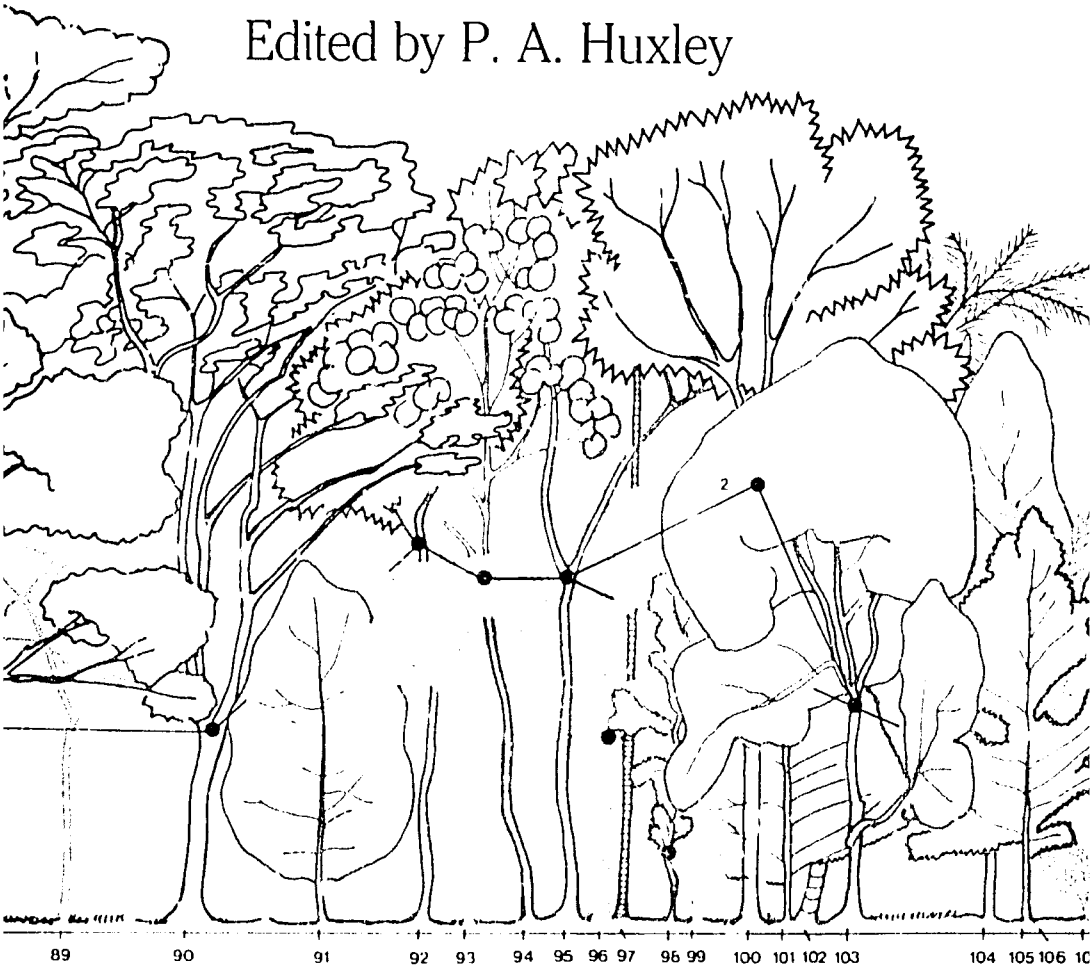
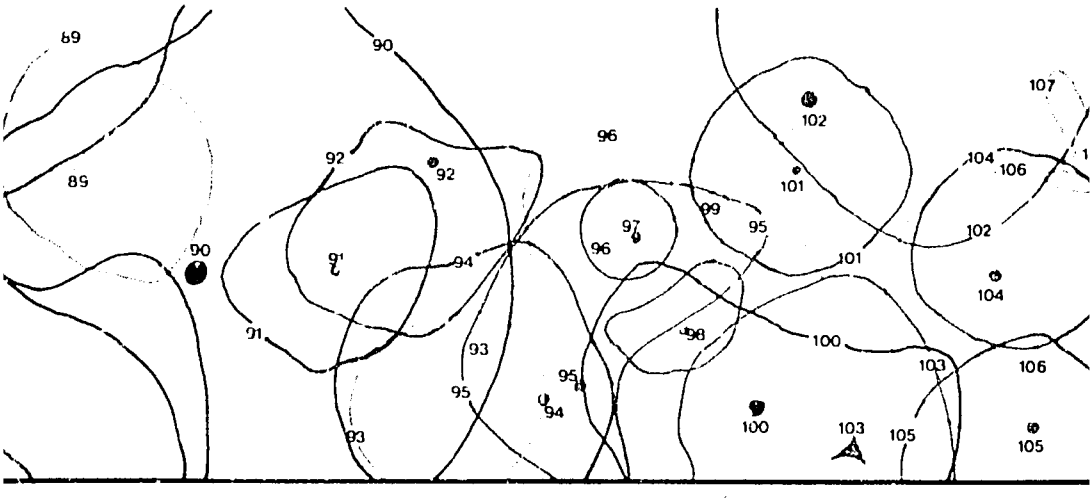
PN-ABE-045

Plant Research and Agroforestry

ICRAF

Edited by P. A. Huxley





PN-ABF-045

Proceedings of a Consultative Meeting held in Nairobi, 8 to 15 April 1981

936-5545A 64257

Plant Research and Agroforestry

Edited by
Peter A. Huxley

ICRAF

Published by the
INTERNATIONAL COUNCIL FOR RESEARCH IN AGROFORESTRY
P.O. Box 30677, Nairobi, Kenya

1983

International Council for Research in Agroforestry
P.O. Box 30677
Nairobi, Kenya

Copyright ©1983
International Council for Research in Agroforestry

No part of this book may be reproduced in any form by photostat, microfilm, or any other means, without written permission from the publishers.

Copies may be obtained from:
I.C.R.A.F., Nairobi, Kenya

Price on application

Printed in Scotland by
Pillans & Wilson Ltd, Edinburgh
from camera-ready copy supplied by
Publication Preparation Service, Penicuik

PREFACE

The reader who expects to pick up this book and find all the answers to how plant science will solve relevant agroforestry problems will be disappointed. In the first place, although many agroforestry land use systems are age-old, and some of the practices well known, agroforestry *research* is a 'new' science and the problems are still being defined. In the second place, the purpose of the meeting from which these contributions arose was definitely exploratory. What did a group of experienced plant scientists, with a wide range of individual expertise to offer, think about the contributions that their subject could make to the development of agroforestry? Some of these plant scientists had first-hand practical experience of agroforestry land use systems, and some not. Even the scope of 'plant science' was chosen to include mainly those areas that link the knowledge of how plants grow and develop to management practices. Several other very important applied aspects, such as pest management or plant breeding, are yet to be explored.

Vast amounts of knowledge and technical/experimental know-how are available, and can be tapped, from conventional agricultural and forestry research experience. What then is different about agroforestry land use systems that they generate problems that require any change in our research approach? To answer this we have to appreciate the fundamental characteristics inherent in all such systems: that they provide *multiple outputs* from the same unit of land in a *sustainable* way; and that there are, in some form or another, *interactions* between the two or more constituent plant species one of which at least (and by definition) is a woody perennial (tree, bush, palm, vine, or bamboo). We are dealing with relatively elaborate systems for which programmes of investigation need to be established that encompass more complex space and time dimensions than those normally found in agriculture and forestry. The kinds of thing we find when we explore the problems and possibilities of intimately mixing trees and agricultural crops and/or grasses, sometimes in conjunction with animals as secondary producers.

If we understand enough about the way the component plant species share environmental resources, and interact both with one another and the soil in such systems (the 'tree/crop interface'), then at least the technical background will be established from which to integrate the other social and economic aspects which are inextricably part of the success or failure of agroforestry in the field. This essential requirement to consider plant science research, at all times, as derived from and leading to the understanding and optimization of a land use *system* was a leading theme of the meeting, as it is of ICRAF's Programme of Work (available on request).

Agroforestry research has to be focused on priority

issues and it must provide at least some indicative information quickly. There are great pressures to obtain rapid solutions to the many land use problems for which agroforestry may provide an answer. If, in any particular set of circumstances, possibilities exist that agroforestry is likely to be better than existing forms of land use, or conventional improvements of it, we need to know. And similarly whether agroforestry is *not* a suitable solution. How then can these decisions be reached? Clearly plant science is just one component of the multidisciplinary approach needed but, in order to set our house in order, we should try to establish how much of the existing knowledge about plants, and the methods used to study them, is relevant to our specific needs. And, especially, whether available research methodologies need to be modified or not.

The reader will have to judge to what extent this first meeting has achieved, or rather partially achieved, these goals. In some subject areas it may well be easier than others. We know, for example, a good deal about how plants of all kinds grow, and how to manage them. Also about the ways that they may interact in different environmental circumstances. Even so we are clearly, as the various authors concerned point out, sadly lacking in many *details* for agroforestry intercropping situations. In agroforestry, the more complex plant associations, and the wide range of plant - environment interactions that are possible, make it essential that we understand how, and to what extent, the major plant growth and development processes will be modified by a change of species, climate, soil and management. Otherwise, the site specificity of any one set of experimental results will severely restrict its value. Some of this information has been considered by various authors, in other cases it is still a question of exposing the wealth of information that the agroforestry researcher can tap *once he has defined his problems and needs more clearly*. Since this meeting was held (in April 1981) some progress has been made. In particular, in outlining at least, suitable research methodologies for the exploration and evaluation of multipurpose tree species, both as sole crops and in agroforestry mixtures (see ICRAF's Technology Programme).

A broad range of contributions were invited for our meeting. The first part of the volume 'sets the scene' by describing some examples of how plants are used in agroforestry and of the plant associated potentials and problems. ICRAF's current work on an agroforestry systems inventory, together with that of many others who are collecting and collating such data, should shortly provide considerably more substantial and detailed information about a wide range of agroforestry land use systems around the world.

Part two of the volume suggests the needs for systems analysis / systems synthesis methods that will be essentially supportive of all the other kinds of investigations. The authors themselves would be the first to agree that, once again, they can rapidly intensify the application of systems methodology to specific problems, once these problems become more precisely exposed. In this respect, the last two years have seen a considerable 'clearing away of the undergrowth in order to expose the trees' (not necessarily a good agroforestry practice!). The

diagnostic methodologies to evaluate land use potentials and problems with regard to the possibilities for agroforestry interventions or improvements has been brought into much sharper focus through the work of ICRAF's Systems Programme. Although much remains still to be done to define how we approach a full technical analysis for the diagnostic and design processes, physical-environmental as well as social-economic information can now be fairly well handled.

In the third section, a series of specific plant related subject areas are explored in order to expose and evaluate, where possible, their relevance to the development of agroforestry research. There are still some topics of considerable practical value that have been covered only cursorily and which yet require a deeper exposition. For example, the practical issues of plant nutrition in relation to management practices and, especially, the possibilities of exploiting di-nitrogen fixation and the benefits of mycorrhizal associations to the best advantage in these more complex systems. Or again, specific examples of what initiatives plant breeders should undertake in order to provide more appropriate genotypes for particular agroforestry plant associations.

The authors were asked to start with the fundamentals of plant behaviour and relate these, as far as possible, to brief explanations of how and why associations of plants in agroforestry might be better or worse than those in other sole crop land use systems; to suggest what potentials there were in such plant associations, and to outline what problems they could envisage. The wealth of ideas, information and comment that emerges from this collection of papers will, it is hoped, form a basis from which to progress further. The various contributions should offer both a stimulus, and some guidelines, for those who wish to undertake plant research for agroforestry. More specific guidance is offered, at the end of the volume, in the recommendations of the various working groups.

Finally, I would like to thank all those who took time off from very busy schedules to come to the Consultative Meeting, and who offered the benefits of their experience and deliberations so enthusiastically. Also to those who helped to implement it. Our gratitude is due to the Swiss Development Co-operation for generously providing the major part of the funding for both the meeting itself and the printing of these proceedings.

In editing so much informative material I have, necessarily, had to exercise some discretion over length and content, but I have tried not to interfere too much with the style of individual authors. Where changes have had to be made I hope they have not detracted from the original in any significant way. A sincere note of thanks goes to Mrs Riet Cannell of Publication Preparation Service, who dealt with the layout editing, typed the camera-ready copy, proofread it and dealt with a multitude of queries; as well as with reading my atrocious handwriting! The errors that remain must be blamed fairly and squarely where they belong — on me!

P.A. Huxley

Nairobi, May 1983

ACKNOWLEDGEMENTS

References are given where any figures or tables have previously been published elsewhere, or where they are re-presented in a modified form. Grateful thanks are due to authors and publishers for permission to reprint in appropriate cases.

Cover design by David Hart
based on sections and plans of village-forest-gardens
(Genevieve Michon)

LIST OF PLATES

PLATES 1-3 Village-forest-garden in West Java.
(Paper 2, G. Michon)

PLATE 4 A home garden in Central Java.
(Paper 2, G. Michon)

PLATE 5 Coppiced *Erythrina poeppigiana* in *Coffea arabica* in Costa Rica.
(Paper 4, G. Budowski)

PLATE 6 *Leucaena* used as support for climbing beans in Colombia.
(Paper 8, K.O. Rachie)

PLATE 7 Open *Acacia tortilis* woodland with *Duosperma eremophilum* understorey in Kenya.
(Paper 11, H.F. Lamprey)

PLATE 8 Goat browsing *Acacia tortilis*.
(Paper 11, H.F. Lamprey)

PLATE 9 Stilt-roots and aerial roots of *Casuarina nobilis* in Borneo.
(Paper 16, E.F. Brunig and N. Sander)

PLATE 10 A mixed maize - soyabean canopy.
(Paper 24, T. Kira and A. Kumura)

PLATE 11 African nutmeg (*Monodora myristica*) near Kampala, Uganda, where it is fully deciduous with short vegetative growth flushes. (Paper 31, P.A. Huxley)

PLATE 12 Interior of root observation laboratory at Auburn, Alabama.
(Paper 32, M.G. Huck)

PLATE 13 Soyabean root system with active nodule development.
(Paper 32, M.G. Huck)

PLATE 14 Secondary root and lateral feeder rootlet of cotton.
(Paper 32, M.G. Huck)

PLATE 15 Ten-year-old coppiced clonal tea bush in Kenya.
(Paper 33, M.J.S. Magambo)

CONTENTS

Preface v

Acknowledgements ix

List of Plates xi

PLANTS AND AGROFORESTRY: SOME EXAMPLES

1 Some characteristics of trees to be considered in agroforestry. 3
P.A. Huxley

2 Village-forest-gardens in West Java. 13
G. Michon

3 Plants and agroforestry in land use systems of West Africa. 25
Bede N. Okigbo

4 An attempt to quantify some current agroforestry practices in Costa Rica. 43
G. Budowski

5 Integrated forestry - agriculture - livestock land use at Jari Florestal e Agropecuária. 63
C.B. Briscoe

6 Agroforestry systems and some research problems. 71
Tran van Nao

7 Agroforestry with coconuts and other tropical plantation crops. 79
P.K.R. Nair

8 Intercropping tree legumes with annual crops. 103
K.O. Rachie

9 The intercropping of grain legumes in agroforestry systems. 117
J.F. Redhead, J.A. Maghembe and B.J. Ndunguru

10 A note on the role of agroforestry in animal-based farming systems in Botswana and Swaziland. 125
W. Godfrey-Sam-Aggrey

11 UNESCO's Integrated Project on Arid Land (IPAL): a silvopastoral approach. 129
H.F. Lamprey

12 Biomass production in agroforestry for fuels and food. 137
D.O. Hall and J. Coombs

UNDERSTANDING AGROFORESTRY SYSTEMS

13 Comments on agroforestry classifications: with special reference to plant aspects. P.A. Huxley 161

14 The design of ecologically sound agroforests. R.A.A. Oldeman 173

15 Systems analysis in production ecology. R.S. Loomis and C.E. Whitman 209

16 Ecosystem structure and functioning: some interactions of relevance to agroforestry. E.F. Brunig and N. Sander 221

17 Crop models: components of and contributors to models of agroforestry plant associations. D.J. Connor 249

18 The role of trees in agroforestry: some comments. P.A. Huxley 257

19 Bioeconomic considerations in the design of agroforestry cropping systems. J.B. Raintree 271

20 The Global Environment Monitoring System: its value for analysis and development of agroforestry land use systems. H. Croze and M.D. Gwynne 291

21 The ICRAF research strategy in relation to plant science research in agroforestry. H.A. Steppler and J.B. Raintree 297

APPLICATIONS OF PLANT SCIENCE TO AGROFORESTRY

22 Aspects of evolution in herbaceous and tree crops relevant to agroforestry. B. Pickersgill 309

23 Photosynthetic systems: implications for agroforestry. L.L. Tieszen 323

24 Dry matter production and efficiency in various types of plant canopies. T. Kira and A. Kumura 347

25 Light climate and crop-tree mixtures. J.E. Jackson 365

26 Crop water use: principles and some considerations for agroforestry. L. Leyton 379

27 Plant stress factors and their influence on production of agroforestry plant associations. D.J. Connor 401

28 The influence of genotype and environment on dry matter distribution in plants. F.T. Ledig 427

29 Plant management in agroforestry: manipulation of trees, population densities and mixtures of trees and herbaceous crops. M.G.R. Cannell 455

30 Plant population and yield of tree and herbaceous crops. M.G.R. Cannell 489

31 Phenology of tropical woody perennials and seasonal crop plants with reference to their management in agroforestry systems. P.A. Huxley 503

32 Root distribution, growth, and activity with reference to agroforestry. M.G. Huck 527

33 Effects of cultural management of tea (*Camellia sinensis* (L.) O. Kuntze) on biomass accumulation and yield. M.J.S. Magambo 543

34 The role of controlled environments in agroforestry research. T.T. Kozlowski and P.A. Huxley 551

MEETING ORGANIZATION AND REPORTS OF WORKING GROUPS

List of Participants 571

Meeting organization 574

Reports of Working Groups

Group 1 - The analysis of plant-to-plant interactions in agroforestry. 575

Group 2 - Ecological considerations. 577

Group 3 - Plant types for agroforestry. 579

Group 4 - Plant management considerations in agroforestry. 582

Index of Plant Names 587

Subject Index 597

Other ICRAF Books 619

PLATE 1 — A view of the village-forest-gardens from the rice-field in West Java (Bogor). Main species are bamboos, durian, coconuts as emergents. *Aglaia dukia*, *Mangifera* sp., *Musa* sp. (Paper 2, G. Michon)

PLATE 2 — Inside the village-forest-garden *(sensu stricto)* in West Java. Tree species are *Dimocarpus longan*, *Aglaia dukia*, *Eugenia caryophyllata*, *Cocos nucifera*, *Bouea macrophylla*. In the background *Musa* sp. Note the houses on the left and sheep on the right. (Paper 2, G. Michon)

PLATE 3. A multicrop field on the border of a village-forest-garden in West Java, with taros, papaya trees, bananas and cassava. (Paper 2, G. Michon)

PLATE 4. A home garden in Central Java (near Solo). (Paper 2, G. Michon)

PLATE 5. Coppiced poró (*Erythrina poeppigiana*) in *Coffea arabica* in Costa Rica. The poró is used to provide both mulch and regulated shade for the coffee and is planted some 6 to 10 m apart (see background). (Paper 4, G. Budowski)

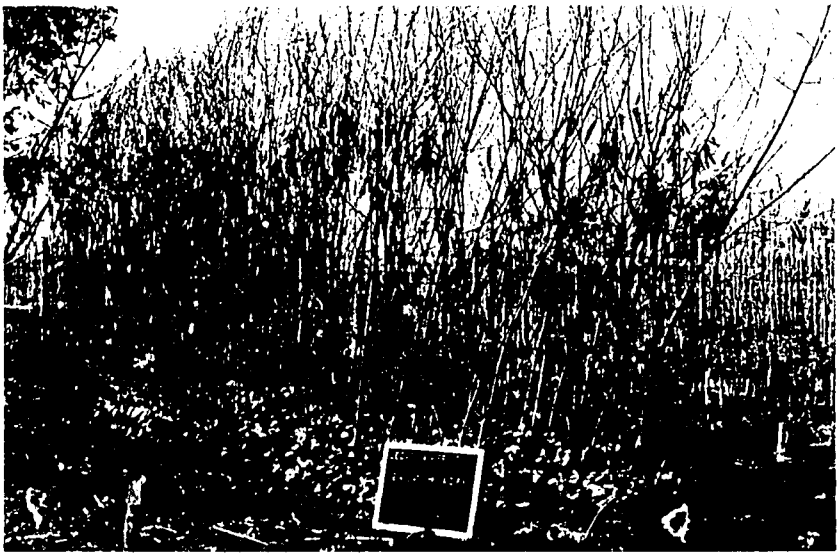


PLATE 6. 'Killed' *Leucaena* used *in situ* for climbing beans at CIAT-Cali, Colombia, 1976. (Paper 8, K. O. Rachie)

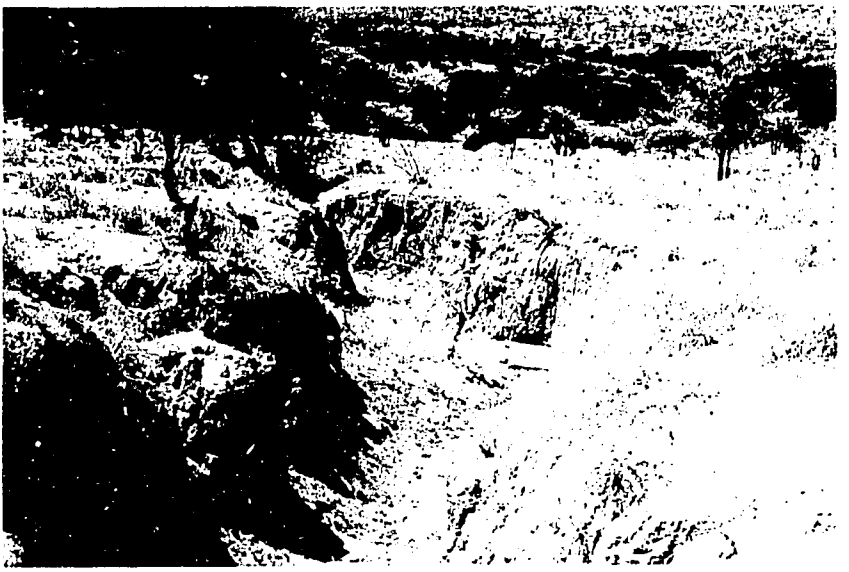


PLATE 7. Open *Acacia tortilis* woodland with *Dinospermum erenophilum* dwarf shrub understorey on the lower fan-slopes of the southeastern Ndoto Mountains in Kenya. The area is subject to severe overgrazing and to excessive tree felling, both of which have resulted in sheet and gully erosion. Management guidelines for this region have been prepared by UNESCO/PAL. (Paper 11, H. F. Lamprey)

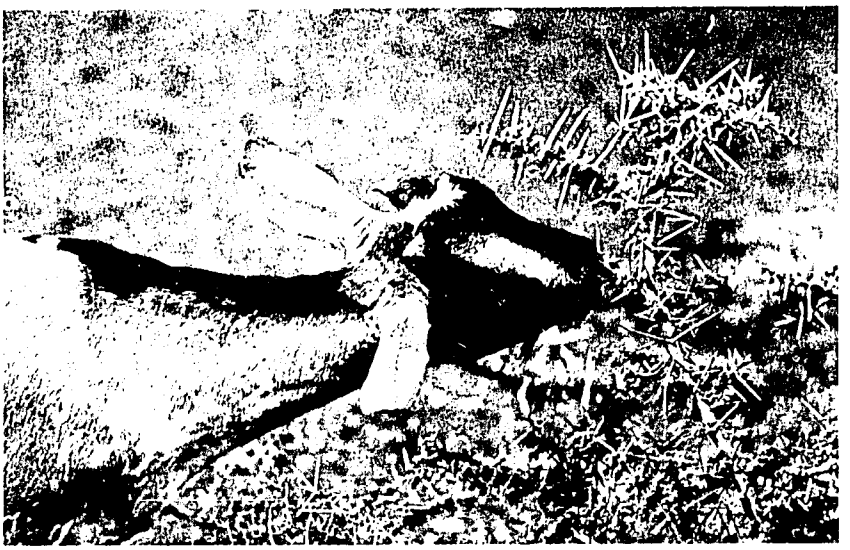


PLATE 8. Goat browsing a small *Acacia tortilis* tree. Heavy browsing frequently prevents *A. tortilis* and other palatable tree species from growing above the reach of goats. Although this species can survive severe browsing for many years, repeated browsing will kill the tree after ca. 20 years. A rotational system of protecting woodland areas for four to five years by the temporary exclusion of livestock is proposed. (Paper 11, H. F. Lamprey)

PLATE 9. Stilt-roots and aerial roots of *Casuarina nobilis* T. C. Whitmore in a wet oligotrophic rainforest. Note the horizontal broom-like roots and partly upward growing roots which embrace the trunk of the neighbouring tree of *Calophyllum teymannianum* and possibly absorb nutrients and rainwater from leaf drip and stemflow. Sabal Forest Reserve, Sarawak, Borneo (Paper 16, E. F. Bruing and N. Sander)

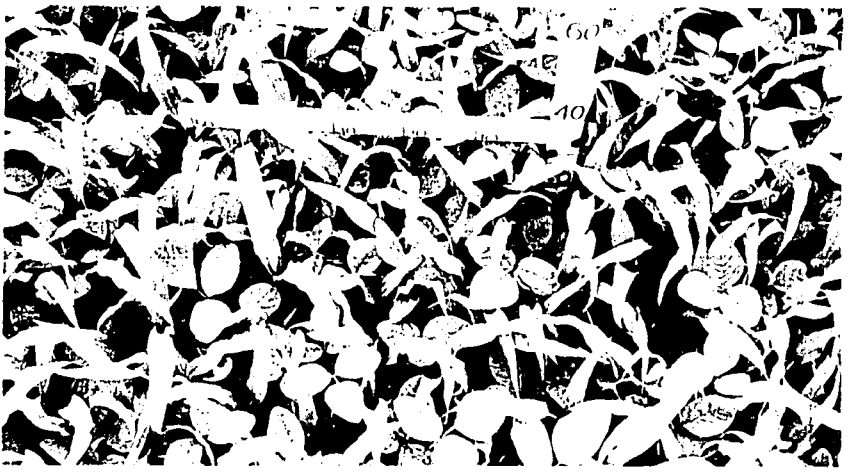


PLATE 10. A plant canopy formed by maize and soyabean. This two-component canopy is relatively 'simple' compared with those found in many agroforestry systems, which can be very complex in terms of geometry, leaf physiology and dynamic changes. Photo by T. Enomoto. (Paper 24, T. Kira and A. Kumura)

PLATE 11. Dormant shoots on a young African nutmeg tree (*Monodora myristica*) growing near Kampala, Uganda (0°20'). This plant is completely deciduous with, usually, two short vegetative growth flushes per year, each lasting only about two months. Flowers are produced from old wood and anthesis accompanies the early stages of a vegetative growth flush. (See Huxley and Van Eck, 1974.) (Paper 31, P. A. Huxley)

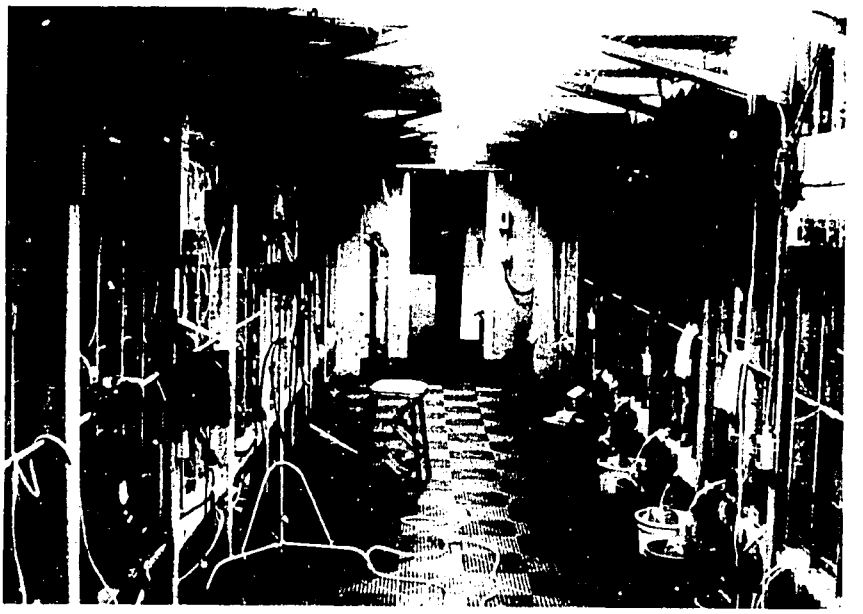


PLATE 12.—Interior of root observation laboratory at Auburn, Alabama. Root growth can be followed at the glass windows by photography or direct visual observation. Instrumentation monitors soil temperature, oxygen concentration, and water status. Drainage water is collected in bottles at lower right for chemical analysis. (Paper 32, M. G. Huck)

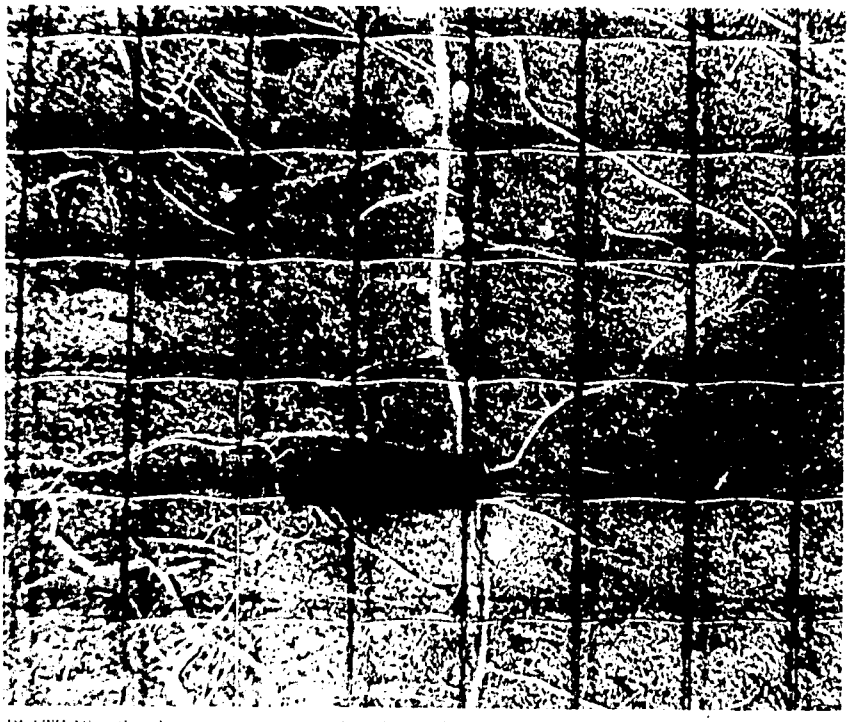


PLATE 13.—Soybean root system with active nodule development (magnified). Note nodule development along main roots; smaller rootlets have a life of only 1 to 2 weeks and so do not develop nodules. The wire grid is 1 cm square. Floodlights have cast a double shadow slightly above and to the right of each embedded wire. (Paper 32, M. G. Huck)

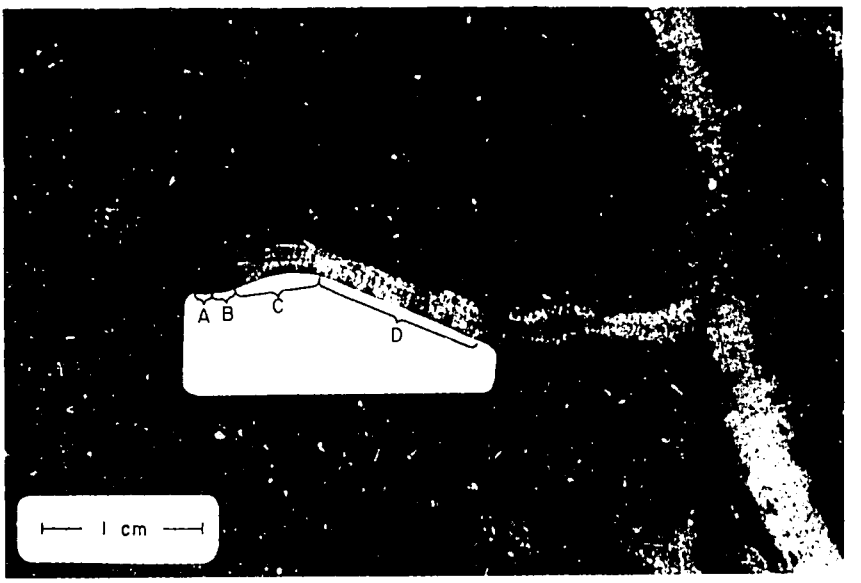


PLATE 14. A lateral feeder rootlet recently emerged from the larger secondary cotton root at the right. Root cap (A), meristematic region (B), cell elongation region (C), and region of maturation (D) with extensive root hair development can be seen. Numerous fungal hyphae are visible in the wet soil behind the glass window. (Photo from Huck, 1977, see Paper 32, M. G. Huck)

PLATE 15. A ten-year-old clonal tea bush at Kericho, Kenya, pruned (coppiced) at 38 cm from the ground. Spacing 1.2 × 1.2 m. Note the amount of woody prunings on the ground. (Paper 33, M. J. S. Magambo)

Plants and Agroforestry: Some Examples

SOME CHARACTERISTICS OF TREES TO BE CONSIDERED IN AGROFORESTRY

P.A. HUXLEY
International Council for Research in Agroforestry,
Nairobi, Kenya.

ABSTRACT. As mainly dominant overstorey plants, trees and shrubs play a key role in agroforestry systems. Agroforestry land use practices can be at various levels of scale but a key to understanding agroforestry systems starts with an appreciation of the environmental and biological processes which occur at the 'interface' between two or more plant components, at least one of which is a woody perennial.

In order to do this satisfactorily it is necessary to have an understanding of the relevant characteristics of the various plant components. Those relating to trees and shrubs are noted in the form of a list of points to consider concerning germplasm, propagation, planting-out, the juvenile phase of growth, mature growth and senescence and replanting; all in relation to technical, managerial and socio-economic considerations.

INTRODUCTION

Agroforestry involves the more or less intimate association of different plant components, always including woody ones, on the same unit of land. Whether the plant components are arranged zonally or in mixtures they will be associated closely enough to interact with one another in some way. Either through environmental processes or through management, for example the transfer of plant material or litter from one zone to another.

CONSIDERATIONS OF SCALE

When examining existing agroforestry land use, or when considering its potential value in place of land use systems of other kinds, we may be involved with different levels of scale. Conceptually we need only three components: two different plant species (one at least woody), and man. Some agroforestry systems can, additionally, include animals of course. In practice any small patch of land with these three (or four) components that

is providing multiple outputs in the form of products and/or environmental benefits may be considered the basic agroforestry unit for purposes of study. Next in the hierarchy is the complete holding or farm. Then any aggregation of land use systems with some common feature (a complete watershed, for example). Finally, the region or, better still, agro-ecological zone.

The problems and potentials of agroforestry will require attention at all four of these levels, and there is no reason why, from the farm up, agroforestry should be considered a sole solution to any existing land use problem. It is merely one logical option which may or may not be valid depending on the circumstances.

AGROFORESTRY AND TREES

In agroforestry we are concerned with the place of trees in the landscape (Steppler, 1981). And these will be in a variety of land use systems some of which, if not all, are providing outputs other than just tree products. However, where isolated plots of trees are being grown as sole enterprises, for example as fuelwood lots, this might more properly be considered as an example of 'mini-' or 'micro-forestry'. This is not just a distinction without a difference because, at least where such fuelwood lots are being established on a community basis, the resource base could be quite different from that available to the individual land user. The tree species chosen may be almost identical to those used by foresters, for example. Nevertheless, when considering larger land units, and even individual farms in some cases, such tree plots may well form part of the overall soil and water conservation strategy for that parcel of land, and thus be generally included within general agroforestry practice.

Again, some managed plant associations, especially in the wet tropics, may consist *only* of woody species. As long as we are concerned with optimizing the outputs from all the components, it may be better to define such systems as 'agroforestry' rather than just 'tropical agriculture'. Certainly, the biological and environmental processes to be evaluated, as well as the socio-economic considerations to be made, will closely approximate to those diagnostic procedures required to understand multiple plant component — multiple output agroforestry systems involving trees/shrubs and herbaceous species or grasses.

The key to understanding what is, or what is not, agroforestry is the appreciation that we start with the environmental and biological processes which occur at the interface between two or more plant components, one of which at least is a woody perennial. Where we draw the boundaries of any classification can then be decided according to the purpose for which it is to be used.

TREE CHARACTERISTICS TO CONSIDER

Trees, shrubs, palms and in the wet tropics woody vines and bamboos as well, are the dominant feature of mature agroforestry systems, and usually the dominant partner of any plant associations within them. The challenge is then to decide: what species?

How many trees? And how should they be arranged? (See Huxley, p.257, this volume). Underlying all three questions is a requirement to understand and appreciate those characteristics of woody perennial species which may, on the one hand, enhance their value or on the other diminish their suitability for any particular agroforestry system.

The lists which follow in Table 1 are intended simply as an *aide-mémoire* for those looking at the role of trees in agroforestry systems, and Figure 1 serves to remind us, simplistically, of the stages that have to be considered.

REFERENCE

Steppler, H.A. (1981). An identity and strategy for agroforestry. Paper presented at the Workshop in Agroforestry in the African Humid Tropics, Ibadan. ICRAF, Nairobi, Kenya.

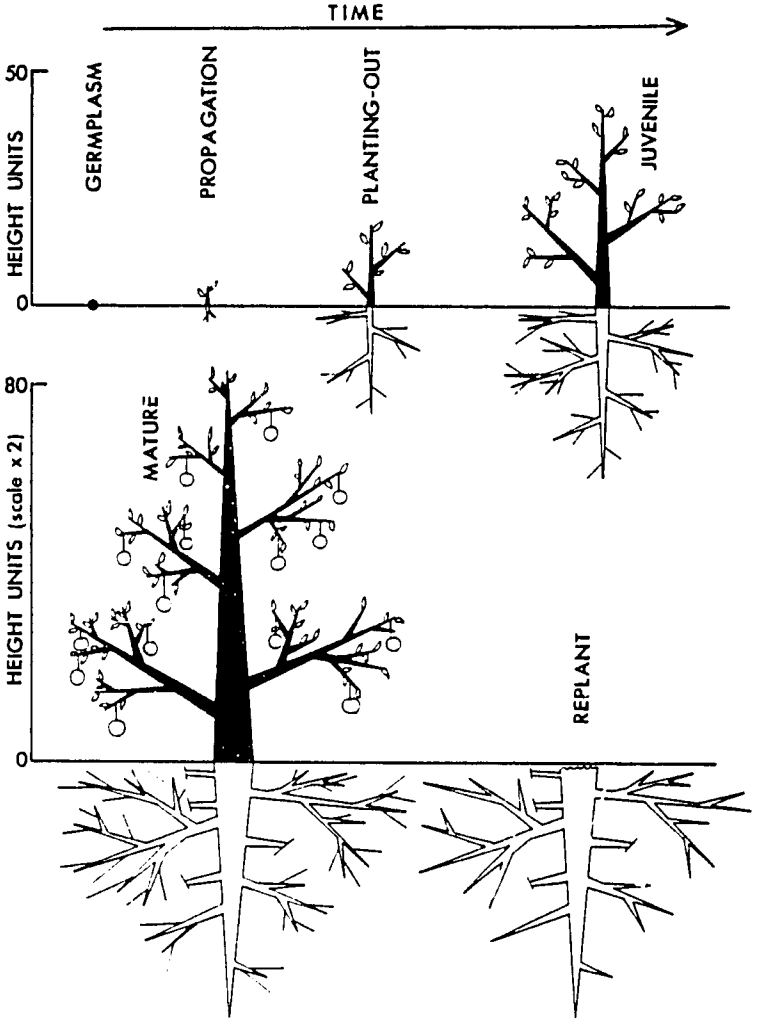


Fig. 1. Diagrammatic representation of the stages in the growth and development of trees related to the sets of considerations listed in Table 1.

Table 1. SOME CHARACTERISTICS OF TREES (AND OTHER WOODY PERENNIALS) FOR CONSIDERATION IN AGROFORESTRY.

Technical	*Managerial*	*Socio-economic*
GERMPLASM • Is this species outbreeding and the germ plasm therefore heterozygous?	- Does a mixture of genotypes matter? - Is germplasm easily and cheaply available? And through what sources?	Can the land user collect and/or distribute his own seed? Or does he have to buy it?
• Are there seed viability problems? If so, does it pay and are there facilities to investigate them?	Will someone have to carry out seed testing? If so, are the necessary skills and equipment available?	Can a farmer easily store seed? Does this put up the cost of seed?
• Are there seed dormancy problems? If so, does it pay and are there facilities to investigate them?	Is any special equipment or technology required to break seed dormancies?	Does this hinder adoption?
• Are seeds commonly attacked by pests and/or diseases?	Are special storage facilities or conditions required?	Will this be a major hindrance to issuing farmers with seed?
• Are there specific seed-borne diseases?	- Is any special treatment of the seed required? - Will the land user have to watch out to eradicate these diseases or treat young seedlings?	Will the land user need special help or advice? And will this be effective and/or costly?
• If tree seeds are not the best or most convenient method of propagation, then what other materials can be tried?	Are the skills and equipment available for collecting and storing propagules (cuttings, bud wood, etc.). Will there be problems associated with using clones, for example, viruses?	What are the comparative costs? And does the farmer already have experience in handling cuttings etc.? (And see next section.)

Table 1 continued

Technical	*Managerial*	*Socio-economic*
	- for as long as he wants them in sufficient quantities and of a type which will survive the distribution and planting systems available?	
PLANTING OUT		
• What are the soil/environmental conditions needed? What is the best season? And are there special soil conservation requirements in this phase?	What site preparation problems are there?	How does it fit in with labour availability and other family needs?
• What is the optimum plant size, and condition, at planting out? (See also above.)	Are proper handling facilities available, and the necessary skills?	Can the necessary care be given?
• Is shelter/support required for the young plants?	What is the easiest to arrange? For example, what local materials are available?	Will the farmer bother? Can he afford it? Will he maintain and manage it and finally remove it?
• Do the young plants need watering, fertilizing or mulching?	Can it be provided?	What is the cost and likelihood of the land user adopting these pro-dures?
• Are pests/diseases/weeds likely to be a problem (and animals/birds)?	Are special chemicals or protec-tive methods needed?	What cost? How does it fit with labour requirements and available skills?

Table 1 continued

Technical	*Managerial*	*Socio-economic*
PROPAGATION • What methods of propagation are available? (And see above.) Seeds; cuttings; budding and grafting; tissue culture, etc.	- What facilities are there for establishing nurseries and distributing plants? - What types of nursery are best? Central, village schools, commercial, etc. - What skills/labour/materials are there for setting up nurseries and distributing plants? And what national organisations and/or infrastructure can help?	- What are the relative cost advantages of direct planting vs using nurseries (transplants and container grown plants)? - What propagating method best suits the land user? - What will the costs be of using different methods?
• What are the specific environmental requirements for germinating seeds and/or rooting cuttings, etc., and for early seedling growth?	Are the facilities (labour and skills) available?	Will the land user easily understand the requirements?
• Are there requirements for seed inoculation (rhizobium, mycorrhizal fungi)?	Will this be done 'on-farm' or for issued seeds?	Will seed be sown in time, and with care, so that inoculation is effective?
• Are there specific pests and diseases in the nursery phase?	Are special procedures involving materials and skills required?	Will the land user suffer severely from a failure to control these properly?
• What is the likely (and optimum) duration of the nursery phase?	Can the nurseries supply plants - when the farmer wants them, and	What are the costs of seedlings? What are the costs of maintaining unsold/undistributed plants?

Table 1 continued

Technical	*Managerial*	*Socio-economic*
JUVENILE PHASE	- Does this affect crops growing nearby? What are the tree/crop interactions?	Will the land-user understand what is required?
• - What is the morphology and early growing habit of the species? - How does it respond to training/ pruning, and what growth responses are there from buds of different kind?	- What training is possible and desirable? - Are plant training skills available?	What are the costs of training vs not training?
• Is the species slow or fast growing in its early stages? (See also above.)	If slow growing will this increase the burden of management operations?	Will a slow growing species be acceptable, however useful and productive later?
• What are the rooting characteristics of the tree species?	- How does this affect management practices (watering, weeding. fertilizing)? - Do early, deep-rooting characteristics affect associated crops and what are the tree/crop interactions at below-ground level? - Will this affect choice of site?	Is the land user prepared to allocate a special site to the trees if needed?
• Is the tree palatable? What is the need for animal protection?	- Are there any effects on animal production if browsing is restricted? - Are people, methods, etc., available for animal protection measures?	- What are the land user's habits with regard to his (or others') browsing animals? - What are the 'costs' of protecting the trees from animals?

Table 1 continued

Technical	*Managerial*	*Socio-economic*
• What are the plants' requirements and responses to shade/shelter, watering, fertilizing, weeding?	What materials, labour and skills are available?	- What are the costs/benefits? - What is the likelihood of adoption of these techniques? What will happen if this is not done?
• What is the duration of the time to flowering/fruiting? (Is the species being grown for fuits?)	What management procedures can be adopted to induce early flowering?	How does this affect incentives to plant?
• How susceptible is this tree species to pests and diseases?	What materials and skills are required?	Will a failure to control these end in disaster?
• What is the phenology of this species? How does this affect the associated crop plants?	How do the time-of-planting restraints and/or other management factors affect the overall management plan, especially with regard to the associated agricultural crop?	How does all this fit with labour availability and social needs?
MATURE GROWTH PHASE AND PERIOD OF MATURITY		
• - What are the morphology and branching habit? - What is the phenology? • shoot dormancies and growth regulation • leaf flush/leaf fall sequences • flowering and fruiting cycles • general source - sink relationships	- Are skills/labour available to deal with training/pruning? - What are the tree/crop interactions implicit in the trees' morphology/phenology and cropping sequences?	- Are there any land user preferences? - What effects are there on the land user's immediate environment (does he want shade/shelter)?

Table 1 continued

Technical	*Managerial*	*Socio-economic*
• Competitiveness (from morphology, etc., above).	What possible operations (for example, lopping) might reduce this and what are the timings?	- What does the land user see as his needs to 'control' the tree? - What are the costs/benefits of doing so?
• Harvestability (single, terminal harvest/sequential harvests).	How does this fit into the pattern of farming operations?	How does this fit into social requirements or market opportunities?
• Needs for weed control.	- Is the necessary labour/equipment available? - How does this fit in with weed control timing and methods for the agricultural crop?	- What methods are best suited? - Will the land-user adopt some form of weed control? - What is the cost/benefit to him?
• Soil management and soil conservation.	- Is the necessary labour/equipment available? - How does this fit in with weed control timing and methods for the agricultural crop?	- Does the land user perceive a need? - Will the land user adopt the appropriate soil management? - What is the cost/benefit to him?
• Pests and/or diseases	- Is the necessary labour/equipment available? - How does this fit in with weed control timing and methods for the agricultural crop? - Can advice be obtained?	- Does the land user perceive a need? - Will the land user adopt the necessary control measures? - What is the cost/benefit to him? - Will there be a disaster if he neglects pest control with these species combinations?

Table 1 continued

Technical	*Managerial*	*Socio-economic*
• Biennial (seasonal) bearing - for fruiting crops.	Are the necessary skills and understanding available to obviate this?	To what extent do variations in seasonal output affect the land-user/markets?
SENESCENCE AND REPLANTING PREPARATIONS		
• What is likely time of onset of ageing/senescence?	What decisions have to be taken on how to remove trees?	How will the land-user perceive the need to remove trees?
• What is the duration of this phase and its effects?	Especially on associated agricultural crops and farm management?	- What are the effects of declining productivity? - Is there a need for credit/help or alternative sources of income?
• What are the options for technical solutions to final harvesting sequences and/or tree removal?	What are the effects on adjacent crops and on the soil?	Are there alternative choices of how to dispose of the trees?
• Are there pests/diseases associated with cutting down trees (including general and specific replant problems)?	Is the knowledge of what to look for available?	Is there a willingness to take care?
• What land preparation is required for replanting?	- What place does this occupy in the whole farming programme? - What is the availability of labour for this?	- What costs are there? - Are there any social implications?
• What crop/soil management is required in the transition period before replanting trees?	What labour/resources are needed, especially for soil conservation in this period?	- Is there a willingness to adopt a a sound plan? - Are there any extra costs?

2

VILLAGE - FOREST - GARDENS IN WEST JAVA

G. MICHON
Institut de Botanique, Montpellier, France.

ABSTRACT. Indonesian village-forest-gardens are distinctive types of agroforestry land use. They are species rich and possess sophisticated spatial structures and dynamics. Although mainly centred on subsistence production surplus products can provide a valuable cash income. Sustained yields are achieved under the present system of home-gardens and village-forest-gardens without any significant input of fertilizers or pesticides. They represent, for the mass of the rural population, the only asset for survival and material autonomy. Until recently, they have been studied only cursorily but these systems, which are far from 'primitive', have many lessons to teach, and they are still susceptible to improvement if we learn enough about them. The two types of gardens are described in some detail and their importance to the farmer is discussed.

INTRODUCTION

Traditional land use systems of the tropical world have long been, and often still are, somewhat despised by agriculturists or economists. That is particularly true with regard to indigenous 'mixed gardens' which too often have been termed 'primitive' or 'archaic'. Nevertheless, most of such systems have survived throughout centuries as the result of long-term adaptations of cultivated plants and cultural techniques to local ecological conditions; and they have, in many cases, reached a noticeable degree of harmonization with the natural environment. The functional relationships of these systems is, in general, little understood.

Examples of some of these age-old land use systems are the Malayan *kebun*, the Indonesian *kampung*, the *jardin créole* of the West Indies, and the dooryard gardens of Central America. Such systems display many agroforestry concepts: their multistoreyed structure and the high diversity of their cultivated species evoke the configuration of tropical forest ecosystems;

diversified agricultural crop types and multipurpose production aims fulfil most of the fundamental needs of local populations. Furthermore, because they have been producing with sustained yields for centuries without causing environmental deterioration they are both ecologically and economically viable and efficient agroecosystems; they are 'sustainable'.

On the island of Java, indigenous village-forest-gardens are mentioned from the tenth century. They have developed up to the nineteenth century but were endangered because of the extension of colonial cultivations and of the establishment of new agricultural systems. However, they are still rather widespread throughout the whole island in spite of an excessively high population density (more than 1000 people km^{-2} in some rural areas), and they make up from 20 to 60 per cent of the total cultivable land of villages.

These Indonesian village-forest-gardens have reached a highly elaborate stage in the imitation of natural forest ecosystems. The Javanese peasant farmer has reproduced in his small parcel a sophisticated producing ecosystem, conditions of which simulate the forest environment, and which is well integrated into the original landscape. In this island, where the tropical rainforest has been almost completely depleted, those artificial 'harvestable forests', which do not deplete natural resources, are a model of land use strategy able to preserve the endangered biological and genetic potential of the environment.

Besides their interest as agroecosystems, their socio-cultural and economic importance is meaningful too. They are both a production unit and a dwelling place and can be considere the result of human cultural activities and traditions.

STRUCTURE OF THE VILLAGE-FOREST-GARDENS IN WEST JAVA

The different types of gardens

From a distance, the village appears as a tangle of houses and disorderly, luxurious vegetation amidst rice fields (*sawah*). In fact, the houses, isolated in groups of two to five, are surrounded by various trees, shrubs, bushes and herbs which fully occupy the space from the ground up to 30 m high. Many animals: sheep, goats and chickens, freely feed among the plants. A fishpond is a common feature of the gardens, and various kinds of fish are fed with vegetable and human wastes. Along the rice fields the village is fenced by a small channel, or by a belt of mixed vegetable fields and of clove, cassava, papaya or banana gardens.

These apparently randomly arranged gardens are, in fact, each a cleverly structured system: every component of which has a precise place and a well-established role. Two main schematic types of garden can be distinguished, and a third is sometimes found.

- The home-garden or *pekarangan* (Figures 1 and 2) is a clean and carefully tended system, just surrounding the house. It is often small (one tenth of a hectare), fenced and planted with various plants from herbaceous vegetable species to medium sized trees up to 20 m high. It has originated in central Java, but has found acceptance in West Java as far

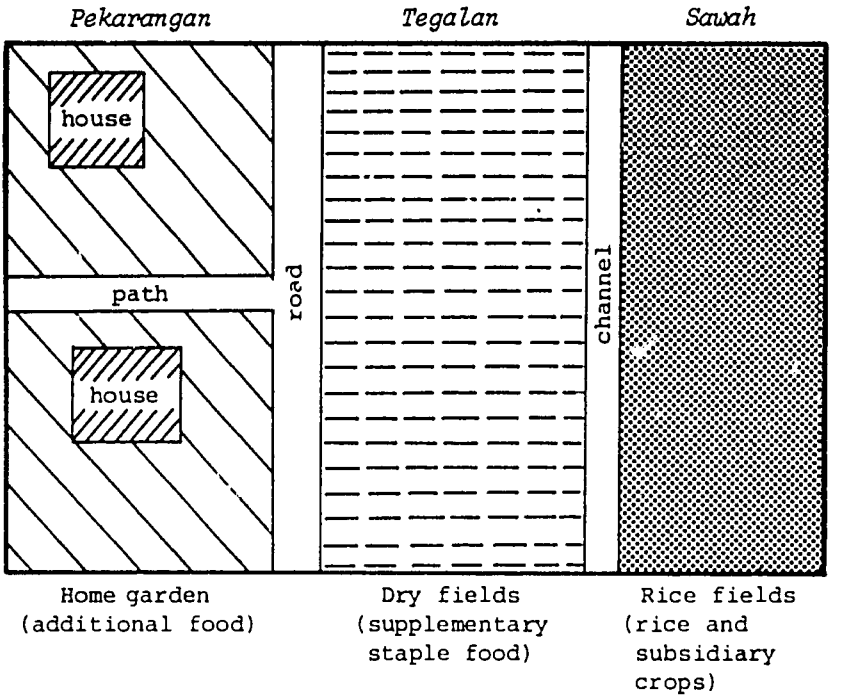


Fig. 1. Layout of a home garden in relation to other fields.

Fig. 2. A schematic aspect of the vegetation in a home garden in West Java. Replacement trees are shaded.

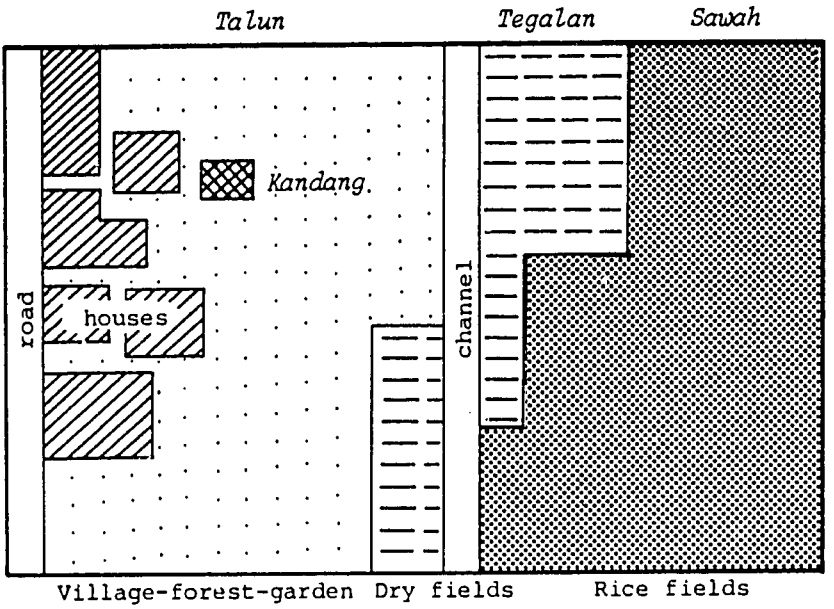


Fig. 3. Layout of a village-forest-garden in relation to other fields. (*Kandang* = cattle stall.)

back as the eighteenth century.

- The village-forest-garden (*sensu stricto*) or *talun* (Figures 3 and 4) is much larger, less densely planted and not so well tended as the home garden. It is planted with higher trees, up to 35 m high, and often contains several spontaneous species of herbs or lianas. It is derived from ancient orchards, and is very common in West Java.
- A third type can sometimes be found in some villages. It is a more homogeneous garden with one dominant species such as clove or papaya, and various herbaceous species. It is often on the edge of the village.

It is actually difficult to differentiate the home garden from the village-forest-garden in West Java. In fact, the succession of gardens that are unfenced, or barely fenced, in those villages forms a continuity, more or less homogeneous, with plots of different aspects reflecting influences or tastes of the owners. But in spite of these local variations, or of differences from one village to another due to sociocultural or ecological factors, the salient features of the village gardens remain uniform throughout the whole island.

The spatial organization

In these gardens the cultivated crop species, from small herbs to taller, emergent trees, perfectly occupy the available space. Many plant species, of different heights and of different architectural types, not planted in any apparently orderly manner, form a multistoreyed and close cover vegetation. Three to five vegetation layers can usually be found (Figure 5).

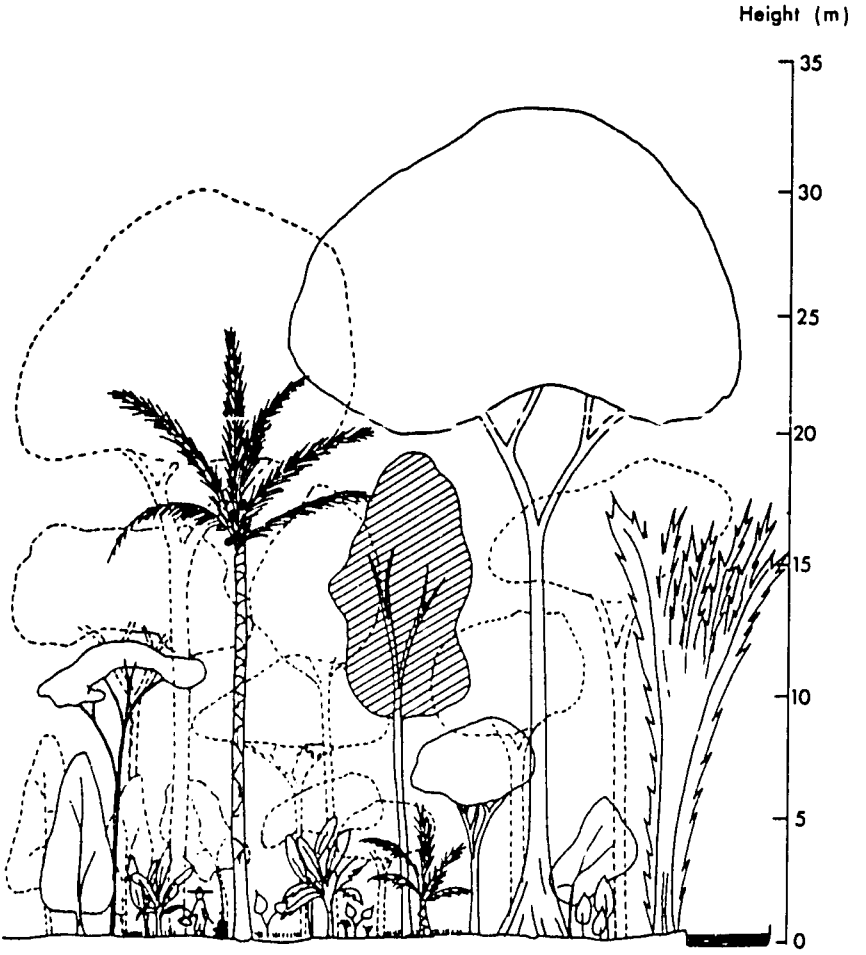


Fig. 4. A schematic aspect of the vegetation in a village-forest-garden *sensu stricto* in West Java. Replacement trees are shaded.

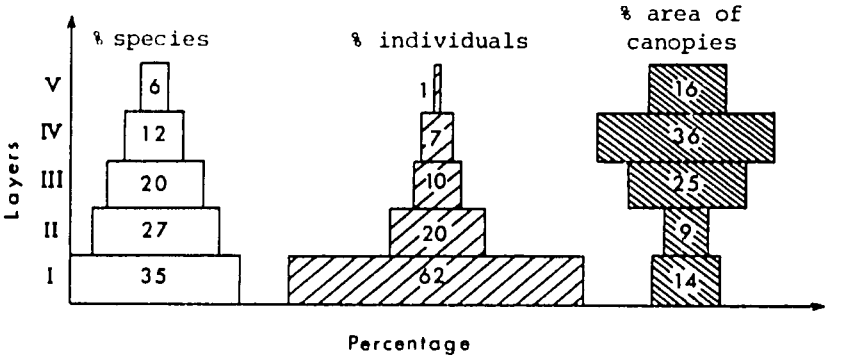


Fig. 5. Structure of *kampungs* vegetation in the home garden (*pekarangan*) in the Citarum watershed in West Java (from Karyono *et al.*, 1978). Layers: I - < 1 m; II - from 1 to 2 m; III - from 2 to 5 m; IV - from 5 to 10 m; V - > 10 m.

- The ground layer, below 1.5 m, is usually dominated by vegetables such as spinach, beans, cucumbers, tomatoes, and so on, by species of the Zingiberaceae or Liliaceae families, by medicinal plants such as *Orthosiphon stamineus*, and *Piper betel*, and by spontaneous herbs. The composition, the specific richness, and the plant density of this level depend on the available light reaching the ground.
- The second layer, from 1.5 to 5 m, is occupied by food plants such as taro, cassava, banana, papaya, salak, and by ornamental bushes and shrubs, such as *Cordyline* spp. and frangipani (*Plumeria* spp.).
- The upper levels consist of trees of different heights, the crowns of which form several layers, all more or less distinct.
  - A lower layer may be formed by small trees such as citrus species, guava, coffee or cacao.
  - The intermediate layer is dominated by various fruit trees such as jack fruit, mango, rambuttan, leguminous species, sugar palm, arek, mangosteen, for example, and also by bamboos.
  - A high layer of taller or emergent trees such as durian or coconut sometimes reaches 35 m above ground.

The height of each level depends on the type of the garden. Also close to the houses trees are usually smaller with medium sized trees about 10 m and taller trees between 10 and 20 m high. Higher branches often are cut away to make the harvest easier, or for safety reasons.

In other gardens which are more distant from the houses, trees are taller (more than 20 m). There can be found tall emergents, and sometimes, wild forest species that seem to be a relic of the ancient tropical forests that have disappeared from these areas during the last century.

The appearance, the structure, the number of plants and the way they occupy the different layers depend on many factors. Sometimes, a layer is incompletely occupied, or is missing; under higher trees, in the village-forest-gardens, the ground layer often is essentially occupied by spontaneous species (germinated seedlings and 'weeds'). In the home gardens, on the contrary, this ground layer is fully planted with vegetables, whereas the upper layers are less occupied and of lower height. Plant diversity, as in forest vegetation, decreases as the height of the plants increases; more species and more plants are found in lower as compared with upper layers.

The temporal organization

The maintenance and the reproduction of these permanent land use types depend on the temporal organization of the cultivated crops, on the replacement rhythm of the perennial plants, and on having a combination of plants with different biological cycles. The villager has to combine short-term and long-term aspects of this production system in order to assure both sustained yields and the durability of his garden.

The permanency of production throughout the year results in

a combination of crops with different production rhythms. Most of the fruit and vegetable species are producing during the rainy season, from November to April. But the flowering and fruiting seasons differ from one species to another, thus allowing a spread of production. For example, the fruiting season of mangoes is September to November, of durians from October to February, and of limes from December to April. However, because of the humid climate of Java, annual plants are grown all the year round, and a certain continuation is obtained, for perennial plants, by the growing of aseasonal species such as cassava, coconut, banana and jack fruit.

The permanency of the producing landscape is a result of a number of factors. Although there is usually no plan for replacing old, unproductive trees or to recolonize new 'chablis' (gaps in a canopy where trees have fallen), the maintenance of a pool of adult, productive species occurs by a mixture of tradition, custom, circumstance and precise observation. A tree may be planted to meet a precise need, for example for economic reasons in the case of commercial tree crops (clove, coconut, coffee, and so on), or in order to replace a valuable but dying tree. But in most cases the young, planted tree is the result of a spontaneously germinated seedling that has been kept and is eventually moved to a more suitable site. It may also be a ceremonial gift on the occasion of wedding or birth.

As in the forest, trees are 'trees of the future', 'of the present' or 'of the past' or, in a different connection, 'not yet productive trees', 'fully productive trees' or 'no longer productive trees'. The layered structure observed is not static, but is an 'episode' in the life of garden vegetation, and the 'producing structure' is also dynamic. Because of the pool of replacement species, the producing landscape is in constant evolution, but its overall structure and function are maintained. The dynamics of such gardens are rapid compared to the turnover in primary forests, both because of the importance of plants with short or intermediate biological cycles, and because of man's intervention in natural processes.

FUNCTIONING OF THE VILLAGE-FOREST-GARDENS

The ecological stability

In these various types of garden the ecological constraints are the same as in natural forest ecosystems. The layered structure of the garden vegetation creates a gradient of light and humidity that plants have to exploit according to their ecological and phytosociological requirements. In spite of the high specific richness of the gardens' vegetation (more than 500 cultivated species can be found in a single village), the place of each plant is carefully chosen, and often corresponds to its ecological niche in the natural forest. Enquiries have shown that people have a certain ecological knowledge in planting their gardens. This knowledge goes together with an individual care towards *each plant* that is in contradistinction to the mass treatment of cultivated crops in monoculture.

This knowledge and respect of ecological constraints, resulting in a 'natural' configuration of garden vegetation, ensures that environmental processes work optimally and render

an ecological stability. Solar energy is well distributed to the plant components of the system, and there is a high level of mineral and organic matter cycling. A recycling of wastes through animals and fishponds maintains soil fertility, and the diversified root systems allow a better use of water and nutrients, and give rise to a good soil structure. The natural specific richness and diversity are a safeguard against pests and diseases. The multistoreyed, relatively dense canopy structure efficiently protects the soil against erosion and leaching; indeed, within the villages erosion is often hardly noticeable, whereas it can be a major problem outside the gardens in some regions of Central Java. These gardens can certainly be considered an ecological 'success' as compared with some other agricultural systems and detailed work is now being undertaken to increase our knowledge of them (Otto Soemarwoto, Institute of Ecology, Padjadjaran University, Bandun, pers. comm.).

A 'man-made' forest

From the original forest ecosystem to these artificial gardens, plants have developed under the influence of human pressures and disturbances. Wild species have been replaced by their domesticated relatives and new species have been introduced, thus producing an environment according to people's needs, as we can see.

- The ground layer has been modified. It is no longer composed, as in the forest, of low shade plants or seedlings of taller trees, but is often partly cleared, except under thinly foliated trees where it is planted with sun- or semishade-loving vegetable species. Such a ground layer may become a free ecological niche opened to colonization. In fact, this population of spontaneous, and often useful 'weed' species, is partly controlled, and the part that is not taken away can serve as fodder for livestock.
- Man has perturbed the reproduction cycles by gathering fruits and seeds, and by favouring vegetative propagation. In a virgin forest seed dispersal occurs naturally by the action of wind, rain and animals, and most of the many seedlings perish because of competition. In the villages, people are responsible for regeneration, and they control this by choosing the place, the time of planting and the number of replacement trees.
- In the gardens plants are not so tall as their wild relatives and trees usually have a rather spheric crown, different from the usual 'umbrella crown' of forest species. In fact, the plant population of the gardens is not as high as in the forest so that soil resources and light are not so limiting, and trees can easily reach a level of sufficient energy to reiterate.
- The colonization of chablis is controlled. When a tree is eliminated the wood is taken away by the farmers for fuelwood or for building material so that the opened place is cleared. It may be kept clear by the villager for growing vegetables, or planted with 'pioneer' cultivated species such as bananas, or some leguminous species (*Albizzia* spp., *Parkia* spp.) under which new semishade-loving species will be grown, thus

restoring the 'forest-garden'.

- The 'forest-garden' is protected and perpetuated by a wealth of knowledge that the local farmers have acquired empirically as well as by custom, superstition and religious laws. Others have tried to imitate it by selecting and siting plant species according to architectural and biological complementarities, but these efforts have usually led to errors, or to badly managed gardens.

In most cases the natural ecological stability, and the integration of sensible management practices, are sufficient to maintain and protect these systems without any significant input of chemical fertilizers or pesticides. Sustained yields have been obtained for centuries and, at the present time, the gardens together with the rice fields, produce enough food for dense settlements without any overexploitation of the natural resources or any deterioration of the system itself.

Importance of the garden for the farmer

Such gardens are essential to support the villagers' life and life style. The cultivated plants, jointly with the products from the rice fields, fulfil most of the fundamental needs of the families.

- Staple foods such as taro or cassava are provided which can, at any time, replace the basic plate of rice. Also various fruits and vegetables that are essential to supply the diet with vitamins and minerals. Such produce may assure more than 40 per cent of the whole calorific requirement (Terra, 1953, 1959; Stoller, 1975). The gardens also provide spices and flavourings, and are a source of raw materials for building and handicrafts, and of fuelwood. The medicinal plants grown in the gardens are the basis for traditional preparations that are the only available medicine. Finally, industrial crops such as coffee, clove, pepper or cacao are a source of cash.

- The combination of the different cultivated plants in the gardens allows permanent production throughout the year. There is *daily* something to harvest, even if it is only a small amount. In the first instance this production is for consumption but any surplus can be sold to local markets, thus representing a safeguard against risk of failure and a security for the interval between rice harvests. This continuous flow of small quantities assists in maintaining an economic and nutritional stability for the villagers; it is, perhaps, the last guarantee against rural poverty (Figure 6).

- The upkeep of a garden requires only a relatively small amount of working time (Table 1). The labour requirement is more or less constant throughout the year, and consists mainly of daily tasks of cleaning or harvesting. Each member of the family, from children to old parents, has a share in this labour.

A village garden is not only an agroforestry system, but also a reflection of the character of a rural society because it has been modelled by social traditions and customs. The ecological

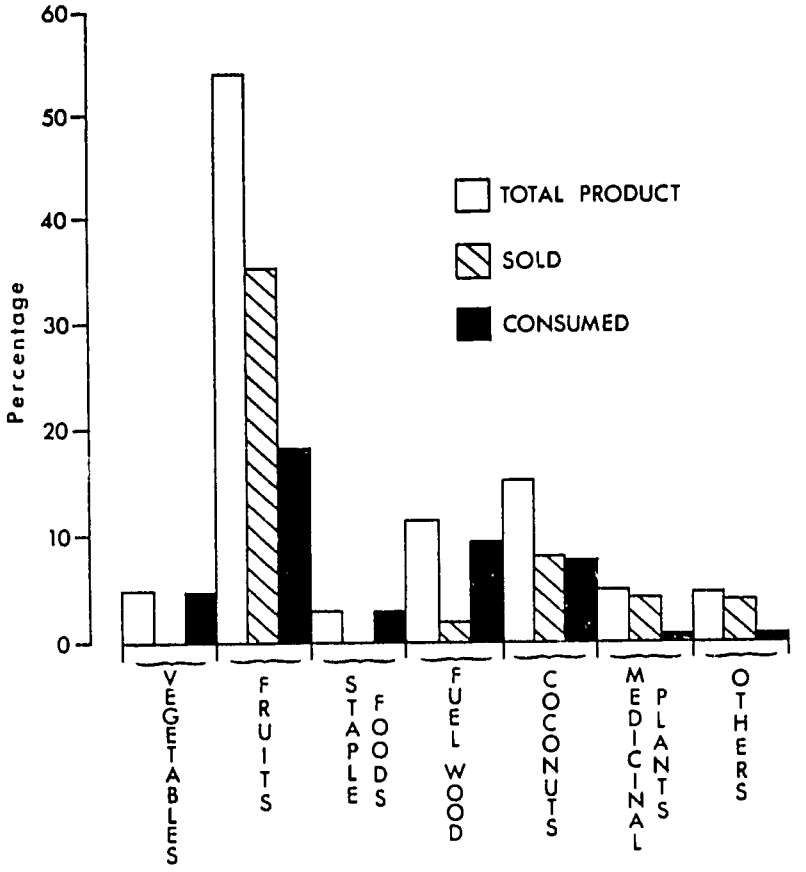


Fig. 6. Distribution of produce from a *kampung* (from Hisyam, 1978).

Table 1. Partition of activities in a Sundanese *kampung* (from Hisyam, 1978). Each member of the family is given a share of the work devoted to each task, as a percentage of his total available time (other activities are not listed).

Activities	Father	Mother	Old parents	Sons	Daughters
	%	%	%	%	%
Work in the garden	13	17	14.3	3	0.9
Work on the pond	1.8	1.7	3.5	0.7	1
Looking after cattle	0.1	0.6	1.9	0.1	0.1
Selling of products	24.2	0.1	-	-	4.2
Total	39.1	19.4	19.7	3.8	6.2

features of such a system can and should not be dissociated from its social and historical background. The present evolution of these garden types expresses a response to the societies' main socio-economical problems, and its aspirations for development along sound agroforestry lines.

PLATES illustrating this paper can be found elsewhere in this book.

NOTE: This contribution was originally presented as a poster paper. For a fuller account see Michon *et al.*, 1983.

REFERENCES

Hisyam, A. (1978). Aspek Social Budaya Pekarangan. [Socio-cultural aspects of home gardens.] Seminar Ekologi Pekarangan II. Inst. of Ecology, Univ. Padjadjaran, Bandung. 126 pp.

Karyono *et al.* (1978). Struktur Pekarangan di Daerah Aliran Sungai Citarum - Jawa Barat. [Structure of home gardens in the Citarum watershed area, West Java.] Seminar Ekologi Pekarangan. Inst. of Ecology, Univ. Padjadjaran, Bandung. 153 pp.

Michon, G., Bompard, J., Hecketsweiler, P. and Ducatillion, C. (1983). Tropical forest architectural analysis as applied to agroforests in the humid tropics: the example of traditional village-agroforests in West Java. *Agroforestry Systems* 1, 117-129.

Soemarwoto, O., Soemarwoto, Z., Karyono, Soekartadiredja, E.M. and Ramlan, A. (1976). The Javanese home garden as an integrated agro-ecosystem. *In* "Science for a Better Environment". Science Council of Japan, Tokyo, Japan.

Stoler, A. (1975). "Garden use and household consumption patterns in a Javanese village". PhD Thesis, Columbia Univ., Dept of Anthropology, New York, USA.

Terra, G. (1953). Mixed garden horticulture in Java. *Malaysian J. Trop. Geog.* 1, 33-43.

Terra, G. (1959). Farm systems in S.E. Asia. *Neth. J. agric. Sci.* 6, 158-183.

DISCUSSION

During the discussion on Javanese village-forest-gardens two different opinions became obvious. One group of participants expressed their interest in these systems, which were new to them, but they did not realize either the need for further research in this field, or the direct contribution of these cropping systems for development in the framework of agroforestry. Some thought that the highly sophisticated structure of those village-forest-gardens made them unsuitable as a model of land use. Others considered them to be very specialized systems, adapted to subsistence agriculture, but without any opportunity for development. Obviously the opinion and the criticisms of this group reflected a traditional agricultural outlook in favour of monoculture, or other monotypic systems.

Others, with personal experience in such systems, immediately recognized the similarities between mixed gardens that

they knew from their own experience in Nigeria, Latin America, and Southeast Asia. They readily acknowledged the need for further investigations, and the wealth of information that could be extracted from these systems concerning the way mixtures of species grow together. (Editor's summary.)

PLANTS AND AGROFORESTRY IN LAND USE SYSTEMS OF WEST AFRICA

BEDE N. OKIGBO
International Institute of Tropical Agriculture, Ibadan, Nigeria

ABSTRACT. The characteristics of the farming systems found in West Africa are briefly outlined and the shortcomings of current land development strategies noted. These include inadequate emphasis on food production research resulting in a continuing expansion of the area under cultivation at the expense of forest resources which are, themselves, increasingly needed for timber and, especially, fuelwood. A solution is to develop integrated land use systems which involve both woody perennials and herbaceous crops and/or grasses. Some suggestions are made on how existing land use systems can be improved in this way.

INTRODUCTION

In many African countries, since independence, the food situation has deteriorated and per capita food production has decreased. Attempts to achieve a rapid increase in food production have relied mainly on the extension of area of land under cultivation. The newly cleared land has either continued to be exploited through outmoded bush fallow systems, which are no longer ecologically stable and productive, or through large-scale farms patterned after the production systems of developed countries. The latter have often produced disappointing results.

The current rapid rate of deforestation in West Africa and other parts of the tropics is largely the outcome of continuing competition from agriculture. It is against this background that recent efforts to improve agroforestry techniques aimed at the integration of compatible components of forestry and agricultural production systems should be viewed.

This paper briefly reviews the rapidly changing traditional farming systems of the major ecological zones of West Africa, and the place of various crop plants, especially trees, in the rapidly changing and evolving land use systems. It develops a conceptual framework for planning and establishing priorities in research aimed at rational, ecologically sound and economically

viable multi-use management of plant resources, with emphasis on the role of agroforestry.

ENVIRONMENTAL SETTING AND TRADITIONAL FARMING SYSTEMS

General description

The relevant area of West Africa extends from latitude 4°N to 15°N, and from longitude 15°E to 16°W. Topographically it consists of undulating plateau of less than 400 m elevation bounded by a coastal plain of varying width and generally from 0 to 90 m elevation. A few hilly and mountainous areas exceeding 400 m, and reaching 1200 m in some places, include the Fouta Jallon Highlands, the Togo-Atakora mountains, the Jos Plateau, the Cameroon mountains, and the Adamawa Highlands.

The region is an area of relatively high annual insolation; mean annual incoming short-wave radiation decreases from about 110 Kcal $cm^{-2}yr^{-1}$ (7.67 GJ $m^{-2}yr^{-1}$) near the coast to over 200 Kcal $cm^{-2}yr^{-1}$ (14 GJ $m^{-2}yr^{-1}$) on the edge of the desert. There is a uniformly high temperature, rarely below 18°C throughout the year and with annual means of around 25 to 27°C. Rainfall is high on the coast and, with the exception of the coastal savanna areas of Benin, Togo and Ghana and coastal areas of Senegal, the usually unimodal annual rainfall may reach 4000 mm with almost no dry season. Further inland rainfall is bimodal, ranging from 1250 mm to 2000 mm, with up to three months of dry season. The rainfall continues to decrease rapidly inland and, at latitude 12°N, it consists of a single peak of less than 500 mm with up to seven months of dry season.

The vegetation consists of climatic climax vegetation zones that have been very much modified by man. These run almost parallel to each other starting from the mangrove and freshwater swamps along the coast, followed by tropical rainforest of mainly broadleaved evergreens which has, in places, been replaced by oil palm bush. This is followed by the forest savanna mosaic, or derived savanna, the southern and northern Guinea savanna woodlands of tall grasses and deciduous vegetation and finally, the Sudan and Sahel savannas of thorn scrub vegetation on the southern border of the Sahara desert.

The soils are highly weathered and of low inherent fertility except where there are young volcanic soils, alluvial flood plains or valley bottom soils. Those formed from pre-cambrian basement complex rocks in well-drained upland areas consist mainly of alfisols of coarse and medium surface texture with a clayey horizon of more than 50 per cent exchangeable base saturation; ultisols, which are similar to alfisols but are highly acid with less than 50 per cent base saturation; oxisols, consisting of strongly weathered soils in parts of southern Benin, Nigeria and the Cameroon Republic; vertisols, which are dark coloured cracking clay soils of the Accra plains, Lake Chad and savanna areas that are difficult to work when wet, and entisols formed from alluvial or colluvial materials in valley bottom soils. Acid sulphate soils (sulphaquents) occur in mangrove swamps near the coast.

There are 18 countries in the region which gained independence within the last 25 years. They all have high rates of population growth (2.5 per cent net increase or above), with over

40 per cent of the population in the 0 to 15 years age bracket, and over 60 per cent of the population engaged in agriculture. They exhibit considerable regional specialization in cash crop production.

Main characteristics of the agriculture of the region

Agricultural activities of the region are related to the prevailing climatic conditions, and the commodities produced are correlated with the vegetation zones and associated agro-ecological conditions. Broadly speaking, the Bandama river forms the dividing line between an indigenous yam dominant staple food crop in the humid and subhumid areas to the east, and a rice dominant area to the west. In general, the farming systems consist of complex enterprises in which there are major staples, cash crops and minor crops, usually associated in some way with varying numbers and kinds of livestock as listed in Table 1.

Other relevant characteristics

Other characteristics of the farming systems encountered in West Africa include the following:

- farm sizes are generally small, with over 70 per cent below 5 ha;
- there is a reliance on bush or grass fallows for the maintenance of soil fertility;
- widespread slash and burn clearance systems exist;
- cropping systems are highly dependent on prevailing rainfall regimes, except for some irrigated agriculture in the Sudan/Sahel savanna;
- simple hand tools and manual labour are used;
- mixed cropping systems aimed at maintaining stable yields of a range of crops to satisfy subsistence and increasing cash requirements at minimum risk are widespread (for example see Lagemann, 1977);
- nomadic herding is common in the Sudan/Sahel zone but, in the southern Guinea and rainforest zones, endemic tsetse borne trypanosomiasis makes cattle keeping and the use of cattle for work and in mixed farming systems impossible;
- there is considerable division of labour between the sexes, and specialization of either sex in growing certain commodities and in some farm operations.

In general the farming systems are complex, with each farmer or farm family operating several field systems located at various distances from a compound garden on which are grown vegetables and various tree crops providing, for example, fruits and nuts (see Fig. 1). The different field systems are devoted to major staples and some cash crops. Dotted about these fields are stumps of fallow trees and protected, useful trees such as the locust bean (*Parkia* spp.) and shea butter tree (*Butyrospermum paradoxum*) in the savanna, and the oil palm, breadfruit (*Treculia africana*), African pear (*Dacryodes edulis*), oil bean (*Pentaclethra macrophylla*), African mango (*Irvingia* spp.) in the rainforest areas. Many of the trees and shrubs are grown either in the compound gardens or are maintained in a protected, semi-wild or wild state. The various field systems are not only sources of food but are often also useful as sources of fibre,

Table 1. Farming systems in West Africa.

HUMID TROPICS/RAINFOREST	
• Dominant crops	
- *Subsistence*	Yams, rice, cassava, maize, plantains and cocoyams in some locations
- *Cash crops*	Cacao, rubber, oil palm, bananas, coffee, coconut
• Minor crops	Vegetables, cocoyam, tree crops, bananas, sweet potatoes
• Livestock	Sheep, goats, poultry
FOREST/SAVANNA MOSAIC	
• Dominant crops	
- *Subsistence*	Sorghum, millet (*Digitaria* sp.), cassava, yams, rice
- *Cash crops*	Soybean, sesame, sugar cane, cotton, tobacco
• Minor crops	Cocoyam, cassava, cowpeas, vegetables, groundnuts, sweet potatoes
• Livestock	Goats, sheep, poultry, few cattle and horses
GUINEA SAVANNA WOODLAND	
• Dominant crops	
- *Subsistence*	Sorghum, millet, rice, maize, cowpea
- *Cash crops*	Groundnuts, sesame, cotton, tobacco, soybean, sugar cane
• Minor crop'	Sweet potatoes, vegetables, bananas, cassava, tree crops
• Livestock	Cattle, goats, sheep, horses, poultry, pigs
SUDAN AND SAHEL SAVANNA	
• Dominant crops	
- *Subsistence*	Millet, sorghum, cowpea
- *Cash crops*	Groundnuts, cotton, some rice, wheat
• Minor crops	Vegetables, rice, sweet potatoes, sesame, tree crops
• Livestock	Cattle, goats, donkeys, sheep, horses, poultry, camels
TROPICAL HIGHLANDS	
• Dominant crops	
- *Subsistence*	Maize, beans, sorghum
- *Cash crops*	Arabica coffee, tobacco, Irish potato tea, subtropical vegetables, cotton
• Minor crops	Sweet potato and Hausa potato (*Plectranthus* and *Solenospermum* spp.), vegetables, cowpea, tree crops
• Livestock	Cattle, sheep, goats, poultry, horses, donkeys

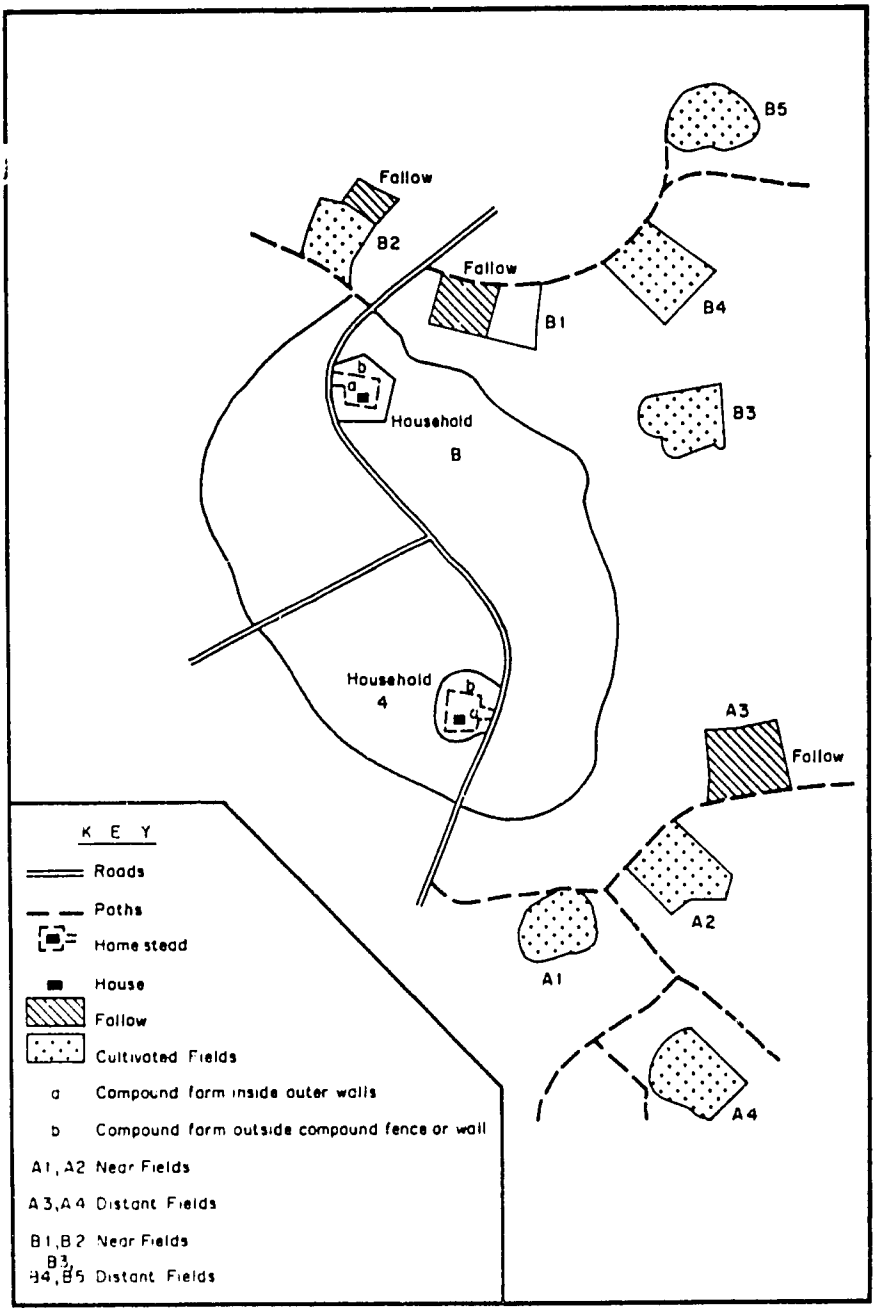


Fig. 1. Schematic diagram of compound farms in relation to associated fields in traditional farming systems of the humid tropics of West Africa.

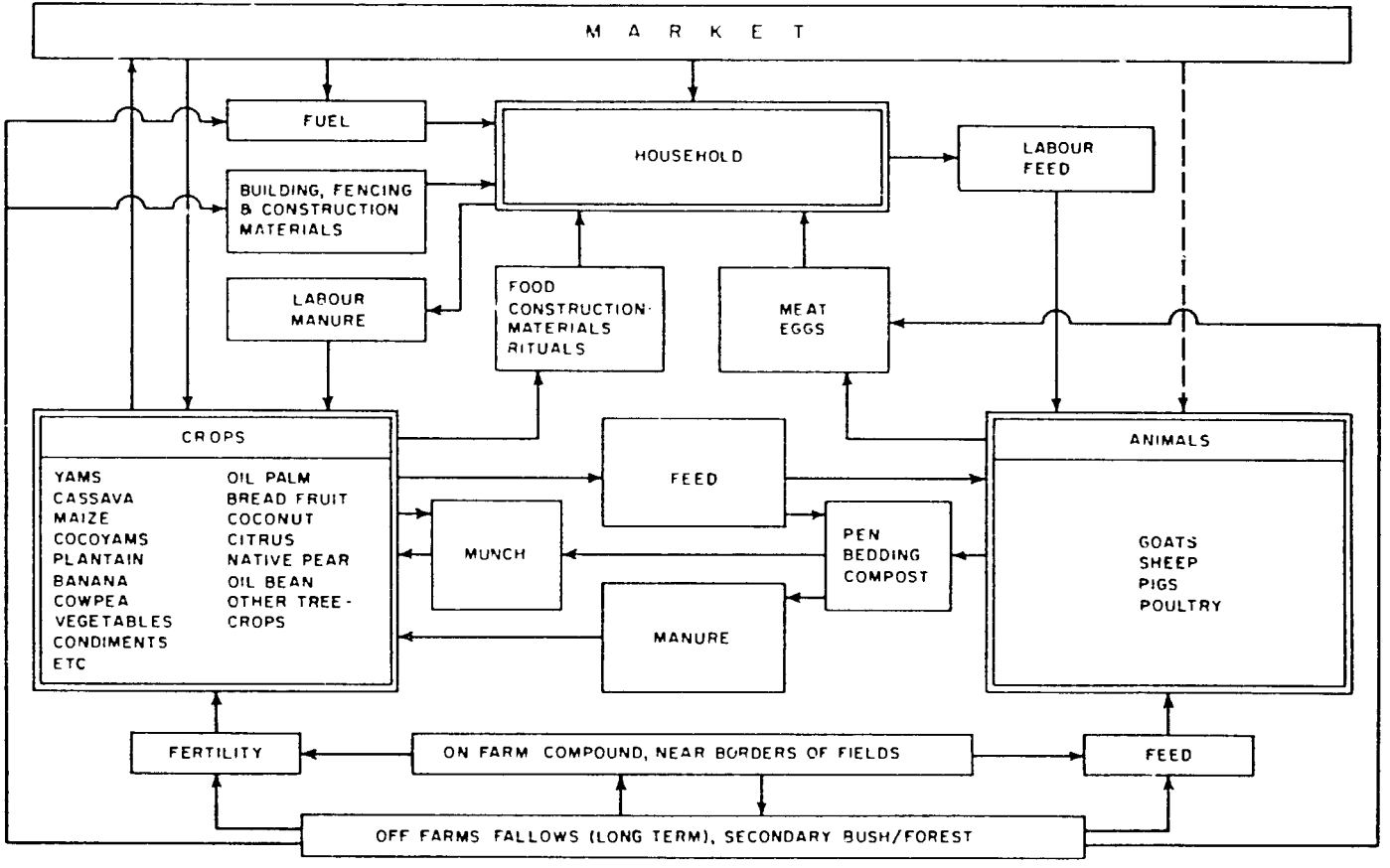

M A R K E T
FUEL
HOUSEHOLD
LABOUR
FEED
BUILDING, FENCING
& CONSTRUCTION
MATERIALS
LABOUR
MANURE
FOOD
CONSTRUCTION-
MATERIALS
RITUALS
MEAT
EGGS
CROPS
YAMS
CASSAVA
MAIZE
COCOYAMS
PLANTAIN
BANANA
COWPEA
VEGETABLES
CONDIMENTS
ETC
OIL PALM
BREAD FRUIT
COCONUT
CITRUS
NATIVE PEAR
OIL BEAN
OTHER TREE-
CROPS
FEED
MUNCH
PEN
BEDDING
COMPOST
MANURE
ANIMALS
GOATS
SHEEP
PIGS
POULTRY
FERTILITY
ON FARM COMPOUND, NEAR BORDERS OF FIELDS
FEED
OFF FARMS FALLOWS (LONG TERM), SECONDARY BUSH/FOREST

Figure 2.

fuelwood, drugs, fodder, and so on. Soil fertility in the compound or homestead garden is often maintained with animal manure, kitchen and compound refuse and crop residues. Thus facilitating a more or less intensive 'garden' or horticultural production system. Two examples of the complexity of farms, in the rainforest zone and in the savanna area, respectively, are shown in Figures 2 and 3.

CONSERVATION VERSUS DEVELOPMENT

Where production objectives were mainly subsistence, original, traditional bush fallow systems were largely in equilibrium with the prevailing ecosystems under low population density, and with fallow periods of more than five years. With increasing pressures of modernization and commercialization, the transitional farming systems of today cannot operate to provide sustainable production, especially where they are based on an arable row crop production technology developed for crops in temperate countries. This is largely because such systems are sustained by mechanization and costly inputs of chemicals, including fertilizers, in areas of low erosion hazard. Similar cropping systems in the tropics pose many problems, especially where fertilizers are not used.

In West Africa, as elsewhere, there currently exist some conflicts between developers and conservationists because of a misinterpretation of objectives. Conservation activities usually tend to be narrowly interpreted to mean the restricted or non-use of resources. Often this arises in response to previous misuse of mismanagement. It is then that drastic measures are needed to save what remains and if possible restore output. We know of many examples for this. For instance, conservation of vegetation in watersheds may be necessary in order to ensure an adequate supply of good quality water. Conservation of vegetation may be necessary to ensure the survival of particular, useful plant species, or in order to study and collect information on the evolution and dynamics of a particular ecosystem so that it can, eventually, be exploited soundly.

By and large conservation measures are not well planned in most West African countries and they are generally limited to the remedial aspects of conservation. More studies and surveys of natural resources are needed which include not only an assessment of the current status but predictions of future ways to develop and exploit the resources prudently and sustainably.

COMMENTS ON SOME IMPERATIVES FOR MULTIPLE LAND USE PLANNING AND RESEARCH

Special reserves

Reserves for hunting and tourism are only just beginning to receive renewed attention in West Africa. Higher priority is

Fig. 2. (*Opposite*) Compound farming, intensive cultivation and bush fallowing in a tropical rainforest region, Imo State, southeastern Nigeria. (Based on Lagemann (1977), adapted from McDowell and Hildebrand (1980).)

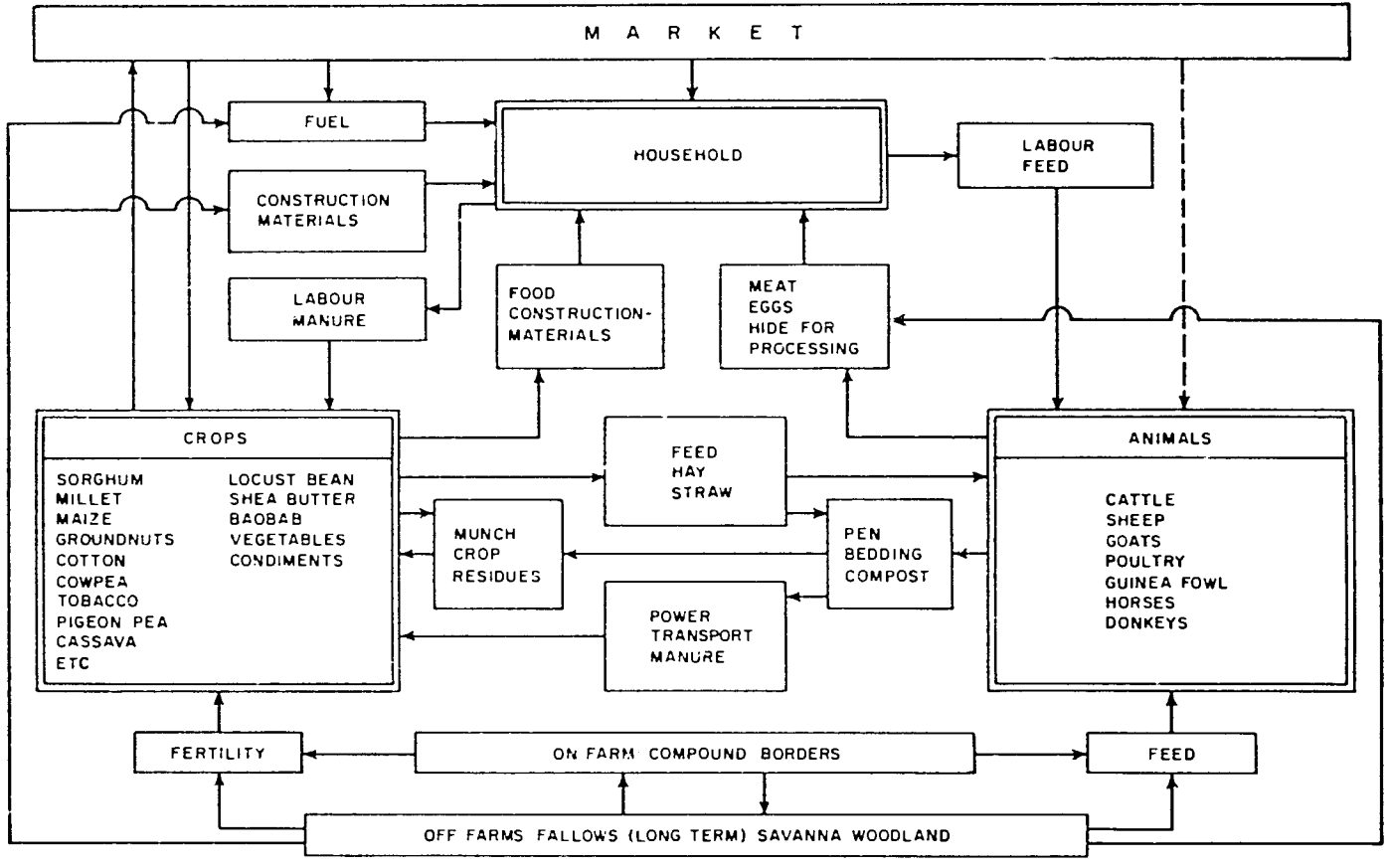

MARKET
FUEL
HOUSEHOLD
LABOUR
FEED
CONSTRUCTION
MATERIALS
LABOUR
MANURE
FOOD
CONSTRUCTION-
MATERIALS
MEAT
EGGS
HIDE FOR
PROCESSING
CROPS
SORGHUM
MILLET
MAIZE
GROUNDNUTS
COTTON
COWPEA
TOBACCO
PIGEON PEA
CASSAVA
ETC
LOCUST BEAN
SHEA BUTTER
BAOBAB
VEGETABLES
CONDIMENTS
FEED
HAY
STRAW
MUNCH
CROP
RESIDUES
PEN
BEDDING
COMPOST
POWER
TRANSPORT
MANURE
ANIMALS
CATTLE
SHEEP
GOATS
POULTRY
GUINEA FOWL
HORSES
DONKEYS
FERTILITY
ON FARM COMPOUND BORDERS
FEED
OFF FARMS FALLOWS (LONG TERM) SAVANNA WOODLAND

Figure 3.

invariably given to tourism as a means of earning foreign exchange than to providing recreational facilities for the local population. However, there are a number of forest reserves established in different countries, principally to supervise forest exploitation. Such reserves are under constant pressure from agriculture and are often damaged by annual fires that are rarely controlled. For example, 'Forest reserves' in Nigeria constitute about 10 per cent of the total land area, but some four-fifths of this is actually savanna, where annual forest fires are difficult to control, and only one-fifth is rainforest which yields most of the timber. Properly planned and supervised reserves are urgently needed to satisfy the needs for vegetation and species conservation, studies of management for sustained exploitation, and for environmental and recreational purposes.

Timber forests

In West Africa, although timber is of considerable commercial importance in national and international trade, some 80 to 85 per cent of the harvested wood from forests is used as fuelwood. The kind of forest and the constituent species are dependent on the climatic zones in which the forest is located. Usually the higher the rainfall the bigger the trees and the greater the timber yield. Similarly, the wetter the area of the humid tropics where a forest is situated, the greater the number of plant species and, generally, the more ecologically stable the ecosystem.

Management of tropical forests is a relatively new development, and much wastage has occurred in the past because exploitation has been limited to only a few species: those that have been well characterized, tested and proven to be of economic value. For example, during the latter half of the nineteenth century, considerable destruction of the tropical forest resulted from destructive exploitation of wild rubbers such as *Landolphia* and *Ficus elastica* spp. as well as species for timber. There are now no longer virgin forests in most of tropical Africa, and even the surviving secondary bush has been very much disturbed.

Destruction of forests is most acute where forests are unmanaged and especially where they are under increasing population pressure. Even where the forests are managed, the prevailing taungya systems used to establish forest plantations are in no way better than shifting cultivation except that legislation is used to guarantee considerably long periods of fallow and establishment of the vegetation before a subsequent harvesting phase is permitted. Usually, the harvesting of timber species and the arable crop production systems practised remain traditional.

Priority should, therefore, be given to improvement of taungya systems of various kinds through research involving the cooperation of agronomists, silviculturists, economists and members of other relevant disciplines. Research in this area

Fig. 2. (*Opposite*) Compound farming with rudimentary sedentary agriculture and bush fallowing in the northern Guinea savanna of northern Nigeria. (Adapted from McDowell and Hildebrand (1980).)

should be related to:

- development of agroforestry systems in which efficiency of harvesting and utilization of the forest products prior to the re-establishment of a plantation is maximized;
- intercropping of various food crops, nonfood industrial crops, or perhaps forage crops in some situations, is carried out with forest trees at the early stage of plantation establishment, with the arable crops gradually being phased out as the tree canopy closes;
- intercropping of arable or perennial food crops, such as plantains, with forest trees on a continuing basis by determining critical planting patterns in time and space.

Tree crop plantations

Tree crop plantations have been found to be ecologically sound production enterprises in the humid tropics, but they are subject to various socio-economic risks related to unstable world market prices and competition with synthetics. Many farming systems that are widely practised in the humid and subhumid tropics involve trees and shrubs. Yet development efforts have mainly been put to converting stable forest ecosystems into fragile food crop production systems involving herbaceous species. These arable crop production systems invariably require higher inputs for sustained high yields that the resource endowment of small farmers permits, resulting in a total breakdown of the system due to soil degradation and weed infestation. This in turn leads to more and more bush or forest clearing, and soil erosion and degradation.

Since the main problem is that of how to provide for subsistence while at the same time ensuring some cash returns to the farmer and some improvement of human welfare, there is need to determine in a given situation in the humid and subhumid tropics what tree crops or forest species can be profitably grown *by the farmer*. Where farm size is not limiting, one or more plantation tree crops can provide enough returns for the farmer to purchase food and fulfil other social obligations. Even fuelwood is now becoming a cash crop in some parts of the world. The situation becomes more complex where, as is often the case, farm size is limiting and the requirements for subsistence, cash and sustainability have to be carefully evaluated (see Huxley, page 257, this volume)

There is a case to evaluate the potentials of plantations of indigenous or exotic tree species grown in mixtures as compared to pure stands, exploring the possibilities of manipulating planting patterns of forest trees in such a way that shade tolerant, useful or economic species can be grown with forest trees and shrubs (as in agricultural relay intercropping). Furthermore, staple food crops can always be intercropped with commercial tree crops during the early period of plantation establishment, and during renovation and re-establishment of unproductive or moribund plantations in such a way as to minimize the cost of plantation establishment. Sparnaaij (1957) has demonstrated this in oil palms and WAIFOR (1960) also recommends planting patterns for growing food crops permanently with oil

palms. Similar systems can be developed for almost all plantation crops. The techniques used for plantation crops can also be practised for fruit trees and horticultural crops consisting of trees or shrubs such as citrus, mango, papaya, and so on, that can be grown for their fruits or processed into products such as jams and jellies which are currently being imported. The fruit trees serve to support agro-based industries aimed specifically at import substitution.

Fallow systems with trees - shrubs - herbs

Traditional shifting cultivation is a slash and burn agricultural system in which generally about one to three years of cropping alternates with more than five years of fallow, during which impoverished soils are rejuvenated. At the end of each cropping phase the farmer shifts to another location and, in classical shifting cultivation, the homestead may be relocated each time the farm is moved. With increasing population pressure and establishment of more sedentary agriculture, shifting cultivation has been replaced by still intermittent bush fallow systems. True shifting cultivation was reported by Morgan (1969) to be restricted to small areas of the Ivory Coast and to the Nigerian/Cameroon border.

In the humid and subhumid areas of tropical West Africa the fallow consists mainly of perennial trees and shrubs with some herbaceous weeds. In the savanna zones the fallow vegetation is made up of natural vegetation but, in southeastern Nigeria, planted fallows may be used of *Acioa baterii*, *Anthonotha macrophylla* and *Alchornea cordifolia* and, in parts of southwestern Nigeria, *Gliricidia sepium*.

Wherever it exists, either as bush or grass fallow systems, trees feature in shifting cultivation in the following ways.

- Cultivated plant components of the compound or homestead garden systems, consisting, for example, of oil palm, breadfruit, coconut, and so on, in the rainforest zone, and baobab mango and so on, in the savanna belt.
- Cultivated or protected food crop components of the outlying field systems associated with a given compound garden (Figure 1) and consisting, for example, of oil bean, *Pentaclethra macrophylla*, *Irvingia gabonensis* in the humid tropics and *Parkia* spp. in the savanna zone.
- Semiwild and wild useful trees and shrubs such as velvet tamarind, *Dialium guineense*, *Vitex doniana* in the rainforest zone, and *Butyrospermum paradoxum* and *Prosopis* spp. in the savanna zone.
- Browse trees and shrubs that may be eaten by livestock, or which are of no specific economic importance except in keeping the soil covered and for mineral cycling and soil improvement, for example, *Raphia nitida*, *Napoleona* spp. and *Uvaria* spp. in the forest zone of eastern Nigeria, and many different shrub species in the savanna.

There is need for research aimed at analysis and study of various components of the existing farming systems, such as the compound farm system and the various field systems shown in

Figures 1, 2 and 3. Such studies should be aimed not only at determining the respective roles in a farming system, but also at identifying targets for improvement; since improvement of each component will give rise to a range of alternative systems that can replace the outmoded traditional or transitional ones. As an example, a compound farm system that contains trees producing fruits, edible seeds, nuts, and so on, also contains herbaceous vegetables and other arable crops. Both the tree and arable crop components may be improved and integrated into an intensive food production, or specialized horticultural system that could satisfy both subsistence and market requirements. There are options for planting patterns in time and space that involve sole crops, inter- and relay cropping systems.

Various field systems contain semiwild, protected or wild edible or useful plant components such as *Treculia africana*, *Dialium guineense*, *Dacryodes edulis*, *Butyrospermum paradoxum* and *Parkia* spp. which would well merit further study and development for systems of horticultural plantations of sole crops, mixtures or special agroforestry systems. In southern Nigeria the African or native mango (*Irvingia gabonensis* var. *excelsa*) is grown for its highly nutritious nuts, and financial returns from it can be higher than that from cacao.

Apart from purely edible plants there are fallow plants such as *Dialium guineense* that can fulfil multiple uses as browse plants, wood for charcoal or fuelwood, and the seeds are high in vitamin C. Some of these plants may not grow as fast as, for example, *Leucaena* but there is need to study *both* exotic and indigenous trees and shrubs.

In agroforestry land use systems, cropping design may involve comparative studies of production systems consisting of:

- modifications of the existing farming or production systems;
- cropping or production systems that mimic natural ecosystems;
- totally new, innovative production systems involving patterns of planting in time and space based on a knowledge of the life cycles and potential uses of the component species.

In all these studies, aspects of both productivity *and* sustainability are equally important.

Special agroforestry systems

Apart from the development of improved agroforestry systems along the lines discussed in previous sections there is a need to test specialized systems which have been shown to be successful elsewhere. For example, the rearing of livestock in pastures under coconuts is widespread in southeast Asia; it is also practised on the East African coast, and in Mauritius and Fiji. Various aspects of this practice in Zanzibar and elsewhere have been reviewed by Reynolds (1980). Similar production systems involving trypanosomiasis resistant animals or small livestock should be explored for West Africa. Some preliminary studies in this area are being initiated by the International Livestock Centre for Africa (ILCA) in cooperation with the International Institute of Tropical Agriculture (IITA). There is also a possibility of developing systems with browse trees and shrubs grown in mixtures with grasses, legumes or both, the species used being related to the ecological zone in each location.

Short term herbaceous perennial and annual fallows

The use of short duration fallows or perennial or annual fallow crops in arable crop production has been tried in the humid and subhumid areas of Nigeria, and reported not to be as efficient in the restoration of soil fertility and productivity as those with deeply rooted shrubs. Moreover, these systems have not gained the acceptance of farmers who prefer trees and shrubs as fallow plants because they fulfil a range of uses in addition to rejuvenation of the soil.

The potential of leguminous and grass cover crops in the rejuvenation of degraded soils in reduced tillage has been reported by Lal *et al.*, (1978); Ruthenburg (1980) reviewed various ley systems in the tropics. Some live mulch systems for maize production involving permanent ground covers of perennial legumes have been studied at IITA. Leguminous shrubs may also be grown along bunds to stabilize the soil and they may serve as windbreaks.

Grazing land

Grazing systems are of widespread use in savanna areas. In such systems trees and shrubs will often feature as browse plants on ranges, and as shade plants in pastures. This important and rapidly developing area is not dealt with here but the extensive literature on the subject is being reviewed by ICRAF (Torres, pers. comm.).

Annual crops

Although many permanent arable crop production systems in the humid tropics require high levels of fertilizers and other inputs if output is to be sustained, there is a new, low input approach that seems promising. This is alley cropping of maize or other seasonal crops between rows of *Leucaena leucocephala*. The leuceana supplies fuelwood in addition to mulch rich in nitrogen and other plant nutrients. Thus this system, in addition to ensuring stable production with minimum soil degradation, helps minimize the use of nitrogen fertilizers. Leucaena can also be grown as a source of *in situ* stakes for yams and other climbing crops (see also Rachie, this volume).

Much remains to be done in determining the potentials of exotic and indigenous tree or shrub species in arable crop production. Comparative studies are needed on management systems in alley cropping as well as a thorough evaluation of the potentials of various species in different ecological zones. Problems of mechanization and appropriate technologies for such production systems also need to receive some attention.

Landscape uses

This aspect of land use may be regarded as of minor importance but it definitely has a place in multiple land use planning, research and development. Apart from the use of trees as a source of poles in industry and mining, no serious attention has been given to their potential for special purposes related either to landscaping or dealing with pollution in urban areas. Similarly, the reclamation of surface and stripmined areas has

received little attention in West Africa. For example, considerable areas near Jos in the Plateau state of Nigeria, which have been dug during tin mining operations remain unreclaimed.

Research programmes should be developed for enhancing use of plants for specific goals in environmental quality maintenance. The high rates or urbanization in West Africa require that more priority should be given to these problems and the trees and shrubs used should not be limited to exotics selected on the basis of research and experience elsewhere. The problem of landscaping is often very serious and it is an aspect of a world culture that should be developed in various parts of Africa.

GUIDELINES FOR RESEARCH IN AGROFORESTRY

Renewable resources have to be managed on a sustained basis, with minimum adverse effects on the environment. Agroforestry is a form of land use which will help to do this. The following guidelines constitute a good starting point in establishing strategies and priorities for research in agroforestry.

- In the humid tropics the exploitation of cash crops, mainly tree species, has far outstripped advances in forest management. Furthermore, to ensure that the increased need for food production is not met at the expense of forestry, ways must be found to increase productivity per unit area by including the very wide range of woody perennial species available. Efforts directed at improving integrated environmental resource management should, therefore, involve manipulation of trees to ensure that maximum advantage is taken of their multiple roles.

- This should begin with a knowledge of the status of trees and their roles in different land use systems, including historical developments, the impact of present activities and projections for future trends.

- The existing forest resources in West Africa cannot satisfy the increasing demands for wood, especially fuelwood, and it is mainly through forms of agroforestry research, training and development that systems of production attractive to small farmers can be developed.

- The alternative agroforestry systems that hold promise of most rapidly providing solutions to the problems being encountered may be developed in three ways:
  - modification of farmers' current or traditional practices;
  - development of new systems which mimic natural ecosystems, (see Oldeman, this volume); and
  - new production systems designed on the basis of our improved knowledge about agroforestry.

  To be attractive to small farmers it will also be necessary that agroforestry systems yield returns in a relatively short time.

- Some alternative land use systems that may be developed to satisfy the above objectives include:

  - tree crop plantations in the humid regions which involve

intercropping with arable food or cash crops, either restricted to the first two to three years of plantation establishment or on a permanent basis;

- specialized horticultural production systems based on fruits, nuts, and so on, with or without arable crop production;
- arable crop production systems involving the use of shrubs such as leucaena, grown with the food crop but managed to serve useful purposes in nutrient cycling, nitrogen fixation, stakes for viny crops, livestock feed, fuelwood, and so on;
- trees, shrubs and/or arable crop production systems integrated with livestock production, involving rangeland or improved pasture management systems.

Other land use systems involving trees and shrubs to which planning, research and development activities should be directed at a lower level of priority include: conservation programmes; special reserves for tourism and recreation; the use of trees and shrubs in landscaping; and reclamation.

- Research on multiple land use with emphasis on agroforestry is essentially multidisciplinary. It involves the manipulation of trees, shrubs, vines and herbaceous species or grasses to different patterns in both time and space. The production systems involved range in complexity from one or two species to many. There is an urgent need to look into the underlying principles of designing and managing such land use systems, to develop research methodology and to undertake training (Okigbo, 1980).

REFERENCES

Lagemann, J. (1977). Traditional African farming systems in eastern Nigeria. Afrika-Studien 98. Ifo-Institut für Wirtschaftsforschung, Munich. Weltform Verlag, Munich.

Lal, R., Wilson, G.F. and Okigbo, B.N. (1978). No-till farming after various grasses and leguminous cover crops in a tropical alfisol. I. Crop performance. *Field Crops Res.* 1, 71-84.

McDowell, R.E. and Hildebrand, P.E. (1980).Integrated crop and animal production: making the most of resources available to small farms in developing countries. A Bellagio Conference. Rockefeller Foundation, New York.

Morgan, W.B. (1969). Peasant agriculture in tropical Africa. *In* "Environment and Land Use in Africa" (M.F. Thomas and G.W. Whittington, eds), pp.241-272. Methuen & Co. Ltd, London.

Okigbo, B.N. (1980). Development of multiple use management for tropical forest through research in Africa. Paper presented at a Conference on Multiple Use Research, May 1980, Flagstaff, Arizona.

Reynolds, S.G. (1980). Grazing cattle under coconuts. *Wld Anim. Rev.* 35, 40-45.

Ruthenberg, H. (1980). "Farming Systems in the Tropics" (3rd edn). Clarendon Press, Oxford.

Sparnaaij, L.D. (1957). Mixed cropping in palm cultivation. *J. West Afr. Inst. Oil Palm Res.* 2, 244-264.

WAIFOR (1960). "How to plant, care for and feed your oil palms." West African Institute for Oil Palm Research, Benin.

DISCUSSION

CONNOR - What about improvement of the woody species in the compound farm?

OKIGBO - In the compound farms in the humid areas of Nigeria and Ghana one finds at least ten useful trees on a single farm. However, there has been practically no research on them. People seem to be more interested in doing research on well-known species. If resources are available investigations on less well-known species would rapidly give valuable results in terms of enhanced production and utilization.

CONNOR - Is it not a characteristic of such species that their produce cannot be stored?

OKIGBO - It varies from species to species, but these aspects have not been investigated.

BUDOWSKI - Some species of woody plants are more useful in certain specific environments than in others, especially as intercrop components. But will the situation be changed where animals are part of the system?

OKIGBO - Most compound farms in Nigeria have at least two or three species of livestock. However, the number of animals, and the intensity of production on the compound farm, varies from one ecological zone to another. Studies conducted by IITA in southeastern Nigeria have indicated that the number of livestock kept increases with human population density. In the humid tropical areas of Nigeria, where small livestock are kept, their uses vary somewhat from those of the savanna areas where cattle may be kept together with small livestock, and the cattle can be used as work animals. In these different situations the roles of the woody components have to be carefully evaluated within each system as a whole.

STEPPLER - The multiple food crop / food tree systems, as exemplified by compound gardens, are obviously highly integrated. If research attention is focussed on, say, a single species, would it not destroy the structure of the farm?

OKIGBO - Probably not, because the compound farms in the humid and subhumid areas of Nigeria consist of multilayered canopies resembling a tropical rainforest, and there is plenty of scope to manipulate such a system. Research work at IITA, and in national research institutes, has given little consideration to the compound farm as one of the target production systems for improvement. Research on arable crops in West Africa is only relevant to some of the outlying field systems located at varying distances from the compound farm, which contain only a few protected, useful trees dotted about them. In the compound farm trees and arable crops, including vegetables, are grown in mixtures without apparently adhering to any planting pattern or spacing. There is a considerable need to determine the best

management methods and planting patterns in order to optimize returns to land in compound farms, so as to grow as many species of edible and useful plants as possible, whether they are improved or not. At the same time there is no doubt that some of the taller trees can be subjected to horticultural methods of improvement which can then allow them to grow less competitively with other crops.

BENE - Presumably there is also considerable scope for tree improvement on non-arable land?

OKIGBO - Yes, but many agriculturists and especially agronomists still do not recognize or appreciate the importance of trees in existing farming systems, so I have emphasized this. Trees are grown both for subsistence *and* cash by small farmers, and this can be done on the same unit of land.

It should be emphasized that in most countries of tropical Africa, expanding the area under cultivation is the most widely practised and effective way of increasing food production. If this is allowed to continue, not only will more and more forests be cleared, but soon the best lands will be used up for arable crop production, and even marginal areas will be utilized. Then very little land, whether suitable or not, will be available for forestry which is very important in meeting the increasing demands for fuelwood, timber and other products. What is needed is increased production per unit area by combining arable crops *and* useful trees of the forest.

AN ATTEMPT TO QUANTIFY SOME CURRENT AGROFORESTRY PRACTICES IN COSTA RICA

G. BUDOWSKI
Centro Agronomico Tropical de Investigacion y Enseñanza, Turrialba, Costa Rica.

ABSTRACT. Measurement data from most agroforestry systems are still either nonexistent or empirical. In Costa Rica some information on components of a number of agroforestry systems has been collected during the last twenty years. A brief account of the results is presented, together with comments on current agroforestry practices.

INTRODUCTION

Quantification of traditional agroforestry practices has always been a difficult task because of their inherent complexity (Combe and Budowski, 1979) and the problems faced in setting up appropriate experimental designs. Most of the studies in Latin America have concentrated on merely describing traditional systems. Some field trials have included economic analyses, but seldom have they been carefully compared with other alternative land use practices. A series of comparisons between selected components of some agroforestry systems and the appropriate monocultures has now been attempted, and a preliminary appraisal has been made of biological, economic and social advantages or disadvantages (Budowski, 1982).

This still falls short of a comprehensive evaluation of the land use systems concerned, and the conclusions drawn are unavoidably tainted with subjective appreciations. However, such preliminary trials have the merit of leading to the formulation of hypotheses, even if their eventual validation will have to await the allocation of adequate experimental resources.

The present description of research carried out in Costa Rica attempts to describe the results achieved over the last twenty years at the Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE, until 1973 the Inter-American Institute for Agricultural Sciences), and the link which can be observed between traditional and relatively recent 'promising' agroforestry practices. CATIE's research, done mostly by staff and graduate students, is carried out on a large estate of 1000 hectares

situated at about 10°N at 600 to 680 m elevation with a mean annual rainfall of 2600 mm and a mean annual temperature of 22.2°C. There is a short dry season lasting one to three months. Soils vary but are usually of good structure and with mostly moderately good fertility.

The reader is referred to the original papers for full details of the experiments.

TAUNGYA

The practice of combining seasonal crops with the initial stages of more permanent tree raising has received much attention at CATIE; mainly through a series of graduate student projects in which different mixtures of crops and tree species have been tried, as well as various tree espacements, techniques for planting trees (seedlings, stumps) and subsequent comparisons of different cultural practices, including weeding schedules and the use of fertilizers (Budowski, 1981). A survey of literature and reports from Asia and Africa, combined with visits by staff to Kenya and Trinidad, to observe pines, cypress and teak planted in association with annual crops, led to the first experiment at CATIE in 1961. The purpose then was to find convenient and economic ways to replace secondary bush by valuable tree crops.

One of the most valuable local timber trees, laurel (*Cordia alliodora*) was used, planted at 3 × 3 m in association with various crops (*Cucumis sativum*, *Cucurbita maxima*, *Manihot utilissima*, *Phaseolus vulgaris* and *Zea mays*) grown on two successive rotations. This proved to be extremely successful with regard to tree survival, growth and form and, the first year after establishment, it yielded an economic benefit of 1410 colones per hectare (in 1963, 1 US$ = 6.63 colones). While the trees, measured 16½ years later, had an average diameter of 19.6 cm, a basal area of 13.2 $m^2 ha^{-1}$ and an excellent form (Aguirre Corral, 1963). (Basal area is the projection of the stem's area at breast height (1.35 m), usually taken with a tape, and avoiding all buttresses.)

A further replicated experiment was begun in 1974, also with *Cordia alliodora* planted at 2.5 × 2.5 m, using either stumps or seedlings, both 13 months old, and associated with maize cultivated traditionally. Half of each plot was given 250 kg fertilizer, using 15-30-8 (N, P, K) for the first application and 20-10-6-5 (N, P, K, Mg) 22 days later (Muñoz, 1975). The results showed a better survival and growth rate for the stumps and no effects from fertilization. This trial indicated a possible advantage of associating maize with laurel without using fertilizers. Furthermore, comparing costs, the establishment of laurel through taungya was 5 to 8 times cheaper than with laurel alone. At 4.6 years of age laurel trees were thinned either by 24 or 40 per cent (see Table 1). These two initial trials led to further investigations with other tree species established by taungya, for example *Eucalyptus deglupta*, *Gmelina arborea* and *Terminalia ivorensis*.

Taungya with Eucalyptus deglupta

In the past several provenances of *Eucalyptus deglupta* were

Table 1. Cordia alliodora, established by taungya after 4.6 years, CATIE, Turrialba, Costa Rica. Mean measurements (taken from Muñoz, 1975).

Treatment	Diameter cm	Height m	Number of trees	Basal area $m^2 ha^{-1}$
		Before thinning		
No thinning	7.74	6.5	1477	7.86
24% of trees thinned	8.21	6.9	1397	8.03
40% of trees thinned	7.88	6.7	1520	8.52
		After thinning		
No thinning	7.24	6.5	1477	7.86
24% of trees thinned	9.15	9.0	1067	7.01
40% of trees thinned	9.37	9.1	960	6.59

introduced to Costa Rica and apparently some cross-fertilization had occurred, producing a vigorous tree locally known as 'Turrialba Eucalyptus Hybrid'. This selection is in demand for banana props and for posts. Growth has been shown to be spectacular, some trees reaching a diameter of over 50 cm in less than 10 years. For the experimental plantation, started in January 1976, 5 randomized blocks were used. Half of the plots had *Eucalyptus deglupta* at two planting distances: 2.5 × 2.5 m and 3 × 3 m, associated with maize. Again half of each plot was fertilized 11 months after planting. Results can be summarized as follows (from Aguirre Castillo, 1977).

- Spacing brought about no significant difference in tree growth in this early stage.
- The best tree growth was achieved with taungya and fertilization, but it was estimated that the high cost of fertilizer did not warrant its use.
- Even non-fertilized eucalyptus associated with maize grew well.
- Economically it was best to grow eucalyptus with maize and without fertilizer in comparison with the other combinations, and compared with eucalyptus without maize it proved 56 to 66 per cent cheaper.

The trees were monitored for a further two years without any additional fertilizer application to give the results shown in Table 2.

Taungya with Gmelina arborea

This trial was initiated in 1977 using the traditional cropping systems of maize (*Zea mays*) and beans (*Phaseolus vulgaris*),

Table 2. Performance of *Eucalyptus deglupta* established at two planting distances in 1976, with and without an assoicated maize crop and with and without fertilizer (after Combe and Gewald, 1979). Figures are overall mean values.

Year after establishment	Second		Third			
Period of observation	Jan. to Dec. 1977		Jan. 1978 to Jan. 1979			
Thinnings	without		without		with	
Increments in:	diameter cm yr^{-1}	height m yr^{-1}	diameter cm yr^{-1}	height m yr^{-1}	diameter cm yr^{-1}	height m yr^{-1}
TREATMENTS						
Spaced 2.5 × 2.5 m						
E. deglupta alone	3.4	4.1	2.2	2.5	3.2	3.1
E. deglupta with maize for first year only	3.3	4.0	2.3	3.5	3.1	3.1
E. deglupta with maize and fertilized for one year only	3.5	4.3	2.5	3.2	3.7	3.5
Spaced 3.0 × 3.0 m						
E. deglupta alone	4.1	4.4	2.9	3.3	3.3	3.7
E. deglupta with maize for first year only	3.6	3.7	3.0	4.9	3.6	4.9
E. deglupta with maize and fertilized for one year only	4.1	4.2	3.0	2.6	3.6	3.5

either separately, or planted together. The first crop of beans, sown in the wetter part of the year, was harvested early for string beans. The second crop was left to mature (total time: 10 months). Spacing for *Gmelina* was 2 × 1 m and 2 × 3 m, and no fertilizer was applied. Half of the trees were planted as stumps, half as seedlings.

A spacing of 2 × 3 m associated with two crops of maize and beans was the most productive and gave a net benefit of 9190 colones (at this time US$1 = 8.54 colones) per hectare (Fernández, 1978). The *Gmelina* trees were measured after ten months: five months after the last harvest of beans. Some results are given in Table 3. As expected, stem diameter of *Gmelina* was greater at the wider spacing but no statistical significance could be detected when the effect of associated crops on *Gmelina* was analysed.

Table 3. Growth of *Gmelina arborea* at 15 months from planting out either alone or under taungya. Annual crops were harvested 5 months before (Combe and Gewald, 1979.) Figures are overall mean values.

Treatment			
Cropping	Spacing	diameter cm	height m
Gmelina alone	1 × 2 m	5.41	6.04
Gmelina with maize (twice)		5.30	5.74
Gmelina with beans (twice)		5.55	5.84
Gmelina with maize and beans		5.70	6.03
Gmelina alone	2 × 3 m	8.80	6.12
Gmelina with maize (twice)		7.52	5.55
Gmelina with beans (twice)		7.31	5.34
Gmelina with maize and beans		7.27	5.38

Taungya with Terminalia ivorensis

Terminalia ivorensis is a valuable African timber tree which had been tested at CATIE over ten years at various sites. It had shown remarkable growth, good form and a striking similarity in branch architecture to *Cordia alliodora*, including light shade and deciduousness in time of water stress. This suggested that it might well be a useful woody perennial component in agroforestry systems and this was tested, first through taungya plantings and, at a later stage, through permanent combinations with perennial crops (coffee, cacao, citrus). All the *Terminalia* trees were planted, in June 1978, at a distance of 3 × 3 m; half of them as stumps, half as seedlings. The wide spacing was intended to allow intercropping for more than a year and no fertilizer was applied. The trial plots were of:

- *T. ivorensis* alone;

- *T. ivorensis* associated with maize followed by beans;
- *T. ivorensis* associated with cowpeas (*Vigna unguiculata*) followed by maize;
- *T. ivorensis* associated with maize and cowpeas together, followed by maize and string beans.

The initial stand of *Terminalia* trees was thinned from 1111 to 694 ha^{-1} six months after crop planting started (Castañeda, 1981).

The results after ten months showed that:

- *Terminalia* stumps survived better and had slightly better growth than seedlings which, in any case, had higher handling and planting costs;
- the best economic combination was the association with maize followed by beans;
- when maize and cowpeas were cultivated together in two periods labour costs were excessive in comparison to the market value of these two food crops;
- all interplanted trees showed greater height than trees planted alone but regularly weeded (Magne, 1979).

When 15 months old the same *Terminalia* plots were underplanted with coffee (*Coffea arabica*), cacao (*Theobroma cacao*) and oranges (*Citrus sinensis*) which were themselves associated in rotations with dry beans followed by green beans (*P. vulgaris* var. Harvester) for half of each plot, and mung beans (*Vigna radiata*) followed by cowpea (*V. unguiculata*) for the other half.

Later observations showed that:

- all *Terminalia* trees associated with crops were growing markedly better than in unassociated plantations;
- the growth of the perennial crops was poor when compared to those grown as sole crops; measurements of the root systems of *Terminalia* showed them to be extensive but superficial;
- the best net benefits derived from the sale of crops were obtained with beans followed by green beans. (In this combination it was possible to obtain a net benefit of colones 2325 ha^{-1}; colones varying between 8.54 and 16.00 to US$1 in this period.)

TESTS OF VARIOUS PLANT ASSOCIATIONS AND ROTATIONS

Starting in 1977, and planned for a period of eight years, an elaborate experiment is being carried out covering several hectares and involving the following 18 treatments with crops, crop associations and rotations of importance in Costa Rica. Each treatment has four replications (Enriquez, 1979; Ensayo Central, 1979).

- Maize (*Zea mays*) followed by maize with beans (*Phaseolus vulgaris*).
- Maize followed by beans and sweet potato (*Ipomoea batatas*).
- Maize and sweet potato followed by bean and sweet potato.
- Plantain (*Musa* sp.) associated with cassava (*Manihot esculenta*) and maize.

- Sugar cane (*Saccharum officinarum*) followed by sugar cane with maize.
- Giant star pasture (*Cynodon plectostachyus*) and laurel (*Cordia alliodora*).
- Giant star pasture and poró (*Erythrina poeppigiana*).
- Giant star pasture.
- Coffee (*Coffea arabica*) associated with laurel, plantain and beans.
- Coffee associated with poró and beans.
- Cacao (*Theobroma cacao*) associated with laurel, plantain, pigeon pea (*Cajanus cajan*) and maize.
- Cacao associated with poró, plantain, pigeon pea and maize.
- Cassava followed by cassava with maize.
- Laurel associated with maize and beans.
- Maize followed by maize (with two tillages for each crop).
- Maize followed by maize (no tillage but herbicides).
- Maize followed by maize (mulching, no tillage).
- Natural vegetation (control, free growth).

The agricultural crops are considered as representative of the basic components of the rural diet, while coffee and cacao are major export crops. The trees used, laurel (*Cordia alliodora*) and poró (*Erythrina poeppigiana*) have totally different functions. Laurel provides a valuable timber; poró is a 'nurse' tree, used for shade and to improve the soil by fixing nitrogen and providing large amounts of organic matter and mulch through periodic prunings. Fertilizers are given to annual and perennial crops but not to the trees, which nevertheless benefit from its use. As yet no conclusive data are available for this experiment. Yield and soil data, and pest records are being collected. So far (1980) random tree diameter and yield measurements show extremely promising results: cacao is fruiting after only three years and laurel, in some combinations, averages over 8 cm in diameter. Other combinations of perennial crops have also been investigated (Zaffaroni and Enriquez, 1979).

MULTISTRATA PERENNIAL SYSTEMS

Coffee (Coffea arabica), *poró* (Erythrina poeppigiana), *laurel* (Cordia alliodora)

This combination of perennials, involving three canopy strata, is frequently used by coffee growers in the Turrialba region and elsewhere in Costa Rica, usually below 800 m elevation (Beer, 1980c). The poró crown is kept at a height varying between 2.5 and 4 m and regular pruning takes place every six months, when the crown has reached an average diameter of 5 to 6 m. Pruning takes little time: usually less than 2 minutes to cut down the branches of a single tree and another 4 to 5 minutes to hack and spread them over the ground.

Gonzalez (1980) compared the net economic production of four treatments common in the Turrialba region:

- coffee with poró and a high plant population of laurel (270 to 410 trees ha^{-1});
- coffee with poró and a moderate density of laurel, that is 120 to 180 trees ha^{-1}; (in both treatments the average

diameter of the laurel varied from 28 to 33 cm, with all trees established through natural regeneration;
- coffee with poró at distances of 8 to 10 m apart;
- coffee with no shade trees.

Three widely separated sites with different soil conditions were studied. The coffee harvests of 1978 and 1979 were measured as well as the diameter increment of laurel. The conclusions showed that:

- the highest coffee yields were obtained by unshaded coffee, but the difference was small;
- the highest economic yields (coffee plus wood production) were found in those treatments where laurel was associated with coffee either at a high or moderate density, and this gave a 10 to 30 per cent cash increase, depending on plots, over unshaded coffee;
- there was, however, a great variation between plots with regard to the volume increment of laurel as summarized in Table 4.

Table 4. Annual volume increment of laurel (*Cordia alliodora*) associated with coffee (*Coffea arabica*) and its economic value on three sites in the Turrialba area (González, 1980).

	Laurel trees ha^{-1}	Volume increment $m^3 ha^{-1} yr^{-1}$	Value of timber increment US\$ $ha^{-1} yr^{-1}$
Site 1	410	5.5	351
	120	5.6	358
Site 2	270	20.1	1285
	180	17.8	1138
Site 3	340	13.4	856
	180	11.4	728

Other measurements of laurel yields in coffee show the increments displayed in Table 5.

Logging trials showed that laurel trees can be felled easily between the rows of coffee and hauled to the road by oxen. Logging is best carried out before pruning the coffee and lopping the poró.

Some interesting additional information was obtained. Farmers sometimes delay poró pruning so as to retard the flowering and harvest periods of the understorey coffee. Unshaded coffee is harvested earlier and, by delaying the harvest through manipulation of poró shade, smallholder coffee growers are able to solve a critical labour shortage (Beer, 1981).

Cacao (Theobroma cacao), *poró* (Erythrina poeppigiana) *and laurel* (Cordia alliodora).

The management of naturally established laurel trees in cacao plantations is a relatively recent phenomenon in Costa Rica.

Table 5. Growth of a naturally established stand of *Cordia alliodora* over coffee shaded by *Erythrina poeppigiana*, the latter planted as large cuttings every 6 m and heavily pruned twice a year (after Combe and Gewald, 1979).

	1977	1979
Estimated age	15 years	17 years
Number of trees ha^{-1}	288	228
Mean dbh (cm)	28.9	30.7
Mean height (m)	22.5	22.9
Total volume with bark ($m^3 ha^{-1}$)	162.3	189.0
Mean annual increment with bark ($m^3 ha^{-1} yr^{-1}$)	10.82	11.12

It was uncommon twenty years ago when cacao shade was provided by a mixture of former rainforest trees, considerably opened up to admit more light. Later legume trees were deliberately planted to favour cacao (Cadima Zevallos and Alvim, 1967). The steep increase in lumber values has undoubtedly encouraged the growing of laurel trees from natural regeneration for cacao shade and these systems have been investigated since 1977 (Beer, 1980a). One measurement over two years in the lowlands close to the coast gave the results shown in Table 6.

Table 6. Growth of a naturally established stand of *Cordia alliodora* (and a few other low shade trees) at Home Creek, Costa Rica (approximate rainfall 3000 mm and mean annual temperature 24.5°C). Unpublished data, Renewable Natural Resources, CATIE, Turrialba, Costa Rica, 1979.

	15 April 1977	16 March 1979	Current annual increment**
Estimated age (years)	20-25	22-27	
Trees ha^{-1}	120	100*	
Mean dbh (cm**)	41.1	43.1	1.0
Mean height (m**)	34.0	35.2	0.6
Total volume in $m^3 ha^{-1}$ (with bark)	271.1	257.0*	14.8

* The figure decreased because many trees were harvested in the two-year period.
** Based on the same trees measured in 1977 and 1979.

Recently a devastating fungal disease, a pod rot (*Monilia roreri*) has appeared in the area and this will undoubtedly complicate future research. Furthermore, lack of income from cacao has prompted farmers to harvest their laurel trees. This is a good demonstration of the need for diversification. Widespread

Table 7. Growth of *Cordia alliodora* in association with *Theobroma cacao* or pasture (Beer, 1981).

Site	Density trees ha^{-1} 1977[1]	1979	1980	Diameter at breast height 1977[1]	1979[2]	1980[2]	Height m 1977[1]	1979[2]	1980[2]
Madre de Dios (cacao)	180	167	180	34.5	36.0	36.6	35.8[4]	35.9	35.8
Patino (cacao)			76			39.6			32.0
Home Creek[3,5] (cacao)	120	100	-	41.1	43.1	-	34.0	35.2	-
Cahuita Plot 1 (pasture)		150	150		30.4	31.3		26.6	26.5
Cahuita Plot 2 (pasture)		208	208		36.7	37.5		33.0	33.8

Site	Basal area[3] (G) $m^2 ha^{-1}$ 1977[1]	1979	1980	Commercial[3] volume (V) $m^3 ha^{-1}$ 1977[1]	1979	1980	Change in[2] (G) $m^2 ha^{-1} yr^{-1}$ 1979-80	Change in[2] (V) $m^3 ha^{-1} yr^{-1}$ 1979-80
Madre de Dios (cacao)	17.6	17.8	17.7	160	168.5	168.7	0.6	5.8
Patino (cacao)			9.9			85.0		
Home Creek[3,5] (cacao)	16.0	14.6	-	141	134			
Cahuita Plot 1 (pasture)		11.4	12.1		81.9	86.1	0.65	4.23
Cahuita Plot 2 (pasture)		22.5	23.5		195.6	206.4	0.94	10.8

1 From Rosero and Gewald (1979).
2 Calculations based only on measurements of trees still standing in 1980.
3 Values affected by felling and natural mortality.
4 Based on a diameter - height regression curve obtained from the 1979 measurements.
5 Remeasurements not taken as, after felling, only six *Cordia alliodora* remained in 1980.

harvesting of laurel has now allowed the estimation of yields (see Table 7) and gross income under present harvesting techniques. It is also possible to start collecting growth data on the new stems arising from the coppiced stumps.

FURTHER EXAMPLES OF TREES IN PASTURES

Laurel (Cordia alliodora) *and cedro* (Cedrela odorata)

The practice of leaving valuable seedlings to grow into timber trees is well known in Costa Rica and elsewhere. Legumes are known to have a favourable influence on adjoining pastures (Baccaret, 1967). In the early fifties Perez (1954) showed that laurel trees 40 and 50 years old were reaching an average diameter of 79 and 89 cm, respectively. The measurements were taken on good soils in the lowlands with close to 3000 mm of annual rainfall and a mean annual temperature of 25°C. An economic rotation of 25 years was recommended, by which time trees average between 40 and 45 cm dbh.

Detailed measurements on one plot gave the results shown in Table 8. *Cedrela odorata* grows very fast when grown in weeded coffee. Also it is able to withstand the attacks of *Hypsipyla grandella*, a destructive shootborer. It was calculated that trees can be harvested on a 15- to 20-year rotation (Ford, 1979).

Table 8. Growth of naturally established *Cordia alliodora* trees in man-made pastures. Cahuita (sea level), 3000 mm rainfall, mean annual temperature 25°C. Unpublished data, Renewable Natural Resources, CATIE, Turrialba, Costa Rica.

	15 April 1977	16 March 1979	Current annual increment**
Estimated age (years)	20-25	17-32	
Trees ha^{-1}	200	190*	
Mean dbh (cm)	37.5	38.6	0.55
Mean height (m)	34.5	35.0	0.25
Total volume in $m^3 ha^{-1}$ (with bark)	380.4	389.1*	13.5

* Some trees were harvested in the two-year period
** Based on measurements of the same trees.

Alder in pastures in the dairy region of Costa Rica

Alnus acuminata O. Ktze. (syn. *A. jorullensis* H.B.K.), a local alder, is widely planted in Costa Rica at between 1400 and 2500 m elevation, either in grazed pastures (mostly 'Kikuyu' grass (*Pennisetum clandestinum*), or where the grass is cut for fodder (*Pennisetum purpureum* and *Axonopus scoparius*) (Alvarez Valle, 1956; Beer, 1980b). Most of the farms are between 3 and 10 ha but income is relatively high in comparison with other regions of the country. The pastures are usually fertilized and fenced, forming small enclosures so as to allow rotations. The spacing

of the alder varies from 8 × 8 m to 12 × 12 m, and sometimes even wider. Occasionally the lower branches are pruned to allow more light. Seedlings from exposed roadsides or riverbanks are used, and they are usually protected from cattle for a few years by wire mesh. Alder fixes nitrogen from the air through the activity of an actinomycete (*Frankia* sp.) that produces large nodules, sometimes over 1 cm thick and of irregular size.

Table 9 shows some growth data for alder. As can be seen, on this good volcanic soil growth is outstanding. Milk production in this region is high, whether alder is part of the pasture or not, and cows are given supplementary concentrates.

Table 9. Growth of alder, *Alnus acuminata* associated with pastures and cut grass in two plots in the highlands of Costa Rica (Combe, 1979a). Rainfall is around 3500 mm and mean annual temperature between 16 and 18°C, depending on elevation.

	Location	
	Las Nubes (Alt. 1700 m)	San Rafael (Alt. 1450 m)
Pasture associated with alder	*Pennisetum clandestinum* (grazed)	*P. purpureum* (cut grass)
Age (years)	15	6
Spacing of trees (m)	8 × 12, and up to 10 × 14	7 × 9 and 7 × 11
Trees ha^{-1} initial	132 approx.	-
present	78	159 and 130
Height (m) mean of 26 trees	22.0	10.0
Mean annual height increment (m)	1.47	1.67
Dbh (cm) mean of 25 trees	44.8	17.0
Mean annual dbh increment (cm)	2.29	2.83

The wide spacing of the trees allows an excellent development of the grass and there is at present an effort by various governmental institutions to plant more alder. A popular manual based on the research work by Poschen (1980) is being compiled. The trees are harvested on a 15- to 20-year rotation when they reach 40 to 50 cm diameter. The medium soft wood is in demand for construction in the highlands, for boxes, crates, coffins, firewood and, lately, for orthopaedic shoes. It has been calculated that about 60,000 ha of land could be devoted to such combinations (Combe, 1979b).

OTHER EXAMPLES OF THE USE OF MULTIPURPOSE TREES

Erythrina poeppigiana *as a multipurpose nurse tree*

This extremely fast growing legume is widely used for 'shade' in coffee and cacao. It is also commonly planted between various annual and perennial crops, as well as in pastures. The leaves are relished by cattle and lopping is often practised. Over the last few years the wood has been purchased by a local paper factory as a substitute for pine. Propagation is usually by large cuttings, 2 m long, which start to produce shoots immediately. Planting distances can vary, but in coffee plantations it is usually 6 to 10 m apart.

Techniques for preparing cuttings and planting them have been described by Lozano (1962), while the amount of biomass derived from *Erythrina* pruned every six months within coffee plantations was investigated by Molleapaza (1979). The latter also calculated the amount of nitrogen that the trees provide to the soil in coffee plantations by measuring leaf fall and the biomass of prunings. This amounted to 80 kg of N ha^{-1} over a period of six months. The nitrogen concentration in leaves fluctuated between 4.2 and 4.6 per cent.

Live fence posts

The practice of planting large cuttings that take root and serve as fences is of ancient origin throughout tropical America, and also in Africa and Asia. In Costa Rica live hedges, with barbed wire strands attached, are a typical feature of the landscape. Even so, there is remarkably little literature on planting techniques, although many of the species are known to produce food, such as fruits or flowers, feed for cattle and rabbits, medicinal products, firewood, posts, and, of course, more fence posts from the branches. There is much empirical knowledge concerning choice of species, planting techniques, management practices such as pruning and renewal, as well as techniques to attach barbed wire. Yet there are regions within the country where few or no live fences are used, even though the climate and soils would make it perfectly feasible to do so. An initial inquiry has shown that live fence posts are usually associated with 'poverty', and that the sophisticated technology to plant and tend live fences may not yet have reached these areas. It points out that sociocultural factors play a most important role in the adoption of live fence post establishment. Some of these ideas are expressed in Table 10 which is based on a series of inquiries and discussions with people knowledgeable about the subject.

CONCLUSIONS

Much of the information obtained so far is empirical and based on common practices within Costa Rica. As yet, there have been few detailed investigations on agroforestry systems in the scientific literature, in contrast to the wealth of documentation on agronomic practices not involving trees. Admittedly research in agroforestry is a complex task (Combe, 1979b) and experiments are not easily set up. Furthermore, there are few scientists trained in the multidisciplinary aspects of agroforestry

Table 10. Comparisons between live and wooden (dead) fences (the latter either naturally durable or treated with preservatives). Both methods use attached barbed wire and are used principally to prevent trespass by cattle (Budowski, 1982).

Factor	Live fence	Wooden (dead) fence
Choice of species	Depends on ecological conditions	Many possibilities: depends on availability
Cost	Relatively low, or free	Relatively high
Handling of post before placing	Needs careful preparation, transport and storage	No special care required
Placing in soil	Needs care, adequate soils	Soil not limiting
Placing of barbed wire	Special techniques in some species	Some skills required
Initial maintenance	Necessary, requires protection against some animals	None, in some cases needs fire protection
Survival	Losses possible	Usually no losses if well treated
When to place wire	Usually when well anchored	Immediately
Increase of post density along fence	Easy and cheap	Easy but expensive
Durability	Usually very long	Variable, limited according to treatment and species
Organic matter production	Varies with species	None
Nitrogen fixation	Possible in some species	None
Effect on soil fertility	Beneficial, specially when branches are pruned and some roots die off (aeration)	None

Table 10 continued

Erosion control	Can be effectively used as barrier	None
Competition for water and nutrients and light with nearby crop	Does exist but varies according to system; organic matter production compensates	None
Protection of crops and/or animals against wind	Effective but varies according to species, height, density	Little or none
'Horizontal' rain (fog drip) from moisture laden winds	Possible	None
Toxic effects	Possible (allelopathy)	None (except when some preservatives are used)
Toxic fauna	Can be sheltered	None (except termites in some cases)
Beneficial fauna	Provides shelter and food (for example for birds, honey bees)	Few, if any
Additional economic products	Many, such as food, feed, medicinal products; also firewood, posts and more live fence posts	None
In case removal is necessary	Difficult and costly	Relatively easy
Labour for management	Periodical pruning is necessary; skills required	Skills also required to place posts and wires and replace them
Acceptance by farmers	Very popular among poorer farmers	Depends on income. More affluent farmers tend to avoid live fence posts
Special limitations	Disliked by aerial crop pesticide sprayers	Firebreaks must be kept clean during fire season
Aesthetics appreciation	Depends on management and cultural background	Depends on investment possibilities and cultural background

research and the sociocultural dimensions of agroforestry must necessarily add complications for the investigator.

Taungya has shown to be relatively successful at CATIE, yet it is practised little in Costa Rica. Nor is any extension effort foreseen in order to transfer this technology.

Regardless of the research carried out at CATIE, or elsewhere, the practice of adding *Cordia alliodora* to coffee, cacao, or other crops is widely practised in the country and the area under this multistrata system is actually increasing. So is the planting of *Alnus* in pastures.

It appears that, for the time being, research under controlled conditions is best directed at understanding and improving practices *already in use* rather than attempting to investigate and transfer new technologies.

A PLATE illustrating this paper can be found elsewhere in this book.

REFERENCES

Aguirre Castillo, C. (1977). "Comportamiento inicial de *Eucalyptus deglupta* Blume, asociado con maíz (sistema 'Taungya') en dos espaciamientos con y sin fertilización". [Initial behaviour of *Eucalyptus deglupta* Blume, associated with maize (taungya system) at two spacings with and without fertilizer.] Mag.Sc. Thesis. URC/CATIE, Turrialba, Costa Rica.

AGUIRRE CORRAL, A. (1963). "Estudio silvicultural y económico del sistema Taungya en condiciones de Turrialba". [Silvicultural and economic study of the taungya system under Turrialba conditions.] Mag.Agr. Thesis. IICA, Turrialba, Costa Rica.

ALVAREZ VALLE, H. (1956). "Estudio forestal del 'jaùl' (*Alnus jorullensis* H.B.K.) en Costa Rica". [Forestry study of 'jaùl' (*Alnus jorullensis* H.B.K.) in Costa Rica.] Mag.Agr. Thesis. IICA, Turrialba, Costa Rica.

Beer, J. (1980a). "*Cordia alliodora* with *Theobroma cacao*: a traditional agroforestry combination in the humid tropics". CATIE, Turrialba, Costa Rica. 4 pp.

Beer, J. (1980b). "*Alnus acuminata* con pasto". [*Alnus acuminata* with grass.] CATIE, Turrialba, Costa Rica. 6 pp.(Mimeograph)

Beer, J. (1980c). "La Suiza study area agroforestry project. Operational plan October 1980 to December 1981". CATIE, Turrialba, Costa Rica. 32 pp. (Mimeograph).

Beer, J. (1981). CATIE-UNU Convenio. [Agreement CATIE-UNU.] *In* Annual Report 1980, CATIE, Turrialba, Costa Rica. (Mimeograph; unpublished)

Budowski, G. (1981). The place of agroforestry in managing tropical forests. *In* "Proc. Intern. Symp. on Tropical Forests: Utilization and Conservation" (F. Mergen, ed.), pp.181-194. Yale University, New Haven, USA.

Budowski, G. (1982). The socio-economic effects of forest management on lives of people living in the area. The case of Central America and some Caribbean countries. *In* "Proc. Workshop on Socio-economic Effects and Constraints in Forest Management" (E.G. Hallsworth, ed.), pp.87-102. John Wiley & Sons, New York.

Cadima Zevallos, A. and Alvim, P. de T. (1967). Influencia del árbol de sombra *Erythrina glauca* sobre algunos factores

edafológicos relacionados con la producción del cacaotero. [Influence of the shade tree *Erythrina glauca* upon certain soil factors related to cacao production.] *Turrialba* 17, 330-336.

Castañeda, L.A. (1981). "Comportamiento de *Terminalia ivorensis* A. Chev. asociada con cultivos anuales y perennes en su segundo año de crecimiento". [Behaviour of *Terminalia ivorensis* A. Chev. associated with annual and perennial crops in its second year of growth.] Mag.Sc. Thesis, URC/CATIE, Turrialba, Costa Rica. 116 pp.

Combe, J. (1979a). Combinaciones silvo-pastoriles en zonas altas de producción de leche en Costa Rica. [Silvopastoral combinations in dairy production in high altitude zones of Costa Rica.] *In* "Proc. Intern. Symp. on Forestry Science and its Contribution to Development in Tropical America". 4 pp.

Combe, J. (1979b). Concepts of agroforestry research techniques. *In* "Proc. Workshop Agroforestry Systems in Latin America" (G. de Las Salas, ed.), pp.48-55. CATIE, Turrialba, Costa Rica.

Combe, J. and Budowski, G. (1979). Classification of agroforestry techniques. *In* "Proc. Workshop Agroforestry Systems in Latin America" (G. de Las Salas, ed.), pp.17-47. CATIE, Turrialba, Costa Rica.

Combe, J. and Gewald, N. (Eds) (1979). "Guía de Campo de los Ensayos Forestales del CATIE en Turrialba, Costa Rica." [Field Guide to the CATIE Forestry Trials.] CATIE, Turrialba, Costa Rica. 378 pp.

Daccaret, M. (1967). "La influencia de árboles leguminosos y no leguminosos sobre el forraje que crece bajo ellos". [Influence of leguminous and non-leguminous trees on fodder plants growing underneath.] Mag.Sc. Thesis. IICA, Turrialba, Costa Rica.

Enriquez, G. (1979). Central trial of perennial crops as compared with some annuals. *In* "Proc. Workshop Agroforestry Systems in Latin America" (G. de Las Salas, ed.), pp.193-196. CATIE, Turrialba, Costa Rica.

Ensayo central de cultivos perennes. (1979). *In* "Guía de Campo de los Ensayos Forestales del CATIE en Turrialba, Costa Rica." [Field Guide to the CATIE Forestry Trials.] (J. Combe and N. Gewald, eds), pp.263-267. CATIE, Turrialba, Costa Rica.

Fernandez, S. (1978). "Comportamiento de *Gmelina arborea* asociado con maíz (*Zea mays* L.) y frijol (*Phaseolus vulgaris* L.) en dos espaciamientos". [Behaviour of *Gmelina arborea* associated with maize (*Zea mays* L.) and beans (*Phaseolus vulgaris* L.) at two spacings.] Mag.Sc. Thesis. UCR/CATIE, Turrialba, Costa Rica.

Ford, L. (1979). An estimate of the yield of *Cedrella odorata* L. (syn. *C. mexicana* Roem.) grown in association with coffee. *In* "Proc. Workshop Agroforestry Systems in Latin America" (G. de Las Salas, ed.), pp.177-183. CATIE, Turrialba, Costa Rica.

Gonzalez, L.E. (1980). "Efecto de la asociación de laurel (*Cordia alliodora* (Ruiz y Pav.) Oken) sobre la producción de café (*Coffea arabica* L.) con y sin sombra de poró (*Erythrina poeppigiana* (Walpers) O.F. Cook)". [Effect of laurel (*Cordia alliodora* (Ruiz y Pav.) Oken) on coffee production (*Coffea arabica* L.) with and without shade from poró (*Erythrina poeppigiana* (Walpers) O.F. Cook).] Mag.Sc. Thesis, URC/CATIE, Turrialba, Costa Rica.

Lozano, O.R. (1962). "Postes vivos para cercas". [Living posts for fencing.] Mag.Agr. Thesis. IICA, Turrialba, Costa Rica.

Magne, J. (1979). "Comportamiento de *Terminalia ivorensis* A. Chev. en su fase de establecimiento, asociado con maíz, caupí y frijol, utilizando pseudo-estacas y planton en el transplante". [Behaviour of *Terminalia ivorensis* A. Chev. in its establishment phase, associated with maize, cowpea and beans, using stumps and seedlings for transplanting.] Mag.Sc. Thesis. UCR/CATIE, Turrialba, Costa Rica.

Molleapaza, J.E. (1979). "Producción de biomasa de poró (*Erythrina poeppigiana* (Walpers) O.F. Cook) y del laurel (*Cordia alliodora* (Ruiz y Pav.) Oken) asociado con café". [Biomass production of poró (*Erythrina poeppigiana* (Walpers) O.F. Cook) and laurel (*Cordia alliodora* (Ruiz. y Pav.) Oken) associated with coffee.] Mag.Sc. Thesis. URC/CATIE, Turrialba, Costa Rica.

Muñoz, M. (1975). "Comportamiento inicial del laurel (*Cordia alliodora* (Ruiz y Pav.) Oken) plantado en asocio con maíz (*Zea mays*) bajo dos niveles de fertilización". [Initial behaviour of laurel (*Cordia alliodora* (Ruiz. y Pav.) Oken) planted in association with maize (*Zea mays*) under two levels of fertilization.] Mag.Sc. Thesis. UCR/CATIE, Turrialba, Costa Rica.

Perez, C.A. (1954). "Estudio forestal del laurel (*Cordia alliodora* (Ruiz y Pav.) Cham.) en Costa Rica". [Forestry study of laurel (*Cordia alliodora* (Ruiz y Pav.) Cham.) in Costa Rica.] Mag.Agr. Thesis. IICA, Turrialba, Costa Rica.

Poschen, P. (1980). "El jaúl con pasto; la práctica de un sistema silvo-partoril en Costa Rica". ['Jaúl' with grass; the practice of a silvopastoral system in Costa Rica.] CATIE, Turrialba, Costa Rica. 6 pp

Rosero, P. and Gewald, N. (1979). Growth of laurel (*Cordia alliodora*) in coffee and cacao plantations, and pastures, in the Atlantic region of Costa Rica. *In* "Proc. Workshop Agroforestry Systems in Latin America" (G. de Las Salas, ed.), pp.205-208. CATIE, Turrialba, Costa Rica.

Zaffaroni, E. and Enriquez, G. (1979). "Asociación de cultivos perennes; una alternativa de diversificación en áreas tropicales para pequeños agricultores". [Association of perennial plants; an alternative for diversification for smallholders in tropical areas.] CATIE, Turrialba, Costa Rica. 17 pp. (Mimeograph).

DISCUSSION

OLDEMAN - Are lopped branches used for fuelwood, and the stemwood as fence posts?

BUDOWSKI - Yes. Fuelwood is often a by-product in such prunings, particularly with some species such as the genus *Inga*, but not others such as *Erythrina*.

OLDEMAN - Cacao under trees needs more light during certain periods and the time of pruning of shade trees must be important?

BUDOWSKI - Time of pollarding/pruning is very important, and it can be used to regulate more uniform flowering or fruiting. By

delaying the pruning of *Erythrina*, the harvesting of coffee has been delayed successfully by one month, for example. This is very important from the point of view of labour availability and labour economy.

OLDEMAN - Are there any adverse effects of one species on another?

BUDOWSKI - Growing citrus species under *Terminalia* has not been successful. Such possible allelopathic effects have been observed with *Juglans* (tropical walnut) also, but not with *Erythrina*. *Eucalyptus deglupta* seems to associate well with other crops and the adverse reports in the literature about *Eucalyptus* in general are, perhaps, exaggerated? *E. deglupta* has certainly been associated successfully with several food species at Turrialba, under high rainfall conditions (2600 mm per year). The situation could be different in dry regions, because of competition for water in the soil.

KOZLOWSKI - *Eucalyptus camaldulensis* can be allelopathic.

BUDOWSKI - Also some grasses, for example *Molinia minutiflora*, where filtrated extracts actually inhibited the growth of trees, as shown in a thesis at Turrialba.

KOZLOWSKI - *Imperata cylindrica* is another such grass species.

LOOMIS - What is the yield of coffee when an estimated 140 kg nitrogen ha^{-1} was added to soil through fixation by *Erythrina* trees?

BUDOWSKI - Coffee yields were high (up to 2 mt ha^{-1}). However, coffee is also fertilized in spite of the nitrogen added by the *Erythrina* trees, often with urea. With little shade and the use of fertilizer, coffee yields per hectare in Costa Rica are second only to those of Hawaii. Additionally, in agroforestry systems, if annual crops are fertilized the tree components also benefit.

LOOMIS - Such situations could readily be quantified using ^{14}N tracer, which is now cheaply available.

BUDOWSKI - Some studies of nitrogen are being done. For example, it has been found that the leaves of *Cordia alliodora*, grown together with *Erythrina* and coffee, had an enhanced nitrogen content (3.1 to 3.9 per cent dry weight).

STEPPLER - What is the influence of *Alnus* on the high milk yields that have been reported?

BUDOWSKI - It is apparently not due to the presence of the trees but to superior management of the cattle, which are fed concentrates; the pastures are also fertilized. Rotations in small enclosures are the rule. A survey of the farmers indicated that some thought the trees benefitted the pastures and the cows, others not; and that possibly the palatability of the grass under trees was better. In any case many farmers like having the trees on the farm. We still know very little about the effect of the trees on the grass.

STEPPLER - Did you analyse the grass?

BUDOWSKI - No, but studies are planned. There are some major limitations also in conducting such studies.

STEPPLER - Reduction of lignification in the grass due to reduced light could be a factor in increasing palatability.

BUDOWSKI - Probably, but there is only limited shading under the trees, which are 8 to 15 m apart; also alder trees have a light crown and are often pruned. Certainly, it is essential to obtain all the relevant data from both the trees *and* the pasture grasses.

63

5

INTEGRATED FORESTRY - AGRICULTURE - LIVESTOCK LAND USE AT JARI FLORESTAL E AGROPECUÁRIA

C.B. BRISCOE
Centro Agronomico Tropical de Investigacion y Enseñanza, Turrialba, Costa Rica.

ABSTRACT. Jari Florestal e Agropecuária is a privately owned company in northern Brazil. On a pulpmill/sawmill industrial base, production of wood, foods, and livestock have been integrated for long-term development. The current operations are briefly described.

The combination of food or livestock production with young trees is relatively simple, but as the trees mature options for integrated management become more limited and technically demanding.

INTRODUCTION

Most agroforestry in the tropics is practised on small or very small farms, much of it operating barely within the cash economy (Chandler and Spurgeon, 1980). Improvements are difficult because of the large numbers and physical dispersion of the landowners, the very low level of capital available, an inadequate research base, a lack of support services, and the complexity of knowledge required from the individual landowner.

The operations of Jari Florestal e Agropecuária are described to illustrate the relative facility, ease and economy of large-scale agroforestry.

Jari is located at 1°S 53°W near the Rio Jari, the last major tributary entering the Rio Amazonas from the north. Elevation is 5 to 500 m. Soils vary tremendously, from deep organic near the Amazon, through dune sand alluvium, to thick residual kaolinite clays. Most are highly leached latosols, high in aluminium and iron oxides and low in phosphorus and calcium (Briscoe, 1978; Chijioke, 1980).

Annual rainfall is 2135 mm, with a dry season from late September into December (Figure 1). March is normally the wettest month, but rainfall is abundant from mid-January through May in an average year. Extreme temperatures recorded are 18°C

In co-operation with SUDAM.

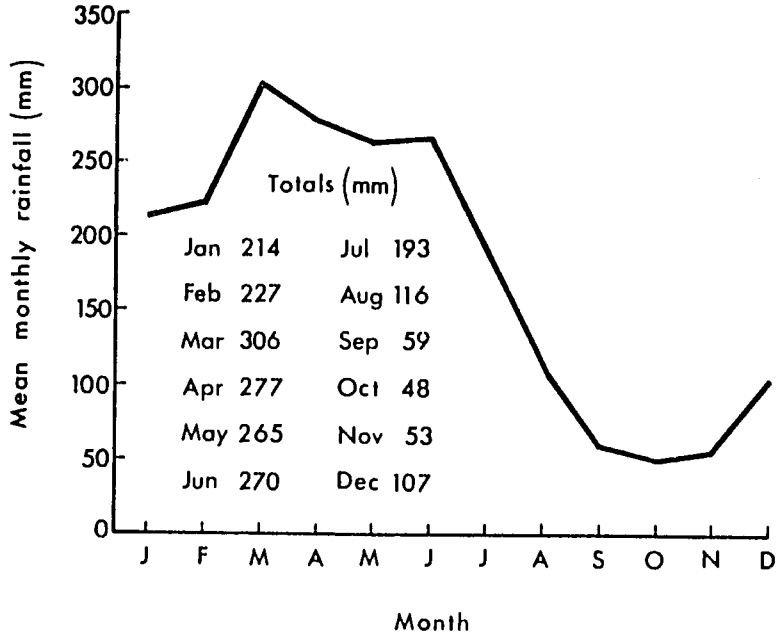


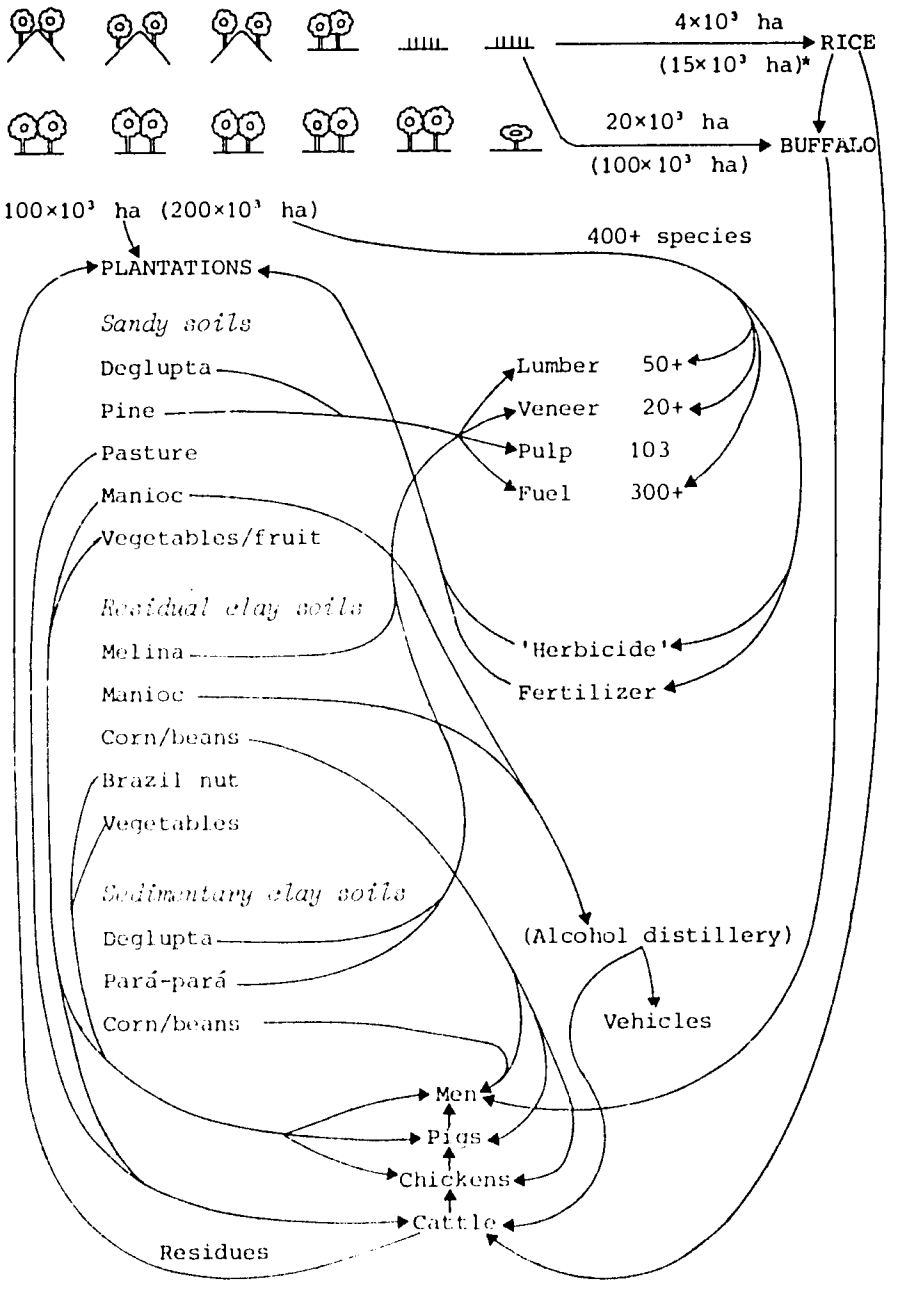
Fig. 1. Rainfall at Jari 1967 to 1980 (means of five stations). Total rainfall is 2135 mm.

and 37°C

CURRENT OPERATIONS

The company began operations in 1967 (the first trees were planted in 1968) after a pan-tropical search for available sites and promising tree species. Initial plantings were melina (*Gmelina arborea* L.), a fast growing species with a good general purpose wood, successfully planted over a wide geographical range. Tests of native and additional exotic species were begun immediately, and commercial scale plantings of Honduras pine (*Pinus caribaea* var. *hondurensis* Barr. & Golf.) were begun in 1973. A third species, deglupta (*Eucalyptus deglupta* Blume) was added in 1978, and cadam (*Anthocephalus chinensis* (Lamk.) Rich. ex Walp.), pará-pará (*Jacaranda copaia* (Aubl.) D. Don), and urophylla (*E. urophylla* S.T. Blake) are being planted on a pilot scale. Total tree plantations to date are slightly more than 105,000 ha, including more than 1900 ha of experimental plantings. Besides the species trials mentioned above and normal studies of spacings, thinning, and pruning, research is also progressing on soils (Woessner and Lopes, 1980), provenance (Woessner and Tiburcio, 1980), melina tree improvement (Woessner, 1980a), pine genetics (Woessner, 1980b), and leafcutter ant control (Ribeiro and Woessner, 1979).

As the company name indicates (it translates as 'Jari Forestry - Agriculture - Livestock') integrated development was the aim from the beginning. Rice (*Oryza sativa* L.) research was begun very early in co-operation with the International Rice Research Institute, and a commercial operation now produces 8 to



* Areas in brackets represent land available.

Fig. 2. The agroforestry system at Jari Florestal e Agropecuária Ltda.

9 m.t. $ha^{-1}year^{-1}$ on about 4000 ha.

The cattle (*Bos indicus*, *B. taurus*) and water buffalo (*Bubalus arnee* f. *bubalis*) herds are for breeding and slaughter and contain a little more than 6000 head each. Buffalo occupy varzea, seasonally flooded lands neighbouring the Amazon, Jari and Parú rivers. Cattle originally moved back and forth between varzea in the dry season and savanna in the rainy season; most are now kept in pine plantations all year. Animal gains are consistently better in the pines on the planted grasses, colonião (*Panicum maximum* cv. colonial), green panic (*P. maximum* var. *trichoglume*), and quicuio amazonica (*Brachiaria humidicola*), than they were while shifting areas. Among the grasses not satisfactory were jaraguá (*Hyparrhenia rufa*), molasses grass (*Melinis minutiflora*), setaria (*Setaria anceps*), and signal grass (*Brachiaria decumbens*).

Buffalo still depend on native forage, except that calves are fed supplements of chopped grass, napier (*Pennisetum purpureum* Schum.) and canarana erecta lisa (*Echinochloa pyramidalis*), and dairy cows are fed rice bran.

The swine herd after staying constant at 1000 to 1200 head for several years is now being expanded to 4000 animals. Fryer chickens are being raised at the rate of 6000 per week from purchased chicks.

Feed, principally corn (*Zea mays* L.) and manioc (*Manihot esculenta* Crantz), for pigs and chickens is grown in the quantities necessary between trees in new plantations.

All the operations mentioned above are shown schematically and simplified in Figure 2. There is nothing included that could not be performed by a resourceful landowner of a relatively small farm if conditions were favourable. Such a person may actually, in many cases, do better because of a more intimate knowledge of microsites and local varieties (Ruthenberg, 1976). However, it would require a very busy and capable small-scale landowner, indeed, to be able to carry out *all* the operations shown.

In the case of Jari we also have a kaolin mine and a 500 ton per day refinery, and we are entering the trial stage of producing refractory bauxite. Any additional noncompetitive source of revenue is, normally, desirable.

There must be a clear definition of objectives in establishing an agroforestry programme. If maximizing employment, especially of small-scale independent landowners, is critical, perhaps the programme should be confined to such. But if maximum production, or maximum income, is at least as important serious consideration should be given to large, integrated industrial operations.

RESEARCH NEEDS

The establishment phase and early operations at Jari have indicated the needs for any similarly integrated operation. These are noted in Table 1.

CONCLUSIONS

Jari has successfully integrated the manufacture of pulp and

Table 1. General and specific categories for consideration in establishing an integrated land use project.

GENERAL	CROPS	SOCIO-ECONOMIC
A. Area necessary: 1. For production: at Jari 170,000 ha (half planted) 2. For infrastructure: 5 per cent B. Transport needs: 1. Internal: all-weather roads, railroad 2. External: deep water port, channels C. Tenure and control: 1. Specific: purchased land 2. General: stable, non-confiscatory government D. Financial: 1. Short term 2. Long term E. Markets: 1. Internal consumption: 30,000 people 2. External sales: Europe, Far East	A. Self-sufficiency: wood, food, minerals B. Cash income: industrial base C. Complementary: corn/melina, cattle/pine D. Storage E. Soil testing/management: organic material! F. Pest monitoring and control G. Species/variety: corn vs. manioc	A. Physical 1. Food, water 2. Shelter 3. Medical 4. Education B. Social 1. Group interaction 2. Competition 3. Advancement 4. Curiosity C. Economic 1. Security 2. Market for surplus 3. Credit 4. Investment of profit

lumber with the growing of trees, rice, livestock, feed for animals, and human food. There remain many opportunities for further development.

The combination of food or livestock production with young trees requires care and common sense, but is not technically demanding.

As the trees mature, options for integrated management become more limited and more demanding.

Establishment of a forestry based industry present almost infinite possibilities for integrated agroforestry, particularly if the industry utilizes short rotation forestry.

REFERENCES

Briscoe, C.B. (1978). Silviculture in plantation development. *In* "Proc. Conf. on Improved Utilization of Tropical Forests." USDA For. Serv. Forest Products Lab., Madison, Wisconsin, USA, pp.83-99.

Chandler, M.T. and Spurgeon, D. (Eds) (1980). "Proc. Conf. on International Cooperation in Agroforestry". ICRAF, Nairobi, Kenya.

Chijioke, E.O. (1980). Impact on soils of fast-growing species in lowland humid tropics. *FAO Forestry Paper* No.21. FAO, Rome. 111 pp.

Ribeiro, G.T. and Woessner, R.A. (1979). Teste de eficiência com seis sauvicidas [illegible] controle de saúva (*Atta* spp.) na Jari, Pará, Brasil. [Tests of the efficiency of six pesticides to control 'saúva' (*Atta* spp.) in Jari, Pará, Brazil.] *Anais Soc. Entomológica Brasil* 8, 77-84.

Ruthenberg, H. (1976). "Farming Systems in the Tropics", 2nd ed. Clarendon Press, Oxford.

Woessner, R.A. (1980a). *Gmelina arborea* Roxb. Variation in wood density, height and diameter of the international provenance trial at Jari. *In* "IUFRO Symp. on Genetic Improvement and Productivity of Fast Growing Trees", Aguas de São Pedro, São Paulo, Brazil. 7 pp.

Woessner, R.A. (1980b). Pine genetic improvement program at Jari. *In* "IUFRO Symp. on Genetic Improvement and Productivity of Fast Growing Trees", Aguas de São Pedro, São Paulo, Brazil. 9 pp.

Woessner, R.A. and Lopes, O.M.N. (1980). Growth of *Eucalyptus deglupta* Bl. at Jari on different soils up through age three. *In* "IUFRO Symp. on Genetic Improvement and Productivity of Fast Growing Trees", Aguas de São Pedro, São Paulo, Brazil. 10 pp.

Woessner, R.A. and Tiburcio, V.A.S. (1980). *Tectona grandis* (DAN/FAO) provenance trial at Jari; an assessment at 5 years. *In* "IUFRO Symp. on Genetic Improvement and Productivity of Fast Growing Trees", Aguas de São Pedro, São Paulo, Brazil. 7 pp.

DISCUSSION

RACHIE - What fertilizers are used in the Jari system?

BRISCOE - None, it does not pay. However, we do give minerals to

the cattle. We have been monitoring the system, doing research on specific plots. We measure nitrogen and carry out soil analyses after each felling, and after one, two and three years, and so on, in representative plots on all plantations.

TRAN VAN NAO - You have many species in the original forest. How many have you looked at to see if you can identify new plants for cropping, food, shade and other purposes?

BRISCOE - We certainly have many fruit trees (taperebá, cupuacú, brazil nut, genipapo, coconut, jambo cacao, jackfruit) and the company town is planted with them and seedlings are given free to anyone who wants to plant them. Also, cassava is native to Brazil and we grow field beans, native vegetables and other useful indigenous plants.

LEDIG - How long do you graze the cattle, and what is the tree density?

BRISCOE - We graze until the system will no longer support the cows. The trees are 1100 ha^{-1} but at six years we thin by 50 per cent. The spacing is 4 × 2.25 m. There is good grass even after six years of tree growth.

LOOMIS - What is the annual nitrogen input due to rainfall?

BRISCOE - I do not know; it is being looked at.

OLDEMAN - We have planted *Pinus* in cleared secondary forest which then needed a large effort to keep it weeded. Grazing with cattle was found to be a solution.

BRISCOE - I do not agree. We found that there were plant species among the native grasses that were poisonous to cattle. Clearing and then broadcasting grass seed did not work either as the cattle damaged the trees. Sowing the grass in strips between the young trees, down the middle, was then tried successfully. In the first year the cattle ate the grass, but the trees remained undamaged. By the second year the grass had seeded itself and spread, but the trees were bigger then. This method reduces competition in the first year so that the trees grow better. The meat brings in the same income as the wood.

RAINTREE - You have a labour-intensive system for forestry, but the agriculture (rice) is heavily mechanized. Why is this?

BRISCOE - I believe in low inputs and intensive labour and am responsible for the trees. The person responsible for the rice believes in mechanization; this reflects his experience. I think that labour is easier to get than spare parts for tractors. Operationally, Jari is making a profit. However, we are not yet able to cover all the infrastructural costs.

AGROFORESTRY SYSTEMS AND SOME RESEARCH PROBLEMS

TRAN VAN NAO
Food and Agriculture Organisation, Forestry Department, Rome, Italy

ABSTRACT. The United Nations Food and Agriculture Organization (FAO) has adopted a policy of incorporating agroforestry practices in all suitable forestry field projects. As of today there are 22 FAO/UNDP projects and 11 WFP assisted projects which include agroforestry activities. A brief account is given of a selection of agroforestry systems which include the rice - *Sesbania aculeata* system; *Sesbania grandiflora* - fruit trees systems; shade trees in tea and pepper estates; systems of *Theobroma cacao* and forest trees; a case of a multipurpose forest plantation using *Prosopis* spp.; and a note on the cultivation of spices and medicinal plants under forest cover. Some research and development problems related to each case are mentioned.

INTRODUCTION

Some years ago the FAO Committee on Forestry Development in the Tropics (First and Second Sessions in 1967 and 1969) discussed the problems of shifting cultivation. Delegates from developing tropical countries were then unanimous in recognizing that a solution to the ill effects of shifting cultivation could be in the application of agroforestry systems because these involve a pattern of multiple land use, combining the production of wood with that of food. This resulted in the incorporation of agroforestry practices in all suitable FAO forestry field projects. A policy that was reaffirmed first at the Fourth Session of the Committee of Forestry in May 1978 with the Secretariat Note COFO 78/3 entitled 'The place of forests and trees in integrated rural development (with particular reference to tropical countries)' and, second, at the Eights World Forestry Congress (October 1978) within the discussion area of 'Forestry for Food.'

At the present time (April 1981), there are 22 FAO/UNDP projects and 11 WFP assisted projects which include agroforestry activities. These include the practice of intercropping, the use of oil and food bearing species in afforestation or enrichment planting, the development of apiculture, fish culture, the planting of fodder species, the establishment of windbreaks or

shelterbelts for the protection of food crops, and the introduction of *Acacia albida* in cultivated fields. In addition, regional studies on agroforestry systems have been undertaken for South Asia and for the French speaking tropical countries in Africa. Other actions are contemplated, budgetary resources permitting, such as: the development of homestead forestry and energy plantations, and the development of forest as a source of food.

RICE - *SESBANIA* SYSTEMS

With Sesbania aculeata

Several species of *Sesbania* used in agroforestry systems are perennial. *Sesbania aculeata* (also called *S. cannabina* or *S. bispinosa*) is annual. *Sesbania aculeata* grows on saline, alkaline and sandy soils, as well as on wet clay soils in the tropics and subtropics. It is usually grown from seeds and the plant's stem resembles a reed with a thin fibrous outer stem filled with a soft pith. The plant matures during a six-month period when the stem becomes woody with a density of about 0.3 kg dm^{-3}. Flowering occurs around the fourth or fifth month from sowing. After six months, under normal rainfall conditions, the plant may have a height of 3 to 4 m and a diameter of 1.5 cm at 0.5 m above ground. However, when the plant grows alongside irrigation ditches, or has access to plenty of water, the stem can be 4 to 5 m in height and 5 to 8 cm in diameter at this time. Table 1 shows a cultivation calendar.

Table 1. Cultivation calendar for *Sesbania aculeata* in an agroforestry system as practised in Viet Nam (Red River delta).*

	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Spring rice cultivation			1									
Summer rice cultivation							2					
Sesbania sown as green manure (to be ploughed in after 3 months)				3								
If summer rice cultivation does not take place, *Sesbania* is left to grow for 6 to 7 months					or	4						
Fish culture						5						

* pers. comm. La Xuan Dinh, 1979.

To cultivate *Sesbania aculeata* in these systems mounds of clay soil, emerging from the water, are made between rice lines at a spacing of 1 m × 0.5 m. At the top of each, 3 to 5 *Sesbania* seeds are sown in March or April, some 1½ months before the

first rice harvest (spring rice). If a second rice season takes place in the summer, from July to October, then the *Sesbania* is ploughed in 3 to 7 days before rice transplanting. At that time about 8 to 10 t ha^{-1} of green manure are returned to the soil. The amount of nitrogen in this is estimated to be 40 to 50 kg (0.5 per cent of the green weight). Whenever a second rice season does not occur the *Sesbania* is left to grow up to October. Yields of about 15 to 20 t ha^{-1} of stemwood plus about 10 t ha^{-1} of roots are expected. In addition, some 400 kg of seed are collected in July to August. When the farmer has the means to pay for fertilizers an additional application of 100 kg ha^{-1} of superphosphate is made before any new transplanting of rice.

This system reflects an intensive use of land which combines both rice and fuelwood production. The contribution of *Sesbania* as fuelwood and fodder is locally very important and the supply of nitrogen and of organic matter for soil improvement contributes to increase the yield of paddy (Tran van Nao, 1979). This combination of *Sesbania aculeata* and rice may gain even more economic and social importance with the potential use of *Sesbania* fibre in pulp and paper making.

Sesbania grandiflora - *fruit tree systems*

In the Mekong delta of South Viet Nam, fruit trees are planted in what are usually called 'home gardens'. These home gardens are modified forest ecosystems with several tiers of fruit trees such as coconuts, mangoes and durian in the upper tier, and orange, mandarin, soursop, papaya and banana in the lower one. *S. grandiflora* is always present as a component in these agroforestry systems, which are known to have existed for hundreds of years.

The association of *S. grandiflora* and fruit trees provides the farmers with a variety of useful products: poles for fishing, fodder for animals, edible flowers, and stemwood for mushroom production (*Auricularia polytricha*). In addition, the soil is improved and the yield of fruit trees increased. As *S. grandiflora* is also viewed as a source of pulpwood this agroforestry system is very promising for rural development schemes as well.

Research and development problems

The traditional experience of growing *Sesbania aculeata* in rice fields for soil improvement and for fuelwood is, unfortunately, known only locally in Viet Nam. There is an urgent need to carry out further trials for the improvement of such practices and to demonstrate them in other, similar paddy cultivation areas in the tropics.

Although the advantages of growing *Sesbania grandiflora* with fruit trees is well accepted the actual nutrient gains provided by its introduction need to be quantified. Various questions need to be addressed such as: at what age or size of tree are the nutrient gains maximized? What would be the optimum number of *S. grandiflora* to be grown per hectare? And are there provenances that yield more?

SHADE TREES IN TEA AND PEPPER ESTATES

The use of shade trees in tea or pepper cultivation has been the subject of much controversy as the cash crop yields may be low in some places where shade trees are grown. However, it has now been observed that tea or pepper plantations without shade trees are often subject to heavy soil erosion. Moreover, as forests are dwindling, it becomes more and more difficult to get an adequate supply of wood to be used as fuel for processing tea or as support for the pepper vines. In the Kandy and Matale provinces of Sri Lanka *Gliricidia sepium* (also called *G. maculata*) has been introduced in the plantations to provide shade and to minimize the harmful effects of erosion. An appropriate pollarding of *G. sepium* plants will supply a certain amount of fuelwood. Particularly interesting is the use of stumps as living support for pepper. When *G. sepium* attains a height of 4 m it can easily be pollarded (and see similar examples in Budowski, this volume).

Research and development problems

To date no quantification has been made with regard to the production per hectare of fuelwood produced from these systems. Nor do we have an estimate of the nutrient gains or of the other benefits in yield provided by the incorporation of *G. sepium* as a shade tree and as a living support.

THEOBROMA CACAO - FOREST TREE SYSTEMS

Cacao has been underplanted in other productive tree crops in several parts of the world. For example, the introduction of *Theobroma cacao* under a rubber plantation maintained at a density of 100 trees ha^{-1} has proved to be successful in Matale Province in Sri Lanka (Tran van Nao, see FAO Travel Report, June 1979). In Mayumbe (Congo Brazzaville) *T. cacao* has been planted in association with limba (*Terminalia superba*), but less successfully. The limba is planted at a density of 70 to 80 ha^{-1} spaced at 12 × 11 m, with cacao at 400 plants ha^{-1}, that is spaced at 5 × 5 m. Limba was planted in 1955 and five years later the cacao was underplanted (Tran van Nao, see FAO Mission Report, May 1980).

Research and development problems

In Mayumbe the limba wood production is satisfactory at the density given above. The mean annual increment is about 6 m^3 $ha^{-1}yr^{-1}$, but cacao production is far from satisfactory. There is a need to know why. From the climatic point of view the situation appears to be similar in both locations and the upper canopy does not appear very different, but the benefits from the systems are not of the same magnitude. This illustrates the extreme care that has to be taken to examine the detailed systems characteristics when attempting to extrapolate, either from one kind of site to another, or when the species mixtures are similar but different.

A CASE OF MULTIPURPOSE FORESTRY

In northwest Peru an afforestation scheme has been developed on

sand dunes of semidesert conditions (see Tran van Nao, FAO Travel Report, April 1979). It covers about 1000 hectares using the following tree species: *Prosopis chilensis*, *Prosopis limensis*, *Prosopis juliflora*. The techniques used have been: direct seeding (five seeds in a hole) followed by irrigation, a spacing of 10 × 10 m, irrigation by gravity through secondary and tertiary canals and then by small rigs using six days of irrigation followed by six days without, and so on until the end of the first year. Along the rigs beans are planted for food.

The scheme has been successful so far and the project is becoming a showpiece of environmental conservation. Trees bear pods after only 1½ years and production is estimated to be 8 t of fruits $ha^{-1}yr^{-1}$. At a price of 5000 soles $t^{-1}ha^{-1}$ income from pods is expected to be some 40,000 soles $ha^{-1}yr^{-1}$ (US$200 ha^{-1}). Table 2 gives a projected production plan.

Table 2. Production plan for afforestation project in northwest Peru.

Year	Products
1 to 4	Beans
4 to 30	Pods of algaroba (*Prosopis* spp.) for animal feed, food, molasses and honey.
4 to 30	Introduction of sheep for grazing (especially for making use of the dry leaf litter).
4	Bird hunting to be allowed.
30	Felling and regeneration (fuelwood production and some timber).

Successful reafforestation of the area is creating resources for a balanced output of food, feed and animal husbandry which were not there before: pods are being converted into food to provide a protein rich flour for humans, but mainly for feed for cattle and pig raising. It will also be possible to raise sheep on a small scale to make use of the dry leaf litter; beekeeping will not only provide another source of income (honey, wax), but will also enhance the pollination process and should significantly increase pod production from the trees; manure from the animals is becoming available to fertilize arable plots; and a small amount of fuelwood is at present obtained from prunings which, although only a minor output now, will be available in much greater quantities later.

Research and development problems

To fully attain the project's objectives there is a need to investigate some problems. For example, *Prosopis* spp. are outbreeding and germplasm is highly heterozygous. All such projects need, therefore, is to search and test for high yielding, adapted provenances. Then again, the feed profile using only *Prosopis* spp. will need to be supplemented at times of the year when algaroba pods are not available and other fodder or forage species can supplement this. This might be done by introducing

other species of trees and/or grasses, or both. For beekeepers other tree species are needed so as to sustain a honey flow over a greater part of the year. Furthermore, as the whole ecosystem improves it is likely that species of perennial fruit trees can be introduced, and the conditions under which this can be done economically need to be investigated.

SPICES - MEDICINAL PLANTS - TUBERS UNDER FOREST COVER

Finally, an agroforestry practice widely adopted in several regions of the world is the cultivation of spices and/or medicinal plants under forest trees, either in plantation or in natural forest. Many examples of this are to be found in Southeast Asia where, for instance, cardamom (*Elettaria cardamomum*), and turmeric (*Curcuma longa*), as well as a variety of other medicinal plants are cultivated under forest cover (for example, see Purseglove, 1968; Nair, 1980). In India, Indonesia and Sri Lanka turmeric (Seth, pers. comm.) is grown under the shade of mango trees, or under forest trees in plantations. Yield may average 1 to 1.5 t ha^{-1} in well-drained, rich soils. Ginger (*Zingiber officinale*) as well as cardamom are also often grown under shade.

At the Research Experiment Station of Cau Hai, North Viet Nam, under a two-storey canopy of *Manglieta glauca*, managed for pulpwood on a ten-year rotation, a *Dioscorea* species is an important component. In addition, *Canna edulis* can be planted. Recently a medicinal plant (*Morinda officinalis*) has been introduced (Tran van Nao, FAO Travel Report, December 1979).

Research and development problems

Unfortunately, detailed accounts of what have often been considered merely as 'minor outputs' are rare. Our information about the species concerned, and their management, is fragmentary and data often only anecdotal in those cases where they have been reported in the literature. Yet it is known that these plants can bring useful additional income to farmers. There is certainly a need to know more about the species concerned and FAO is addressing this problem. This has to be followed by investigations to show how best to optimize planting arrangements and management in order to satisfy particular requirements for outputs and sustainibility in the systems in which these species can play an important part.

CONCLUSIONS

The examples of agroforestry given above are only a selection. Hopefully, they serve to show that, throughout the world, there are many types of landuse systems working in a pragmatic way which merit further study *in situ*. Such an approach has an advantage compared with the establishment of field experiments on agroforestry because these will take a number of years before results can be analyzed and conclusions formulated. Moreover, establishing field experiments throughout the world, under varying ecological conditions, is a costly undertaking requiring large inputs in manpower and important investments.

A start in collecting information on *existing systems* will certainly be a fruitful way to provide a cost-effective impetus

to agroforestry development in general.

REFERENCES

Nair, P.K.R. (1980). "Agroforestry Species: A Crop Sheet Manual". ICRAF, Nairobi, Kenya.

Purseglove, J.W. (1968). "Tropical Crops: Dicotyledons" and "Tropical Crops: Monocotyledons". Longmans, London, UK.

Tran van Nao (1979). *Sesbania* species in two agroforestry systems. *In* "Proc. Workshop on Agroforestry for Rural Communities", Chiang Mai University, Thailand. United Nations University, Tokyo, Japan.

DISCUSSION

JACKSON - The emphasis on studying existing agroforestry practices is certainly valid. There will be a need to initiate new research programmes, however. Starting a research programme now will bring results in five to ten years, after which useful information will continue to become available.

LEYTON - A good start for research might be to seek out some existing agroforestry experiments.

OLDEMAN - There are also many abandoned projects which could provide relevant subjects for study in the light of new developments.

GETAHUN - Experiments with *Sesbania grandiflora* have been carried out, also, at IITA. It was considered more suitable than leucaena for wet sites but, at IITA, it is subject to severe insect attack and the likelihood of nematode damage. What is the reason for this? Is it poor genetic material? Are these problems known in Southeast Asia?

TRAN VAN NAO - [illegible] Southeast Asia it grows very well. There are no problems. Per[illegible] the site in Nigeria is not wet enough?

GETAHUN - It is not that the site is too dry, but every November it gets severely damaged by grasshoppers.

TRAN VAN NAO - It grows very well from the humid part of India all the way to Indonesia. There is no report of disease or insect problems.

AGROFORESTRY WITH COCONUTS AND OTHER TROPICAL PLANTATION CROPS

P.K.R. NAIR
International Council for Research in Agroforestry, Nairobi, Kenya.

ABSTRACT. The perennial plantation crops of the tropics occupy about 8 per cent of the total arable area in developing countries and are very important, both economically and socially. Research has helped to increase substantially the yields of many in the recent past. Modern plantations maintain their traditional monocultural production strategy but smallholder farmers tend to adopt less well studied integrated and intensive land use practices, often combining perennial cash crops with the production of food crops and livestock in what are, essentially, subsistence production units. Some of these systems are noted.

The coconut palm is one of the most widely grown tree crops in the tropics with a total area of over 6 million hectares, mostly as smallholdings in densely populated areas. The growth habit of the palm is remarkably suited both to small-scale production and to combination with other crops. The age and stand density of the palms is an important factor in determining the type and form of crop association. Integrated mixed farming in smallholdings, and grazing of cattle under extensive stands of palms, are also common. Where the intercrop and the coconut crop are properly manured and well managed, a substantial number of additional crops can be produced without impairing long-term productivity. Commensal interactions in some such plant associations have been noted. Such intensified systems are well suited to smallholder situations.

The examples given of intensive coconut based systems are relevant to other smallholder plantation crops using some form of plant association or mixed farming technique that will result in higher income and land equivalent ratios per farm. As with the development of the coconut systems, their development will need to be supported by adequate research efforts.

TROPICAL PLANTATION CROPS

General considerations

These crops, which include oil palm, rubber, coconut, cacao, coffee, tea, cashew, and others, are usually cultivated intensively, with a high input of labour, and often on large holdings on a monoculture basis. Their economic produce, harvested regularly, forms after processing high value commodities in international trade. According to the United Nations Food and Agriculture Organization (Food and Agriculture Organization, 1978) permanent crops occupy over 8 per cent of the total arable area in the developing countries. Most of such permanent crops belong to the category of tropical plantation crops; pineapple, sisal and sugar cane are of relatively shorter duration and can best be referred to as perennial field crops. They are not considered here (see Table 1). The high export value of tropical plantation crops, and the high input of manual labour required, make them very important, both economically and socially, in the major producing countries or regions.

Table 1. Production statistics of major plantation crops.

Crop	Total area ('000 ha)	Total production ('000 tonnes)	Major producing countries/regions
Coconut	6865	4765 copra 3321 oil	Philippines, Indonesia, India, Sri Lanka
Oil palm	2519*	3751 palm oil	Malaysia, Nigeria, Indonesia, Ivory Coast
Rubber	6732	3613 dry rubber	Malaysia and other Asian countries
Coffee	9085	4340 green beans	Brazil, Colombia, Ethiopia, East Africa
Tea	1567	1758 made tea	India, China, Sri Lanka
Cacao	4684	1408 dried beans	Ghana, Brazil, Nigeria
Cashew	1740**	540.4 nuts	Mozambique, Tanzania, India

Source: 1977 FAO Production Yearbook No.31.
* From Hartley (1977)
** From Ohler (1979)

Commercial yields of some of these crops have increased considerably whereas, for others, it has been remarkably stagnant. A notable example of the former group is rubber, a recently domesticated plant, the average yield of which has increased over 17-fold in a century. In the latter group are crops like the coconut palm, cultivated since very early times, the economic value of its many products well known to man, and yet its average yield has remained low for a long time. This contrasting situation can be related to the research effort that

has gone into the development of these crops. Thus, crops like rubber, coffee, cacao and, to some extent, oil palm, have received considerable research attention, and the commercial yields of some of them have increased substantially, compared with crops like coconut and cashew.

Research efforts with tropical plantation crops have been, essentially, commodity oriented. The production strategy with respect to land use patterns has not changed, so that modern plantations maintain their traditional characteristics: monocultural production of an export crop, extensive and, in some cases, underutilization of land, and a high manual labour input. As indicated by Johnson (1980), the plantations, as they typically have been functioning, have seldom been concerned with annual crops except in the case of intercropping during the early stages of plantation establishment; nor with livestock raising, except to supply the needs of the plantation itself. With the realization of the importance and necessity for intensification of land use in the context of increasing population, planners and policy makers have turned towards proposals to integrate plantation crops, annual crops, livestock raising and forestry. Such integration is far more feasible in the case of those plantation crops, such as coconut, which have received relatively little research attention and are predominantly for smallholders.

Scope for integrated land use systems with plantation crops

Modern commercial plantations of crops like rubber, coffee and oil palm represent a well-managed, profitable, and environmentally stable land use activity in the tropics. The scope for integrative practices involving plant associations is limited, except perhaps during the early phases of plantation establishment, because the commercial production of these crops has been developed with the single commodity objective to such an extent that multi-use resource development in such large-scale plantations is not found to be attractive. And such diversified production strategies impede modernization of the traditional plantation management technologies. Thus, it seems that there is no rationale for diversified production from such plantation areas; nor has the technology for such possibilities been adequately developed to make such alternatives economically more remunerative than at present.

On the other hand, the situation is quite different under the smallholder farming conditions, where the two major production functions: land and capital, are limiting, and the farmer's objective is not to maximize the production of a single commodity. In many such cases, especially in the densily populated areas, farmers usually integrate crops and animal production with the perennial crops, primarily to meet their food requirements. It is for these populous smallholder crop areas that perennial crop plant associations and integrated land use practices are becoming increasingly important.

Common smallholder systems with plantation crop species

The various types of cropping systems with perennial crops that are practised in different parts of the tropics have been

described by Ruthenberg (1980). Some of the most prominent among these that are practised by the smallholder farmers are the following.

- Cacao and food crops in Ghana, Nigeria and Trinidad.
  Cacao in Latin America is mainly a forest crop, maintained under shade trees, with no fertilizers or pesticides. On the other hand, most of the cacao in West Africa is produced in smallholdings, mostly in association with a specific crop such as maize, cassava, banana, cucumbers, and sweet potato, especially in the first three to four years after planting cacao. Such plantations are established usually in areas close to the roads and the size of the plantations varies widely between families.

- Integrated farming systems (food crops and poultry) in rubber smallholdings in Malaysia, Thailand, Nigeria, India and Sri Lanka.
  Plots of rubber of less than 10 hectares are considered smallholdings in Malaysia, although the average size of such smallholdings is 1 to 3 ha. These smallholdings usually have a different appearance than the neat rows and weed free stands of commercial rubber estates. In the smallholdings rubber is planted mixed with fruit trees, pepper, coconuts, and arable crops such as soya bean, maize, banana, and groundnut. Poultry raising in rubber stands is also a common and remunerative practice in Malaysia (P.D. Abraham, pers. comm.).

- Coffee smallholders in East Africa, Colombia, Ivory Coast and Madagascar.
  The banana [illegible] coffee smallholdings of Bukoba District, Tanzania; the coffee and maize holdings at Jimma in the Ethiopian highlands; the coffee and plantain systems in the steeply sloping land of Colombia; and the integrated land use of smallholder coffee with dairy milk production in Kenya, are some of the notable examples of this production system.

- Intercropping and cattle raising with coconuts in India, Philippines, Sri Lanka and the Pacific Islands.
  Commercial production of coconuts is mostly in numerous smallholdings in the Philippines, India, Sri Lanka, and Malaysia. A large number of annual and perennial crops can be seen interplanted with coconuts in these smallholdings. Grazing under coconuts is also extensively practised in Sri Lanka and the Pacific Islands.

- Cashew holdings in India, Tanzania, and Mozambique.
  Cashew is considered to be a crop of the wastelands, where only very few other species survive well. Moreover, cashew is adapted to a wide range of ecological conditions; most of the cashew trees have not been systematically planted, so that trees appear scattered in the farm holdings in a wide range of situations. As a consequence, smallholding cashew stands are often grown intermixed with other cultivated species. Grazing under cashew is also very common as, for example, on the East African coast.

There are some characteristics, both socio-economic and

biological, that are common to all such systems, more particularly their subsistence nature. In such smallholdings the resources available to the operator, including capital, severely limit opportunities for improvement, farm size is often small, and family labour is usually underutilized on a year-round basis but inadequate during periods of peak requirements. Smallholder land use systems using plantation crop species are characterized by the availability of low cost labour with, usually, a higher employment turnover — more working days per worker, as well as more hours per working day — as compared to arable cropping. Modern production technologies that are well adapted to the commercial plantation are of little value to such small farms, mainly because lack of resources on the part of the farmer does not allow him to adopt them.

Such perennial crops do, however, encourage the farmer to take up a more settled form of livelihood, with greater motivation for investment in permanent improvements such as houses, irrigation systems, and so on. Perennial crops are often considered a basis for a family's wealth and security. The relative constancy of yield and aseasonality of production of some of the perennial crops, for example coconut and rubber, have made them a reasonable insurance against the risk of total crop failure that is so common for rainfed, seasonal crops in the tropics.

Crop systems consisting of perennial plant associations offer improved chances for conserving the soil and soil fertility through the presence of a permanent plant cover and the addition of litter to the soil, and they lend themselves, in some cases, to reduced tillage operations.

Disincentives can be the relatively long time-lag between planting and profitable production, the fact that land is committed to a crop for several years, or even decades, the high initial investment in capital and labour costs, the processing requirements of some crops, and the special management skills and different kinds of work that are usually needed.

SMALLHOLDER SYSTEMS WITH COCONUT - SOME NOTABLE EXAMPLES OF INTEGRATED LAND USE

Coconut is one of the most widely grown tree crops in the tropics. It is found mostly on islands, peninsulas and along coasts, covering an area of over 6 million hectares. More than 90 per cent of the crop is in Asia and Oceania, the major producing countries being the Philippines, Indonesia, India, Sri Lanka, Malaysia and the Pacific islands. Although the coconut is sometimes thought to be a large-scale plantation crop, most of the world's production of coconuts is from numerous smallholdings (Table 2).

The rationale for intensive land use with coconuts

Intensification and a greater integration of land use systems are a logical development in smallholder areas where coconuts are grown because of the demographic and socio-economic characteristics of such areas and the growth habit of the coconut palm which lends itself to such use. The transmission of light to the lower profiles in palm stands of varying age groups, and the general pattern of coverage of the ground by a coconut canopy,

Table 2. Estimated total and smallholder areas of coconut and the common land use systems involving coconut. (Adapted from Child, 1974 and Plucknett, 1979.)

Country/region	Total * coconut area ('000 ha)	Smallholder area (% of total area)	Size of the smallholdings (ha)	Common land use systems in coconut areas
Philippines	2100	90	0.1 - 20	Intercropping with food and cash crops; cattle grazing.
Indonesia	1800	>90	not specified	Intercropping with food crops; cattle grazing.
India	1100	>90	<2	Intercropping with food and cash crops.
Sri Lanka	445	75	<8	Intercropping; cattle grazing.
Papua New Guinea	250	33	not specified	Intercropping; cattle grazing.
Malaysia	246	87	<40	Intercropping with perennial cash crops and food crops.
Oceania	297	not available	not specified	Intercropping; cattle grazing.
Africa	208	not available	not specified	Intercropping; cattle grazing.
Central and S. America	108	not available	not specified	Intercropping with other species.
West Indies	79	not available	not specified	Intercropping with food crops.

* Reliable statistics on coconut areas are difficult to obtain because the palms are widely spread all over the area and plant associations of varying intensities are common.

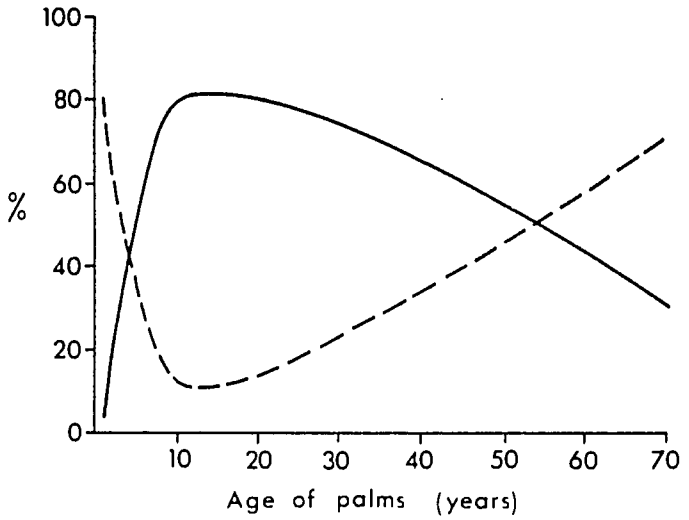


Fig. 1. Ground coverage by coconut palms of different age groups planted at 7.5 × 7.5 m (from Nelliat *et al.*, 1974). ——— Apparent coverage of the ground. — — — Light transmission through the canopy.

are shown in Figure 1. Except during the period from about the eighth to the twenty-fifth year of the palm's growth, there is sufficient light reaching the understorey to permit the growth of other compatible species. The rooting pattern of the palm is also such (Fig. 2) that most of the roots are found near the bole (Kushwah *et al.*, 1973), and the overlapping of root systems of the palm and the intercrop species can be minimal. These situations have been examined in detail by Nair (1979) who suggested a plant association pattern for coconuts of different age groups (Fig. 3).

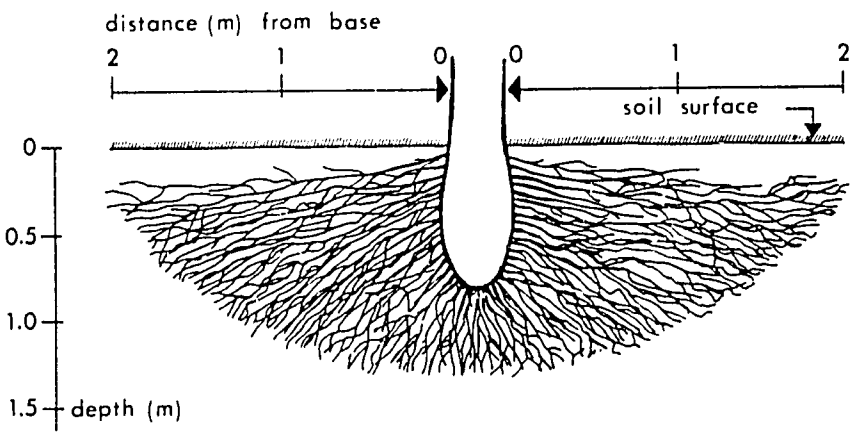


Fig. 2. Schematic presentation of the rooting pattern of an adult coconut palm. (Nair, 1979, from Kushwah *et al.*, 1973.)

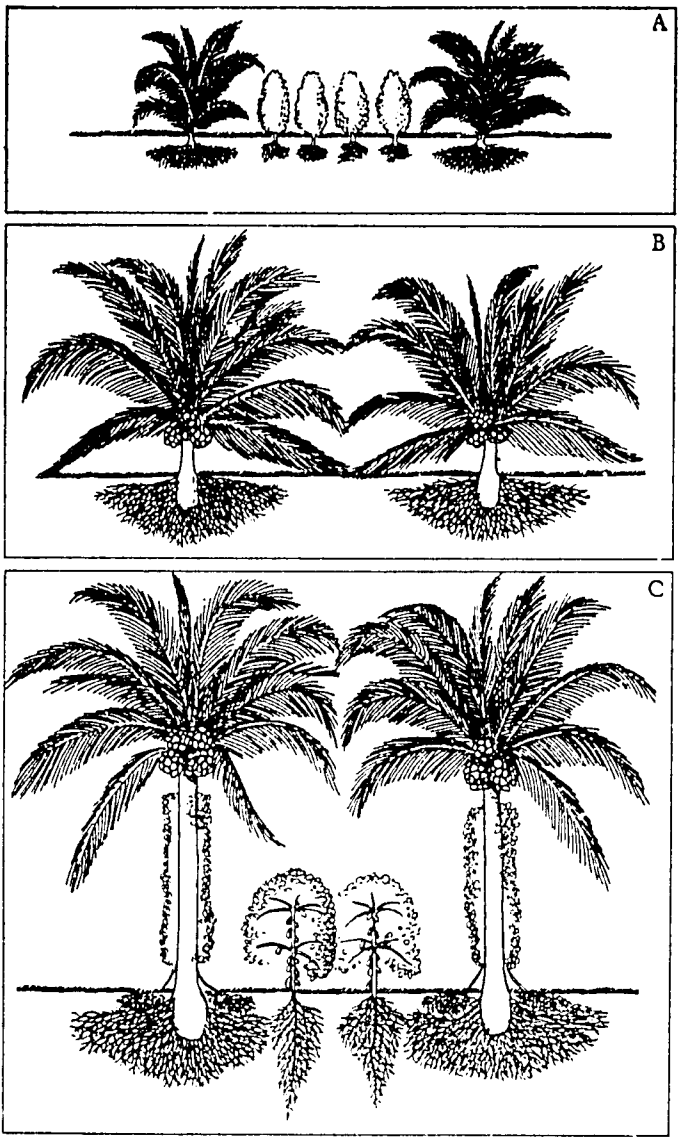


Fig. 3. Schematic presentation of the growth phases of coconut palm indicating possibilities for crop combinations.
A. Early phase, up to about 8 years: canopy develops gradually; much scope for intercropping.
B. Middle phase, about 8-25 years: greater ground coverage by canopy; little scope for intercropping.
C. Later phase, after about 25 years: increased scope for intercropping; a multistoreyed combination of coconut, cacao, and black pepper is depicted. (Nair, 1979.)

Common intensive land use systems with coconuts

Just as there is no uniformity in palm spacing, planting pattern or palm age in most of the smallholder coconut areas, so there is no regularity or systematic pattern for intercropping. In many cases a number of crops are grown together on the same piece of land in complex systems. In India the term intercropping is used for the practice of growing annuals or other short-duration crops under perennial species, whereas growing other perennials in the interspaces of perennials is called mixed cropping. Multistoreyed cropping is a term used to refer to multiple species crop combinations involving both annuals and perennials (Nair, 1977), and mixed farming refers to combined crop and livestock production.

Crop combinations. Because of the diverse conditions under which coconuts are grown, they can be seen interplanted with a large number of other economic species; the species diversity being more in less intensively managed holdings. In well-maintained holdings farmers exercise some care in the selection of the other species grown among coconuts but, invariably, food crops that give a reasonable yield under partial shade are a natural choice. For example, various tuber crops such as cassava, sweet potato and different species of yams, as well as several kinds of vegetables. There are also other annuals such as ginger and turmeric, biennials like the banana and pineapple, and an array of perennials such as cacao, clove and cinnamon that grow well with coconuts. Where the population of palms per unit area is less, and other conditions are favourable, crops which require abundant sunlight such as cereals and grain legumes, are also grown profitably among coconuts.

A list of crops commonly grown with coconut on small farms across the world is given in Table 3. It can be seen that the intercrops range from staple food crops to cash and export crops. The choice of the intercrops and their cropping pattern depend on a number of factors such as demand or market for the product, climatic and soil factors, age and management level of the palms, growth habits of the intercrop, and so on. The planting schedule for a number of intercrops for the high rainfall areas on the west coast of India is shown in Figure 4. In Sri Lanka, Santhirasegaram (1967) has divided the coconut lands into three rainfall zones, based on their suitability for intercropping, and has suggested different cropping patterns for the 'wet', 'intermediate', and 'dry' zones. However, since coconuts do not grow well in areas with less than about 1000 mm of appropriately distributed rain, the areas that he classified as 'dry' are not truely arid or semiarid according to the general meaning of these terms.

Numerous reports are available on the yield performance of various coconut intercrops under different conditions. As expected, there is a considerable amount of variation. As an example, yields of some intercrops grown under coconut in the Philippines, presumably under low management levels (Table 4), are much lower than the research station yields obtained in India (Table 5), where both the coconuts and the intercrops were separately fertilized and managed well. However, in general, the yield of a species grown as an intercrop will be less than the

Table 3. Crops commonly grown with coconut (excluding cover crops and fodder species). (Adapted with modifications from Plucknett, 1979.)

Crop	Scientific name	Country	Important references
1. CEREALS			
Rice	*Oryza sativa*	India	CPCRI, 1976; Child, 1974
Finger millet (and other millets)	*Eleusine coracana*	India, Sri Lanka	Child, 1974; Albuquerque, 1964
Maize	*Zea mays*	Philippines	Celino, 1963
2. PULSES			
Green gram (mung bean)	*Vigna radiata*	India	Albuquerque, 1964; Nair, 1979
Black gram (Urd)	*Vigna mungo*	India	Albuquerque, 1964; Nair, 1979
Pigeon pea	*Cajanus cajan*	India	Albuquerque, 1964; Nair, 1979
Cow pea	*Vigna unguiculata*	Sri Lanka	Child, 1974
Soya bean	*Glycine max*	Philippines	PHILCOA, 1974
Groundnut	*Arachis hypogaea*	Philippines	PHILCOA, 1974
3. ROOT CROPS			
Cassava	*Manihot esculenta*	India	Nair, 1979
		Sri Lanka	Child, 1974
		Philippines	Celino, 1963
Sweet potato	*Ipomoea batatas*	India	Nair, 1979
Yams	*Dioscorea* spp.	India	Nair, 1979
Elephant foot yam	*Amorphophallus campanulatus*	India	Nair, 1979
Taro, cocoyam	*Colocasia* spp.	India	Nair, 1979
	Xanthosoma spp.	Philippines	Gomez, 1974
		Fiji	Hampton, 1972

Table 3 continued

4. SPICES AND CONDIMENTS			
Ginger	*Zingiber officinale*	India	Nair, 1979; Balasundaram and Aiyadurai, 1963; Menon and Pandalai, 1958
Turmeric	*Curcuma longa*		
Minor spices	e.g. *Coriandrum sativum*, *Trigonella foenum-graecum*		
Cinnamon	*Cinnamomum zeylanicum*		
Chillies	*Capsicum annuum*	Sri Lanka	Child, 1974
Clove	*Syzygium aromaticum*	Tanzania (Zanzibar), Seychelles	Child, 1974
Black pepper	*Piper nigrum*	India, Philippines	
5. FRUITS			
Pineapple	*Ananas comosus*	India, Sri Lanka, Philippines, Malaysia, Pacific islands, Caribbean	Nair, 1979; Celino, 1963; Child, 1974; Gomez, 1974
Mango	*Mangifera indica*		
Banana	*Musa* spp.		
Papaya	*Carica papaya*		
Breadfruit	*Artocarpus altilis*		
6. TREE CROPS			
Arecanut	*Areca catechu*	India	Menon and Pandalai, 1956
Cacao	*Theobroma cacao*	India, Malaysia, Philippines, Oceania	Child, 1974
Coffee	*Coffea canephora*		
7. OTHER CROPS			
Cotton	*Gossypium* spp.	India, Sri Lanka	Albuquerque, 1964; Child, 1974
Sesame	*Sesamum indicum*	Philippines	Seshadri and Sayeed, 1953
Abaca	*Musa textilis*		
Sugar cane	*Saccharum officinarum*		

yield of the same species in pure stands when other conditions are similar. A detailed discussion on these aspects is given by Nair (1979).

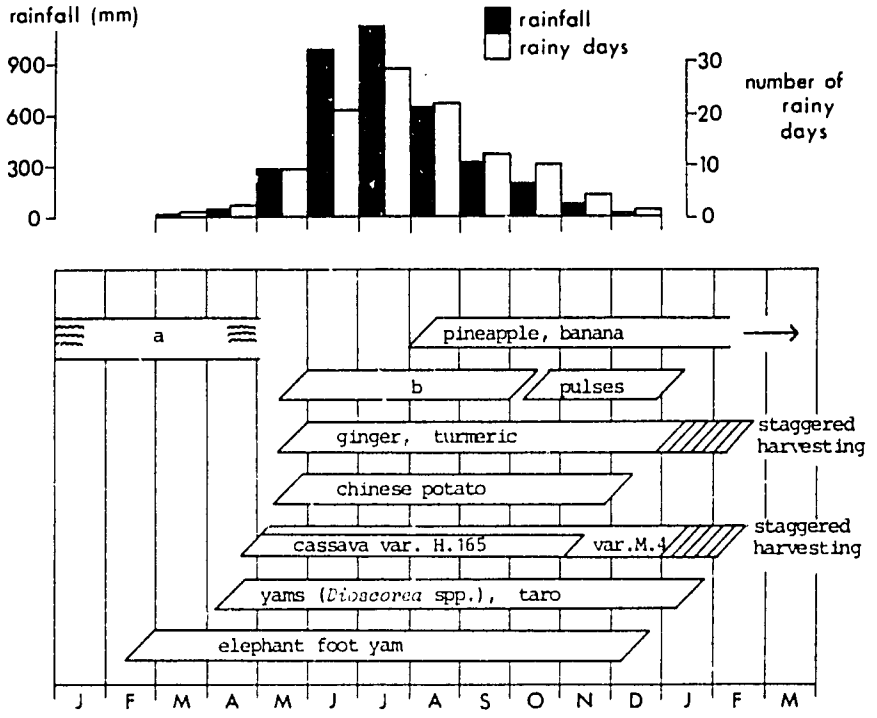


Fig. 4. Schedule of some intercrops with coconuts and the average rainfall pattern at Kasaragod on the west coast of India (Nair, 1979). (a) Irrigation to standing crop. (b) Sweet potato, upland rice.

Table 4. Yield of annual field crops under coconuts, Philippines (Paner, 1975).

Crop	Yield under coconut	
	Yield (t ha^{-1})	Percentage yield compared to crop grown in open
Maize	1.17	37
Soya bean (*Glycine max*)	0.41	34
Black gram (*Vigna mungo*)	0.58	85
Peanut (*Arachis hypogaea*)	0.93	45
Sunflower (*Helianthus annuus*)	0.63	95
Jute (*Corchorus* spp.)	0.52	29
Kenaf (*Hibiscus* spp.)	1.47	30
Ramie (*Boehmeria nivea*)	0.16	135
Taro (*Colocasia esculenta*)	5.48	367
Cassava (*Manihot esculenta*)	0.98	14
Arrowroot (*Maranta arundinacea*)	0.98	14

Table 5. Cultivation details and yield of some intercrops under coconuts in India. (Nair, 1979; Nelliat and Bhat, 1979.)

Intercrop	Per hectare of coconut area				
	Net area of intercrop	Fertilizers for intercrop			Yield
		N	P_2O_5	K_2O	
	(%)	(kg)			(t)*
Cassava *Manihot esculenta*	75	75	75	75	14.82
Elephant foot yam *Amorphophallus campanulatus*	70	75	75	75	13.46
Sweet potato *Ipomoea batatas*	70	52	35	52	8.38
Greater yam *Dioscorea alata*	70	75	75	75	13.61
Lesser yam *Dioscorea esculenta*	70	75	75	75	9.26
Chinese potato *Coleus parviflorus*	70	80	60	80	7.32
Ginger *Zingiber officinale*	70	80	60	80	8.61
Turmeric *Curcuma longa*	70	80	60	80	10.94

* All yields are 60 to 75 per cent of the open area yield of the same species.

Integrated mixed farming in smallholdings. In addition to intercropping systems there are also examples of integrated, labour intensive systems of livestock production with coconuts in smallholdings. Experiments with these have been in progress at the Central Plantation Crops Research Institute (CPCRI), Kasaragod, India, since the early 1970s. The basic unit consists of a farmer with a holding of one hectare, or perhaps more, of coconut land who maintains a few milk animals. The interspaces between coconuts are planted with fodder grasses and legumes which are manured with the cow dung and the barn wastes. A gas plant working with the cow dung will meet part of the farmer's domestic energy requirements. One or two rows of food crops such as cassava, banana, yams, or other suitable species grown around the periphery of the plot provide subsidiary food for the farmer and planting and harvesting is staggered through the year. Trials at the CPCRI have shown that the net annual income to the farmer from mixed farming in a one-hectare plot would be 50 per cent more than that of the sole crop stand of coconut (CPCRI, 1979; Nair, 1979). Guatemala grass (*Tripsacum laxum*), hybrid Napier grass (*Pennisetum purpureum*) and Guinea grass (*Panicum maximum*) yielded 50 to 60 t ha^{-1} of green fodder annually,

whereas the fodder legumes stylo (*Stylosanthes guianensis*) and cowpea (*Vigna unguiculata*) yielded 30 t ha^{-1}. At a daily feeding rate of 30 to 35 kg green fodder in a 3:1 proportion of grasses and legumes per animal, the fodder requirement of four milk cows could be met from one hectare of coconut land.

Grazing under coconuts

Grazing of cattle on the pastures grown under coconuts is another major land use activity in coconut areas in many parts of the tropics (see Table 2). Cattle raising in most such areas involves grazing on pastures composed of natural species but, in some, growing of special fodder plants is also practised. In the natural stands, the most important plants for grazing, as would be expected, are grasses and legumes, although many types of plants that can be grazed and provide some feed for livestock can be seen growing. A list of the common species occurring in natural pastures in coconut areas is given in Table 6. Some of the species which are considered 'weeds' in coconut gardens are also grazed. Moreover, cover crops such as kudzu (*Pueraria phaseoloides*), centro (*Centrosema pubescens*) and calopo (*Calopogonium mucunoides*) can also be found in natural pastures.

The carrying capacity of unimproved natural pastures varies widely because it depends upon a number of factors such as the type of plants, climatic condition, age and stand density of the palms, degree of weediness, and so on. Plucknett (1979) has surveyed the available literature on the subject and, in most cases the carrying capacity on natural pastures varied from 1 to 2 hectares per head of cattle. This form of cattle raising on natural pastures under coconut is an extensive land use system with little management input. Usually many grasses, broadleaved plants and shrubs grow as weeds in these natural pastures reducing the quality and production of forage.

On the other hand, improved pasture species and good pasture management techniques are common in several coconut growing areas, especially in the Pacific islands. The species that are commonly used are also listed in Table 6. Management practices include different stocking rates, grazing with various classes or types of animals, seasonal grazing, use of different grazing systems, use of fertilizers, selection of the proper pasture species or mixtures, weed control, fencing, and so on. The management system will vary greatly depending upon climatic factors (particularly rainfall), soil type and the farmer's skill. The effect of grazing and improved pasture management techniques on coconut yields has also been studied in detail, particularly at the Coconut Research Station in Sri Lanka. The results have indicated that, as with the case of intercropping, the pasture will not have depressive effects on the yield of palms if fertilizers are applied to both (Santhirasegaram, 1967, 1975; Santhirasegaram *et al.*, 1969).

Factors favouring intensification of land use with coconuts

Perhaps the most important incentive for adopting intensive land use systems with coconuts are the immediate economic benefits which accrue. Some data on the labour requirement, costs of cultivation, net economic returns, income equivalent ratios, and so

Table 6. Common pasture and forage species occurring under coconuts. (Adapted from Plucknett, 1979.)

Common name	Scientific name	Comments on occurrence and use
NATURAL PASTURE GRASSES		
Carpet grass	*Axonopus compressus*	Pacific islands, Jamaica
Sour paspalum	*Paspalum conjugatum*	High rainfall areas in the Pacific islands
Bermuda grass	*Cynodon dactylon*	Pacific islands
Buffalo grass	*Stenotaphrum secondatum*	New Hebrides
Guinea grass	*Panicum maximum*	Wide adaptability
LEGUMES		
Sensitive plant	*Mimosa pudica*	Widely distributed
Desmodium	*Desmodium trifolium*	Malaysia, Indonesia, Western Samoa
Hetero	*Desmodium heterophyllum*	South Pacific
Centro	*Centrosema pubescens*	Mostly as a cover crop
Alyce clover	*Alysicarpus vaginalis*	Sri Lanka
IMPROVED PASTURE GRASSES		
Palisade grass	*Brachiaria brizantha*	Wide adaptability
Signal grass	*B. decumbens*	
Cori grass	*B. miliiformis*	
Koronivia grass	*B. humidicola*	
Para grass	*B. mutica*	
Congo grass	*B. ruziziensis*	
Alabhang	*Dicanthium aristatum*	East Africa, India
Rhodes grass	*Chloris gayana*	
Pangola grass	*Digitaria decumbens*	
Batiki blue grass	*Ischaemum asistatum*	Fiji
Molasses grass	*Melinis minutiflora*	
Guinea grass	*Panicum maximum*	
Scrobic	*Paspalum commersonii*	Mostly as fodder
Napier grass	*Pennisetum purpureum*	Fodder species
LEGUMES		
Green leaf desmodium	*Desmodium intortum*	Wetter subtropics
Kaimi clover	*Desmodium canum*	Pacific islands
Perennial soya bean	*Glycine wightii* (syn. *G. javanica*)	East Indies
Leucaena (Ipil-ipil)	*Leucaena leucocephala*	Wide adaptability (except acid soils) for fodder
Siratro	*Macroptilium atropurpureum*	
Stylo (Brazilian lucerne)	*Stylosanthes guianensis*	Adaptable to infertile soils; also used as fodder

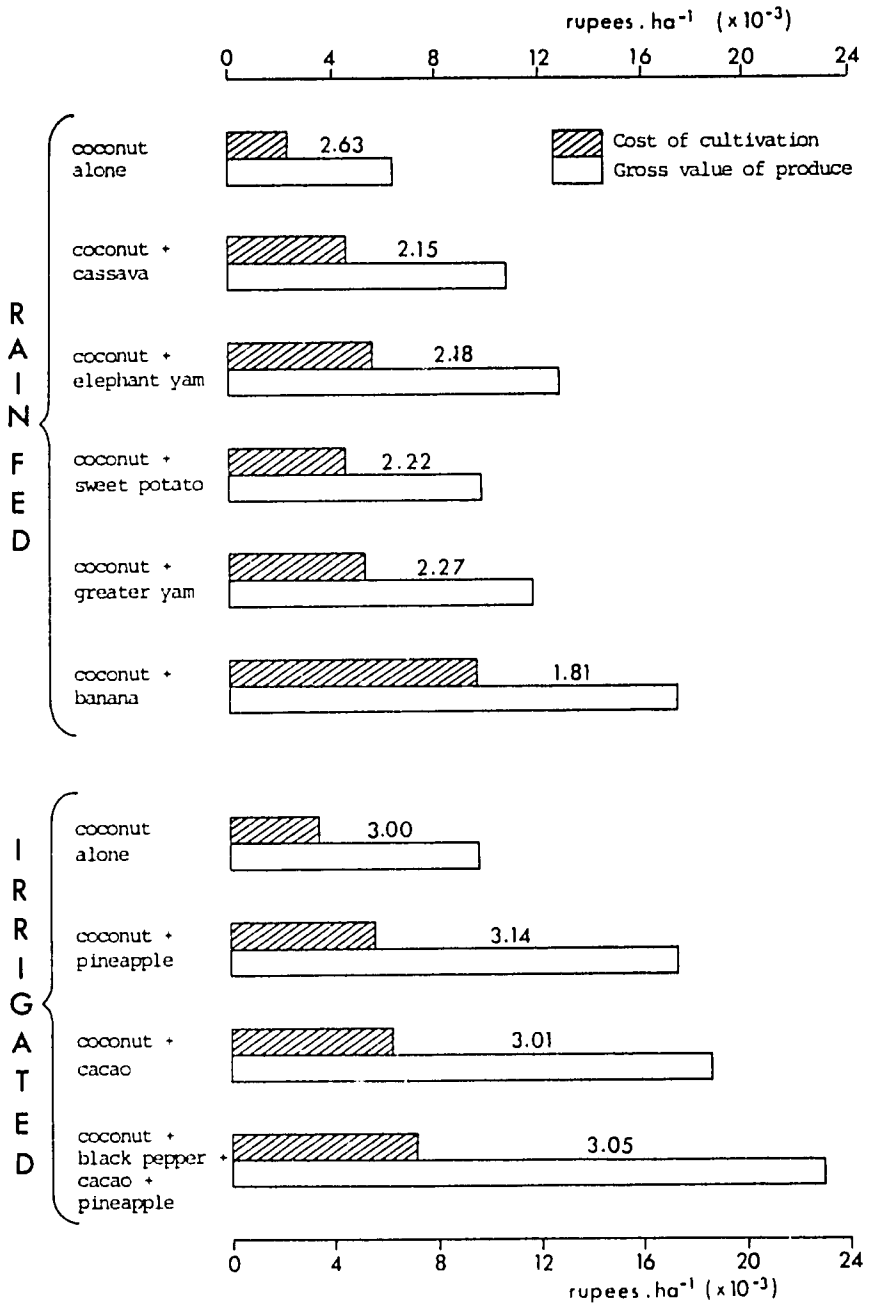


Fig. 5. Economic aspects of some crop combinations with coconuts (Nair, 1979). The figures along the bars indicate the gross value of the produce per unit amount of cost of cultivation.

on of several intercropping systems in smallholdings have been reported by Nair (1979) and Nelliat and Bhat (1979). A summary of some data is given in Figure 5.

Notwithstanding these economic benefits, the desirability of intercropping from the point of view of long-term productivity has been raised frequently. Published reports and experimental evidence indicate that the crux of the problem is the level of management. If both the main crop and the intercrop are adequately manured and managed well, intercropping is not harmful to coconut production. This has been shown in several investigations at the Central Plantation Crops Research Institute, Kasaragod, India (CPCRI, 1979; Nair, 1979). On the other hand, if the additional crop is allowed to be a 'parasite' on the main crop, the yields of both components of the mixture will be adversely affected.

A major consideration in the productivity of such plant mixtures is the extent of plant-to-plant interactions. Neighbouring plants will often be drawing on the same pool of environmental resources at both aerial and root levels (see Connor, p.401). In crop combinations with coconuts lower storey species are likely to be subjected to competition only for aerial growth factors. Fortunately, there are a number of species of economically useful plants, adapted to a range of ecological conditions which can give a reasonable yield under conditions of restricted light, for example Nair (1980), and see Table 3. Below the ground the distribution patterns of the roots of individual species are very important. The favourable rooting configurations in a multistoreyed crop combination of coconut and cocoa and pineapple are shown in Figure 6.

Interaction between neighbouring plants need not always be competitive. Plants may complement each other in sharing resource pools and thus achieve a more complete utilization of these. They may also affect the ecoclimate in ways which favour associated species. Such an example of biological complementarity has been noticed in a crop combination of coconut and cocoa at CPCRI (Table 7) and could be the outcome of a large number of factors including a modified ecoclimate (Nair and Balakrishnan, 1977), the favourable activity of beneficial micro-organisms (Nair and Rao, 1977), and others. The exploitation of beneficial interactions could substantially enhance the productivity of coconuts and other species in a combined system (Figure 7).

The intensification of land use in existing coconut areas is not without problems and limitations. Nor is it of universal applicability. The potential is confined to those areas where soil and other physical conditions permit such practices. Environmental resource limitations may impose restrictions on the crops and cropping patterns; a lack of proper management of the crop combination could also result in undesirable effects; and certain pest problems can be enhanced by growing two or more crops together. As regards the availability of area for intercropping, the shade cast by the palms, which depends upon the age of palms and their planting distances, is the most decisive factor.

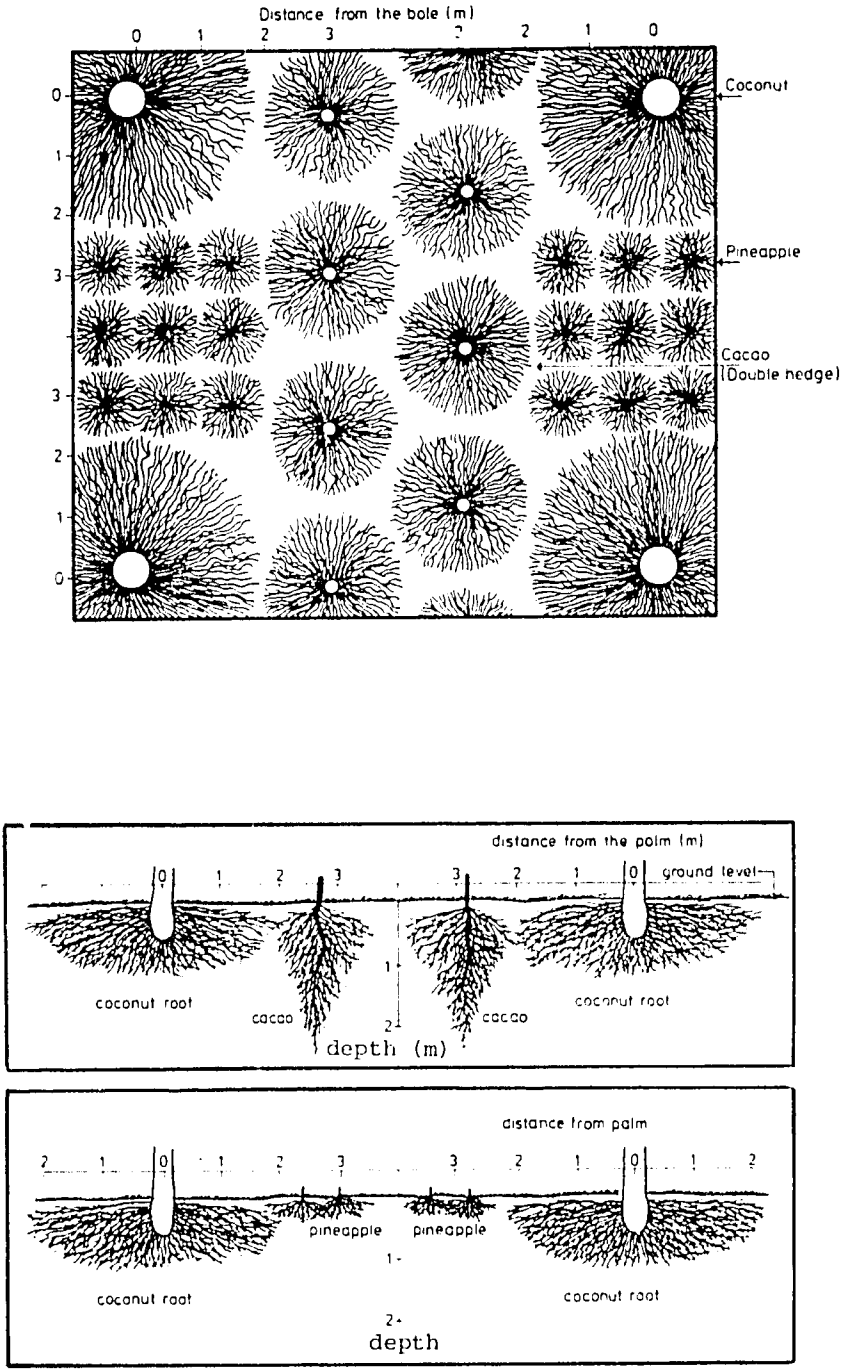


Fig. 6. Schematic presentation of the horizontal (above) and vertical (below) distribution of roots of a multistoreyed crop combination of coconut, cacao and pineapple. (Nelliat *et al.*, 1974).

Table 7. Biological complementarity of crop combinations: yield of coconut in the coconut + cacao mixed cropping experiment at CPCRI, India. Cacao was planted in 1970 when coconuts were 20 years old. (Nair, and Varghese, 1979; Nelliat and Bhat, 1979.)

Cropping system	No. of plants ha^{-1}		Annual yield of coconuts (nuts per palm)		
	Coconut	Cacao	Pre-experimental period (means for 2 years)	Experimental period 1972 - 1978 (means for 6 years)	Increase over pre-experimental period
Coconut alone	175	-	68	122	54
Coconut + cacao as single hedge between coconuts	175	350	57	121	64
Coconut + cacao as double hedge between coconuts	175	600	39	101	62

The plots were irrigated in the summer months during the experimental (but not during the pre-experimental) period.

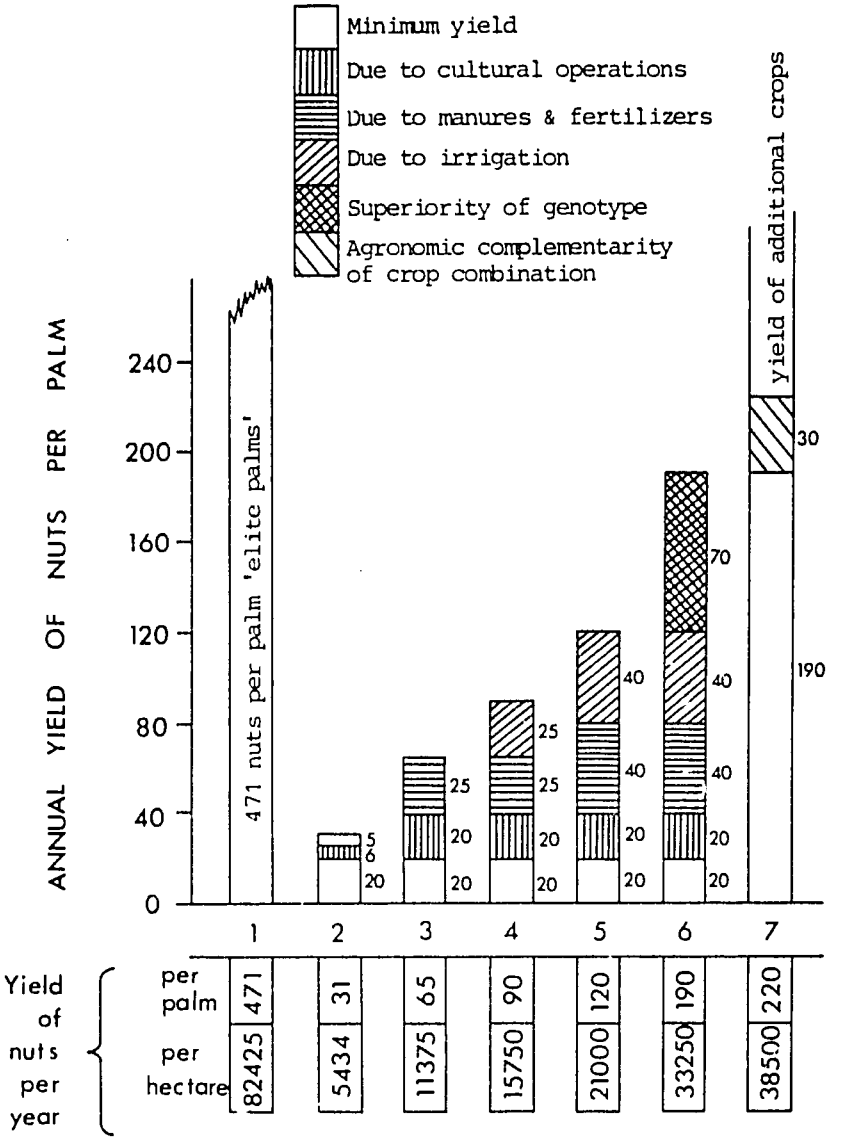


Fig. 7. Yield levels of coconut in India under different management conditions.

1. Performance of the so-called 'elite' palms; only a few such palms have been identified so far.
2. National average yield.
3. Ordinary management by average farmer; no irrigation.
4. Ordinary management with irrigation.
5. The common Tall variety under good management.
6. High yielding genotypes under good management.
7. Good genotypes grown in association with compatible intercrops; the increase in yield over (6) can be considered to be due to the complementary interaction with the associated species.

(Adapted from Nair and Varghese, 1979.)

CONCLUSIONS

Research on intensifying land use in coconut areas must be based on sound principles and it is undoubtedly one of the most important scientific initiatives in the improved management of coconut based agro-ecosystems, especially for smallholdings. Fortunately, and unlike many other scientific initiatives in the farming sector, the new technology is not confined to research stations alone; farmers are taking the initiative. Intensification practices are of particular importance in the areas affected by 'root wilt' disease of coconut — a disease syndrome of unknown aetiology that poses a great threat to coconut production in India. The productivity of such affected lands can be increased by the new technology, apart from the possible ameliorative effects of crop combinations in reducing the disease intensity.

The emphasis in intensification is to increase the productivity of areas that are already planted with coconuts. These areas are 'committed' to the crop, and it is neither desirable nor feasible to convert them to other forms of land use. The activities described conform very well to the concepts and principles of agroforestry. And like other forms of agroforestry, the history of the practices, in some form or other, is ancient. It is only now, however, that research is being organized to refine and to improve these intensive systems. In the few instances where the new technology has been introduced, a substantial number of additional crops have been grown without impairing the productivity of the coconut palm, and good use has been made of surplus human labour.

These examples of successful coconut based systems can serve as a guide to what might be done in some other smallholder perennial plantation crop areas. Some intensification of land use is a natural consequence wherever demographic pressures are high, but this need not necessarily be in the form of intercropping. Intimate crop associations on smallholdings can lead to more efficient use of land and other available resources, and thus result in better land and income equivalent ratios. Especially if managed in such a way that the combined attention given to all the species exceeds that usually prescribed for monoculture. Such intensive land use practices need to be supported by adequate research. Without this, attempts at innovation and extrapolation could have disastrous consequences; and therein lies the challenge to scientists.

REFERENCES

Albuquerque, S.D.S. (1964). Coconut cultivation in Mysore. *Coconut Bull.* 18, 249-256.

Balasundaram, E.K. and Aiyadurai, S.G. (1963). Grow spice crops in the shade of coconut palms. *Coconut Bull.* 17, 182-184.

Celino, M.S. (1963). Increasing income from coconut lands. *Coconut Bull.* 17, 169-172.

Central Plantation Crops Research Institute (CPCRI) (1976). Annual Report for 1975, pp.24-27. CPCRI, Kasaragod, Kerala, India.

Central Plantation Crops Research Institute (CPCRI) (1979). Annual Report for 1977, pp.31-34. CPCRI, Kasaragod, Kerala,

India.
Child, R. (1974). "Coconuts" (2nd edn). Longman, London.
Food and Agriculture Organization (1978). "FAO Production Yearbook No.31, 1977". FAO, Rome.
Gomez, A.A. (1974). Intensification of cropping systems in Asia. *In* "Interaction of Agriculture with Food Science" (R. MacIntyre, ed.), 93 pp. Int. Dev. Res. Centre, Ottawa, Canada.
Hampton, R.E. (1972). Vegetables. *In* "Record of a Coconut Industry Workshop", pp.72-74. Dept. of Agriculture, Fiji.
Hartley, C.W.S. (1977). "The Oil Palm" (2nd edn) (pp.590-596). Longman, London.
Johnson, D. (1980). Tree crops and tropical development: the oil palm as a successful example. *Agric. Admin.* 7, 107-112.
Kushwah, B.L., Nelliat, E.V., Markose, V.T. and Sunny, A.F. (1973). Rooting pattern of coconut (*Cocos nucifera* L.). *Indian J. Agron.* 18, 71-74.
Menon, K.P.V. and Pandalai, K.M. (1958). "The Coconut Palm - A Monograph". Indian Central Coconut Committee, Ernakulam, India.
Nair, P.K.R. (1977). Multispecies crop combinations with tree crops for increased productivity in the tropics. *Gartenbauwissenschaft* 42, 145-150.
Nair, P.K.R. (1979). "Intensive Multiple Cropping with Coconuts in India: Principles, Programmes and Prospects". Verlag Paul Parey, Berlin.
Nair, P.K.R. (1980). Agroforestry species. *In* "A Crop Sheets Manual" ICRAF 003e, pp.161-166. International Council for Research in Agroforestry, Nairobi, Kenya.
Nair, P.K.R. and Balakrishnan, T.K. (1977). Ecoclimate of a coconut plus cacao crop combination on the west coast of India. *Agric. Meteorology* 18, 455-462.
Nair, P.K.R. and Rao, N.S.S. (1977). Microbiology of the root region of coconut and cacao under mixed cropping. *Plant and Soil* 46, 511-519.
Nair, P.K.R. and Varghese, P.T. (1979). Recent advances in the management of coconut-based agro-ecosystems on the west coast of India. *In* "Tropical Ecology and Development" Part I, (J.I. Furtado, ed.), pp.569-580. Int. Soc. for Tropical Ecology, Kuala Lumpur, Malaysia.
Nelliat, E.V. and Bhat, K.S. (Eds) (1979). Multiple Cropping in Coconut and Arecanut Gardens. Tech. Bull. No.3, CPCRI, Kasaragod, India.
Nelliat, E.V., Bavappa, K.V.A. and Nair, P.K.R. (1974). Multistoreyed cropping - new dimension of multiple cropping in coconut plantations. *World Crops* 26, 262-266.
Ohler, J.G. (1979). Cashew. *In* "Comm. No.71, Dept. of Agricultural Research", pp.144-146. Royal Tropical Inst., Amsterdam.
Paner, V.E. Jr (1975). Multiple cropping research in the Philippines. *In* "Proc. Cropping Systems Workshop", pp.188-202. Int. Rice Research Inst., Los Banos, Philippines.
Philippine Coconut Authority (PHILCOA) (1974). Annual Report 1973-74. Agric. Res. Dept PHILCOA, Quezon City, Philippines.
Plucknett, D.L. (1979). "Managing Pasture and Cattle under Coconuts". Westview Press, Boulder, Colorado, USA.
Ruthenberg, H. (1980). "Farming Systems in the Tropics" (3rd edn). Clarendon Press, Oxford, UK.

Santhirasegaram, K. (1967). Intercropping of coconuts with special reference to food production. *Ceylon Coconut Planters' Rev.* 5, 12-24.

Santhirasegaram, K. (1975). Effect of associated crop of grass on the yield of coconuts. Paper read at the 4th session, FAO Tech. Working Party on Coconut Production, Protection and Processing, Kingston, Jamaica. 11pp.

Santhirasegaram, K., Fernandez, D.E.F. and Goonesekera, G.C.M. (1969). Fodder grass cultivation under coconut. *Ceylon Coconut Planters' Rev.* 5, 160-165.

Seshadri, C.A. and Sayeed, P.M. (1953). Profitable subsidiary crops. *Coconut Bull.* 7, 19-21.

DISCUSSION

COOMBS - The new, high yielding cultivars of coconut are short-statured. Their growth habit and light penetration pattern are different from that in the system you describe. Are these dwarf plants used in new plantings?

NAIR - Yes, but they have been planted only recently and will not be a significant part of the total coconut area for at least the next twenty years. We now want to improve the situation where the older, tall cultivars are planted, and these may live for 60 to 100 years.

JACKSON - Did you say that light penetration increased as the palms became older just because the canopy moves up?

NAIR - The effect is perhaps caused by a change of leaf orientation with age *vis-à-vis* light penetration.

CROZE - Certainly, raising the canopy alone could not have much effect on total light penetration to the ground surface.

JACKSON - I agree. Changes in leaf area, leaf size and aspect must also occur?

NAIR - The number of leaves in the crown, the size of leaves, and the number of leaflets per leaf, and probably the total leaf area, are similar for adult palms of different age groups.

LUNDGREN - In these small plantations does light infiltrate from the edges?

NAIR - No; the 'edge effect' has been avoided in these measurements.

OLDEMAN - How did you observe the rooting patterns?

NAIR - Soil was removed from one quarter segment, layer by layer; it was washed away with water. Visual records were made of the roots seen.

LEYTON - Were the coconut and cacao root patterns based on such observations when they were growing together?

NAIR - The coconut root system was depicted based on monoculture observations, but cacao roots were actually observed as they grew under coconut.

LEYTON - Would some intermixing of at least the finer roots of the two species be expected?

NAIR - The roots of coconut are fairly thick and easily seen. Cacao and coconut roots can be distinguished easily. The root systems were mainly separated.

INTERCROPPING TREE LEGUMES WITH ANNUAL CROPS

K.O. RACHIE
The Rockefeller Foundation, 1133 Avenue of the Americas, New York, USA.

ABSTRACT. Trees have many roles to play in tropical land use systems and woody perennial legumes are an extensive and important group to consider. Some of the factors to take into account when choosing an appropriate species are outlined.

Preliminary observations from intercropping trials at IITA and CIAT in which *Leucaena leucocephala* was used have indicated the potential for mixing annual food crops with such a woody leguminous species, and have shown some of the management needs for these systems. Some optional cropping schemes with leucaena are outlined.

Less familiar perennial food crops such as breadfruit, pejibaye, palm species (for oil), caryocar, jojoba, cow tree, perennial pigeon peas, mesquite, acacias and chestnuts are noted as having considerable potential for contributing to the more usual production from annual staple crops. However, the need for research to develop the new technologies, especially for intercropping situations, is essential. This must include plant exploration for economically useful woody perennial species, their selection for complementarity with other crops, genetic improvement and appropriate management techniques.

INTRODUCTION

The development of viable technologies for small farmer systems in the tropics is a challenge for today's agricultural scientists. Alternatives to slash-and-burn practices are needed to improve the productivity of traditional farming systems, and to conserve the soil resources of deforested lands. Currently, scale-neutral technologies are being tested in order to lower input requirements in crop and animal production. This is a step in the right direction, but the most important consideration is the return on investment. Monoculture systems do not meet the farm families' needs, nor make optimal use of available land, labour and financial resources. Mixed cropping systems supply more of the families' basic requirements and provide insurance

against unfavourable conditions. Trees are often included in these complex cropping systems but have the potential for an even greater role in improved productivity and conservation of the environment.

TREES IN TROPICAL LAND USE SYSTEMS

The inclusion of woody plants in tropical land use systems offers many advantages at virtually no expense. The judicious use of leguminous trees can aid in recycling plant nutrients and water from the deeper soil profiles, fix nitrogen from the air, intercept fog drip, reduce soil evaporation, lower soil surface temperatures, provide shade for animals and crops (coffee, tea and cacao), contribute animal feeds, supply human food, and generally increase off-season production to achieve more effective year-round use of labour (Douglas, 1972; Kirby, 1976; MacDaniels and Lieberman, 1979; Vietmeyer, 1979; Myers, 1980; National Academy of Sciences, 1980).

Characteristics desired in perennial legumes

Several factors should be considered in choosing tree species and varieties for smallholder cropping systems. However, water limitations may restrict the situations under which trees can be intersown with annual crops. If planting of trees would actively compete for moisture available to the annual crop, it may be prudent not to mix perennials with annual species. Alternatively, woody legumes may be grown in waste places or low lying areas where the foliage can be harvested and utilized as organic manure or for feeding of animals. In this paper, it is assumed that woody perennials draw most of their water and nutrients from depths below those at which annual crops feed; and that appropriate management of the woody species would reduce competition for water and nutrients in the upper layers of the soil profile during the main growing season for annual crops.

The choice of woody legumes for intercropping with annuals in the lowland tropics should be based on several criteria. Different situations will dictate the specific requirements, but the following factors often have to be considered.

- Ease of establishment from seeds or seedlings.
- Rapid growth and high productivities of foliage and wood.
- Limited maximum size (small trees may be optimum).
- Good coppicing ability (regrowth following topping).
- Effective nutrient recycling abilities; and especially di-nitrogen fixation.
- Multiple uses: food, feed, firewood, construction materials and other products, and 'services' (shade, shelter, etc.).
- Spinelessness (although sometimes spines are desirable).
- Minimal competition with shallowly rooted annual crops.
- Good quality (for example, high protein) foliage, fruits and seeds.
- Small leaflets readily detached when dried and quickly decomposed when used as fertilizer.
- A high proportion of leaves to secondary branches.
- Good stress tolerance: against drought, low fertility, extremes of pH, and others.

- Freedom from pests and diseases.
- Ease of control or eventual elimination.

Considering this list of desiderata, it is not surprising there has been so much popular interest in *Leucaena leucocephala*. This species is widely adapted from 30°S to 30°N and up to an elevation of about 1500 m. It grows in areas with from 600 to 1800 mm of annual rainfall (National Academy of Sciences, 1977; Brewbaker and Hutton, 1979; Vietmeyer, 1979). However, many other promising tree legumes have not yet been studied, some of which may be superior to leucaena, particularly in respect to tolerances to stresses like seasonal drought, extremes of soil pH, aluminium and manganese toxicities, and cool temperatures (Bogdan and Pratt, 1961; Douglas, 1972; National Academy of Sciences, 1975, 1979; Felker, 1979). Several genera should be considered in the following families.

- Mimosoideae: *Albizia*, *Acacia* (especially the spineless types like *A. muricata*), *Calliandra*, *Enterolobium*, *Inga*, *Lysiloma*, *Parkia*, *Pithecellobium*, *Prosopis* and *Samanea*.
- Papilionoideae: *Centrolobium*, *Clathrotropis*, *Dahlbergia*, *Erythrina*, *Flemingia*, *Glyricidia*, *Lonchocarpus*, *Ormosia*, *Piscidia*, *Pterocarpus* and *Sabinea*.
- Caesalpinioideae: *Cassia*, *Dialium*, *Haematoxylum*, *Hymanea*, *Peltogyne* and *Tamarindus* (excluding ornamentals).

Model species

The requirements described above for tree legumes in arable cropping systems are most closely met by three or four species. The most actively studied of these is probably *Leucaena leucocephala*; but *Gliricidia grandiflora* and the honey locust (*Gleditsia triacanthos* L.) are two other widely adapted and potentially useful species for such cropping systems. Other members of the genera *Acacia*, *Prosopis*, *Desmodium*, *Cassia* and *Tamarindus* (Caesalpinioideae) may have useful characteristics for various situations (Bogdan and Pratt, 1961; Felker, 1979; National Academy of Sciences, 1979). The great range of variation within each of these genera should be studied to assure the best possible genotypes for intercropping research.

OBSERVATIONS ON INTERCROPPING WITH TREES

Intercropping observations in Africa

My work in tropical Africa during the early 1970s stimulated a search for alternative cropping systems which, while avoiding the high inputs of modern agriculture, would be more appropriate for various environmental conditions and more productive than the long fallow system practised locally. At the International Institute of Tropical Agriculture (IITA) at Ibadan, Nigeria, the effects of erosion occurring on the Alfisols (primarily Egbeda, Iwo and Apomu series) under the intense tropical rainstorms are severe. High surface soil temperatures (sometimes exceeding 50°C) inhibit crop growth and reduce productivity. These problems are exacerbated by clean cultivation systems. Experimental objectives were to maintain plant cover throughout most of the year to reduce erosion, moderate surface soil

temperature, suppress weed growth and recycle nutrients. Another goal was to provide a more effective and less costly system of supporting the climbing crops so widely used in the low, humid tropics.

These studies demonstrated the benefits of 'alley' cropping of leucaena grown in alternate 1.20 to 1.80 m strips with annual food crops such as maize, rice, root and tuber crops. Leucaena prunings applied to the adjoining rows of maize contributed to increased yields when nitrogen fertilizers were not available. Other woody legumes such as *Cajanus cajan*, *Tephrosia candida* and *Glyricidia sepium* may also be successful in this management scheme (IITA, 1980).

The potential of *Leucaena leucocephala* has been earlier recognized by workers in Hawaii, the Philippines and Australia (National Academy of Sciences, 1977; Guevarra *et al.*, 1978a, b). Improved varieties of leucaena from Hawaii were planted at Ibadan, Nigeria, and proved exceptionally well adapted. It was further demonstrated that: plant growth was rapid; the foliage provided an excellent source of forage; various planting configurations were possible; it was relatively compatible with annuals in associated plantings; growth could be controlled or modified by hand or machine pruning; and it seeded profusely.

Biological fixation of nitrogen is an important attribute of many legumes. Under favourable year-round growing conditions, dinitrogen fixation rates as high as 500 to 600 kg $ha^{-1}year^{-1}$ have been measured (Guevarra *et al.*, 1978a, b). The stimulation of regrowth following pruning in leucaena and other legumes has recently been shown to have a stimulating effect on dinitrogen fixation, causing a surge of nitrate production during or immediately following regrowth. Thus, leucaena is more efficient both in growth and dinitrogen fixing ability following topping as compared with normal growth.

Intercropping studies in Latin America

Observations made in tropical Africa were used as the basis for the design of experiments on intercropping of perennial legumes with annual food crops at the Centro Internacional de Agricultura Tropical (CIAT) in Cali, Colombia (CIAT, 1977, 1978). Two 'model' perennial legumes were used for these studies. One was the non-viny, vigorous and highly persistent ground cover, perennial peanut (*Arachis glabrata*). The second was *Leucaena leucocephala*. Preliminary observations under controlled conditions at the experiment station were needed before attempting longer-term studies on the less fertile and erosion prone lands of nearby regions.

Field trials with leucaena were established at the beginning of 1976 on the comparatively fertile soils at CIAT in the Cauca Valley of Colombia (3°27'N, 1000 m elevation). Seeds were obtained from an earlier introduction by CIAT (CIAT 871) and were treated with hot water (80°C) for one to two minutes, which successfully increased germination from 20 to 96 per cent. Longer exposure to the treatment tended to reduce seed viability but treated seeds retained a high germinability in storage for several months following treatment.

Intercropping with maize. *Leucaena leucocephala* cv. CIAT 871 was established at the beginning of 1976 and four months later was approximately 2 m tall (CIAT, 1977). At this time it was cut to 20 cm and the branches uniformly distributed over the soil surface where maize was to be planted. In one trial, maize (cv. H-207), was planted at 25,000 and 50,000 plants ha^{-1} in leucaena populations of 0, 10,000, 20,000 and 40,000 plants ha^{-1}. In the second trial, the maize population was 60,000 plants ha^{-1} and the leucaena was planted either on the same ridge as the maize (40,000 plants ha^{-1}), or on every second (20,000 plants ha^{-1}) or every third ridge (13,000 plants ha^{-1}). Thirty days after planting the maize, the leucaena had regrown considerably and appeared to be competing with the maize. It was cut to 10 cm and the branches were distributed uniformly around the maize plants.

At maize planting time, the fresh weight in nitrogen, phosphorus and potassium contents of leucaena was determined (Table 1). The highest leucaena population produced significantly more fresh weight in nitrogen, phosphorus and potassium than the lower ones. Nevertheless, all populations accumulated significant quantities of nitrogen and potassium in the foliage. Moreover, the leaves contained 27.4 per cent protein which could readily be incorporated into animal diets.

Table 1. Fresh weight and nitrogen, phosphorus and potassium contents of the leaves and branches of four-months old leucaena plants at CIAT, Colombia.

Leucaena population	Fresh weight[1]	Nutrients released (kg ha^{-1})								
		N			P			K		
plants ha^{-1}	t ha^{-1}	L	B	T	L	B	T	L	B	T
40,000	17.8	127	45	172	7	6	13	53	46	99
20,000	9.3	66	25	91	4	4	8	28	24	52
13,000	8.2	59	22	81	3	3	6	24	21	45

L = leaves B = branches T = total

1 The leaves and branches had 64 per cent moisture content.

Maize yields varied only slightly under various treatments as shown in Table 2. This indicated very little competition by the leucaena. The slight decrease in maize yields grown in association with leucaena is understandable since CIAT soils are relatively highly fertile, and therefore little response from nutrients recycled by leucaena foliage was expected at the outset. However, some reduction in plant height occurred in maize intercropped with leucaena, although this effect was not apparent in the final yields.

Results were similar in the second trial (Table 3). Maize yields were only slightly reduced by the highest populations of leucaena. There was no appreciable difference between the two maize populations (25,000 and 50,000 plants ha^{-1}). These observations suggest that leucaena populations of 10,000 to 20,000 plants ha^{-1} are, at CIAT, adequate to provide sufficient foliage

Table 2. Maize height reduction and grain yields when grown in association with leucaena at CIAT, Colombia.

Leucaena population plants ha^{-1}	Planting distance cm	Maize Height reduction[1] %	Maize Yield[2] t ha^{-1}
0	-	0	5.4
13,000	24 × 300	16	6.0
20,000	25 × 200	16	5.5
40,000	25 × 100	25	4.9
40,000	50 × 50	29	4.5

1 Forty days after planting compared to check.
2 Adjusted to 15 per cent moisture content.

Table 3. Maize height reductions and grain yields when grown in association with leucaena at CIAT, Colombia. (Second trial.)

Leucaena population plants ha^{-1}	Maize population plants ha^{-1}	Maize Height[1] reduction %	Maize Yield[2] t ha^{-1}
0	25,000	0	4.6
0	50,000	0	5.2
10.000	25,000	2	4.7
10,000	50,000	11	4.6
20,000	25,000	0	4.2
20,000	50,000	12	4.9
40,000	25,000	10	3.5
40,000	50,000	15	4.9

1 Forty days after planting compared to check.
2 Corrected to 15 per cent moisture content.

to cover the soil and supply significant quantities of nutrients without competing with maize.

When weeds are troublesome in establishing leucaena stands, a companion crop can be planted to reduce weed competition and provide income during the three to four months of initial growth. When bush beans (*Phaseolus vulgaris* cv. Calima) were interplanted in one metre rows, the early development of the leucaena was not affected, nor did the beans appear adversely affected by the leucaena, when it was coppiced frequently. Alternatively, selective and general herbicides can be used to control weeds. Initial observations showed that alachlor, H-22234, nitrofen, DNBP, Linaron, vernolate, and bentazon could be used selectively without affecting the leucaena. However, other formulations were non-selective including metribuzin, liuron and trifluralin.

Leucaena support for climbing beans. The maize/leucaena intercropping experiments were followed by a leucaena/climbing bean association trial. Thirteen herbicides were applied singly or in combination as sprays to the lower trunks of leucaena in an attempt to kill the stand, or temporarily set it back to minimize competition with the climbing beans. Basal spray applications of the herbicides were compared with mechanical ringbarking of the trunks at a height of 50 cm, which allowed the leucaena to regrow later from below the rings. Climbing beans were then planted two weeks after the treatments were made.

A 2,4-D ester and picloram as a 4 per cent spray were much more effective than other treatments in killing the leucaena, but their residual effects were long-lasting and completely inhibited bean germination even after repeated replantings. Applications of 2 per cent 2,4,5-T effectively killed the leucaena, and did not inhibit bean germination after two weeks. Application of chemical formulations with a brush should be tested, in order to avoid the soil sterilization effect of spray applications.

In the ringbark treatment, regrowth of leucaena did not appear to affect the early development of beans on the dead leucaena superstructure (3+ m tall). The bean vined rapidly on the main axis and branches of the killed leucaena, and production of beans appeared comparable to that of constructed trellis supports. Following bean harvest, the dead stems and branches of leucaena could still be removed for fuel or construction, allowing new growth to develop.

DISCUSSION OF THE INTERCROPPING STUDIES

The inclusion of new long-term perennial species in complex cropping associations with annuals offers new opportunities for increasing productivity in smallholder agriculture in developing countries. There are many promising 'new', or rather unfamiliar plant species which could be tried in these systems (Bishop, 1978; Guevarra *et al.*, 1978a; MacDaniels and Lieberman, 1979; Myers, 1980). However, there will inevitably be problems to identify and solutions to work out, as with any new technology. And any intensive, complex system is unlikely to be attractive to extensive, mechanized farms (but see Briscoe, this volume).

Optional cropping systems

In some tropical areas with favourable year-round growing conditions, it should be possible to plan cropping sequences around a permanent planting of tree legumes. For example, the following two-year sequence might be considered for the subhumid to humid rainfall regions of the low elevation tropics of Latin America.

FIRST YEAR

First rains - simultaneous planting of bush beans and leucaena (during establishment of the leucaena).

Second rains - cut leucaena and plant maize in rows; top the leucaena again 4 to 6 weeks after planting the maize.

Third season (dry) - allow the leucaena to regrow on residual soil water and utilize the foliage as a protein 'bank' for

livestock.

SECOND YEAR

First rains - plant cassava with leucaena (topped at intervals), which would require the rest of the year. Alternatively, ring-bark or kill upper storey foliage (above 10 to 15 cm) for use as *in situ* trellis support for yams or climbing beans.

Second rains - following bean or root harvest, remove new sprouts and dead stems of Leucaena for firewood or construction; allow leucaena to resprout and plant rice or maize and top leucaena after 4 to 6 weeks.

Dry season - allow resprouting of leucaena for use as dry season forage (protein bank).

This scheme demonstrates that it is possible to make more intensive use of the land if moisture is available, assuming a reasonable level of soil fertility (except for nitrogen). Year-round production from the land is possible, yielding crops and high protein foliage for livestock feed during the dry season when other forage is scarce (Douglas, 1972; Kirby, 1976; Bishop, 1978; MacDaniels and Lieberman, 1979). Under this system, crops such as maize, beans or starchy food plants may not achieve the maximum yields that are possible when they are grown under optimal fertility and moisture conditions. However, it should be possible to stabilize production at an intermediate level which would at least double the current mean yields of the region.

Drawbacks

There are several drawbacks in developing these production systems.

Moisture limitations. Intercropping of species results in competition for available water and nutrients. Although the available precipitation is seldom utilized optimally in most of the tropics, modifications of the system would be essential when water is limiting.

Management requirements. These systems are more labour intensive and require more manipulative husbandry. They are, therefore, better suited to smallholder agriculture.

Recycling of nutrients. With the exception of the biologically fixed nitrogen, other plant nutrients, especially phosphorus and potash, will be extracted more rapidly from the limited soil reservoir particularly on less fertile tropical soils. Some systems of production tend to export essential plant nutrients more rapidly than other systems

Eliminating woody plants. The removal of woody stumps and root systems requires considerable effort and could pose a major problem in situations where special equipment is unavailable. The presence of woody plants may also limit the flexibility of land use.

Refuge for pests. A permanent stand of woody legumes could

provide a refuge for some pests and diseases including unwanted birds, rodents and other animals which prey on crops and domestic animals.

Inputs

In the proposed systems the moderate use of key inputs is likely to pay off handsomely in many situations. For example, a judicious intervention with appropriate pesticides during vulnerable periods of plant growth, or the restoration of non-renewable plant nutrients, particularly phosphorus and potassium which are often lacking in tropical soils. Phosphate deposits are more widely distributed than earlier suspected, and the use of raw rock phosphate on acid tropical soils can often be as effective as acidulated forms of phosphorus at only a quarter of the cost (CIAT, 1977, 1978).

Providing trellises or supports for climbing crops can be an expensive input requiring considerable materials and labour. However, the support poles or sticks can usually be produced locally or grown *in situ*. Construction can often be done with excess labour during the slack season, thus providing a means of intensifying production on smallholdings.

Future research needs

Initial observations and experiments on cropping systems comprising both annuals and perennials (especially legumes) are scanty. Much more evaluation of legume species needs to be done. This includes examining the variation within species and compatibilities between species, both of annuals and perennials; investigating the management of growth, including temporal, spatial and manipulative management; studying short- and long-term soil effects and plant nutrient requirements; looking into the water relations of mixed communities, both with regard to species requirements in terms of spatial and seasonal availability; understanding pest and disease dynamics; and many other aspects.

THE FUTURE PROSPECTS

It is likely that productivity will increasingly be evaluated on the basis of returns on effort (or energy) rather than simply on yield *per se*. A greater reliance on perennials (especially trees) as sources of food, feed, fibre and fuel could have a major impact on agriculture in terms of energy efficiency (National Academy of Sciences, 1975, 1979, 1980).

Some suggestions

Among the less familiar perennial food crops which might usefully add to some of our annual staples are the following.

The breadfruit. *Artocarpus* spp. is an exceptionally high yielding, moderately nutritious fruit which can be used much like a cereal.

Pejibaye. The Amazon peach palm (*Bactris gasipaes*) produces excellent yields of highly edible fruits which are comparable to cereals in nutritional value and can produce two and a half times

the yields of maize with only a small fraction of the effort.

Exotic oil palms. The African oil palm is the most efficient solar energy converter of all cultivated crops, including sugar cane; but there are at least two other obscure palm species (*Oribygnia* spp. and *Jessenia polycarpa*) with exceptional potential for vegetable oil production which have not yet been intensively studied or developed.

Pittosporum resiniferum. This tree is used in the Philippines for several purposes including food and medicine, and as a liquid fuel. Up to 60 litres are produced per tree which is 16 per cent alcohols and 20 per cent hydrocarbons.

Caryocar species. These trees produce fruits high in oil content and yield two edible oils, from the pericarp and from the kernel. Caryocar kernels are reputed to be the most delicious edible nuts in the tropics.

Jojoba. *Simmondsia chinensis*, a hardy desert shrub, produces a highly valued liquid wax. The seeds were once an important food staple for Indians in southwestern USA and northern Mexico.

Cow tree (ramon). This tree (*Brosimum alicastrum*) produces edible leaves, chestnut-like seeds and a free-flowing milky latex which can be eaten by humans and animals.

Perennial pigeon peas. These peas (*Cajanus cajan*) used both green and dried, and as edible browse, are really short-term perennials, although some bushes (small trees) have been reported to live for 'decades' unless injured or attacked by insects and diseases. The stems are useful as a limited fuelwood source.

Mesquite. Several *Prosopis* species produce edible pods (up to 30 per cent sugar) and seeds which are still used for food in some areas, (although their importance has diminished in recent times). Some species are also useful as a dry season browse.

Acacia. There are about 800 acacia species, some of which provide edible seeds, pods and foliage. The phyllode acacias are particularly worth investigating.

Chestnuts. The chestnut (*Castanea* spp.) is well adapted in subtemperate regions. It produces one of the few tree seeds which might possibly substitute for cereals.

The value of trees

From the national and community standpoint trees can be used to help conserve both the soil and the growing environment. They can greatly reduce fossil fuel requirements for agricultural production and extend the use of fragile environments and marginal lands. For the farmer, especially smallholders, trees can increase returns on human effort; provide multiple uses for his family; lower capital requirements for mechanization; and seasonally extend photosynthetic capacity.

The primary concern of the smallholder is to increase

productivity and other economic returns, mainly from his own effort. Often, he is season bound and constrained by lack of machines and draft power to cultivate a sufficiently large area to feed his family throughout the year, and to provide for other needs and improvements. A benefit would be to reduce the seasonal requirements for primary tillage and intercultivation of newly emerging crop plants. The use of long season perennials and trees can help do this through a mulch farming approach and so extend the productive season as well as spreading labour requirements. The wider use of nitrogen fixing tree species could become an important factor in maintaining an enhanced nitrogen status in many tropical land use systems.

GENERAL RESEARCH NEEDS

The most urgent research needs in my opinion would be to carry out plant exploration for economically useful new perennials and tree crops. Thus survey need not be limited only to those species currently in use by man, but should stress the need for several uses and economic products. The discovery of cereal-equivalent products from trees and perennials would be particularly interesting, since very few good possibilities are available at present (only breadfruit, pejibaye, cow tree or ramon, and plantain meet this definition). The next step would be to determine the adaptive limits and potential uses of the more promising new species based on a reasonable range of variation within each of them. Those with established potential should then be more extensively collected for further study and to provide a basis for future genetic improvement if and when justified.

Those tree and perennial species which clearly show potential should be considered for genetic improvement and manipulation through the use of plant breeding, genetic engineering, tissue culture and grafting. Improvement objectives would certainly include increased productivities, improved quality of product, broader adaptation, greater tolerance of stresses, resistance to harmful biota, ease of establishment and handling, multiple uses and other characters.

As an adjunct to genetic improvement, research would be needed on pest management, general cultural practices and plant nutrient and water requirements. These would need to be correlated with crop physiological studies aimed at providing information for improving management practices. Such investigations could lead to greatly increased production on both arable and marginal lands, reduced energy and input requirements, and higher returns on human effort.

A PLATE illustrating this paper is elsewhere in this book.

REFERENCES

Bishop, J.P. (1978). The development of sustained yield tropical agro-ecosystems in the Upper Amazon: a stable agro-silvo-pastoral system. *Agro-Ecosystem* 4, 459-461.

Bogdan, A.V. and Pratt, D.J. (1961). Common acacias of Kenya. Ministry of Agriculture, Animal Husbandry and Water Resources. Grassland Research Stations, Kitale and Marigat, Kenya. pp.15.

Brewbaker, J.L. and Hutton, E.M. (1979). Leucaena: versatile

tropical tree legume. *In* "New Agricultural Crops", pp.207-259. Westview Press, Boulder, Colorado, USA.

Centro Internacional de Agricultura Tropical (1977). Annual Report for 1976, pp. G.35-G.39. Cali, Colombia.

Centro Internacional de Agricultura Tropical (1978). Annual Report for 1977, pp. F.5-F.12. Cali, Colombia.

Douglas, J.S. (1972). Tree crops for food, forage and cash. *World Crops*, January/February, pp.15-19.

Felker, P. (1979). Mesquite: an all-purpose tree. *In* "New Agricultural Crops", pp.89-132. Westview Press, Boulder, Colorado, USA.

Guevarra, A.B., Kitamura, Y., Whitney, A.S. and Thompson, J.R. (1978a). Yield of *Leucaena leucocephala* and its nitrogen contribution to intercropped maize. *Agronomy Abstracts*, November p.99. American Society of Agronomy, Madison, Wisconsin, USA.

Guevarra, A.B., Whitney, A.S. and Thompson, J.R. (1978b). Influence of intra-row spacing and cutting regimes on the growth and yield of leucaena. *Agronomy J.* 70, 1033-1037.

International Institute of Tropical Agriculture (1980). Research Highlights for 1979, pp.5-14. Ibadan, Nigeria.

Kirby, J.M. (1976). Forest grazing; a technique for the tropics. *World Crops*, November/December, pp.248-251.

MacDaniels, L.H. and Lieberman, A.S. (1979). Tree crops: a neglected source of food and forage from marginal lands. *BioScience* 29, 173-175.

Myers, N. (1980). The conversion of tropical forests. *Environment* 22, 6-13.

National Academy of Sciences (1975). "Underexploited Tropical Plants with Promising Economic Value". National Academy of Sciences, Washington D.C., USA.

National Academy of Sciences (1977). "Leucaena: Promising Forage and Tree Crop for the Tropics". National Academy of Sciences, Washington D.C., USA.

National Academy of Sciences (1979). "Tropical Legumes: Resources for the Future". National Academy of Sciences, Washington D.C. USA.

National Academy of Sciences (1980). "Firewood Crops: Shrub and Tree Species for Energy Production". National Academy of Sciences, Washington D.C., USA.

Vietmeyer, N.D. (1979). Tropical tree legumes: a front line against deforestation. *Ceres* (71) 12, No.5, pp.38-41.

DISCUSSION

NDUNGURU - Are you suggesting substitutions of existing food crops by trees; that is, a change in the pattern of production?

RACHIE - We have not done this but I suggest that such a practice has advantages, in theory, since trees can be maintained on low inputs once established. What you need is a product with a food profile with a reasonable protein content of 5 to 10 per cent, say 5 per cent oil; a high level of starch, and not too much fibre. That is one that matches the composition of a required diet. One tree which fits this description is pejibaye (*Bactris gasipaes*, also known as the Amazon peach), indigenous to Central and South America. It requires about 1500 mm of rain,

and it is adapted to tropical conditions at elevations up to about 1500 m. The tree can produce up to 2.5 times as much useful nutrients as maize, without the need for tillage inputs. It has few pest problems.

CROZE - My reservation relates to the relative costs and benefits of integrating trees and crops in intercrop situations. It would appear that there could be only marginal benefits, but increased costs, from the necessity of cutting the leucaena in your example.

RACHIE - I agree, but several years of trial may be necessary to establish feasibility and an economic evaluation.

TORRES - The sustainability of the systems also needs careful evaluation.

RACHIE - I agree, and we should also look at these systems on marginal lands. The ones I have described were on good soils.

STEPPLER - After coppicing, how fast was the decay of the leucaena loppings; that is, how fast did the nutrients get back into the nutrient cycle? Furthermore, what were the effects of woody parts that decayed slowly, especially on the succeeding maize crops?

RACHIE - Not known.

LOOMIS - I am not sure about what you said concerning soil temperature. If you include trees, you may reduce the ground cover under the canopy, so that the net effect on soil temperature may be difficult to predict.

RACHIE - Yes. In general the high incident solar radiation in the tropics may typically result in an air temperature of 30 to 35°C, but the soil surface may exceed 50 or 55°C, if not shaded.

LOOMIS - But the field crop is at ground level, interacting with the soil through mineralization, improving water-holding capacity and cooling through evapotranspiration. The organic matter level under the trees may be less. Therefore are you really saving more water and keeping the soil cooler under trees? This certainly needs more study for particular situations and tree species.

TIESZEN - Soil temperature will be considerably affected by the presence of a plant canopy. The advantage of many trees is that this is continuous in time, whereas that of a field crop is not.

LOOMIS - You are losing the water whether the tree is there or not.

TIESZEN - Not necessarily from the same part of the soil profile though, because the field crop may take water from the surface, whereas tree roots can go deeper and may utilize water not accessible to the field crop.

LEYTON - What matters is the difference in the extent of annual

cover; that is, how long during the year is there a canopy?

TIESZEN - Assuming at least some competition for water, you have also said that there is better water economy in the mixed crop / tree system. Why?

RACHIE - You have to be careful in generalizations on water management. In Latin America with 2000 to 3000 mm of precipitation a year mixing trees and field crops intimately may not be a problem. In the Sahel with only between 60 to 800 mm, say, you have to look at the situation quite differently. It is also a question of compatibility of tree and field crops. Root systems are often quite different, depending on the species and the site, and there may or may not be an opportunity for sharing resources without competition. This is something that needs looking into for agroforestry combinations.

JACKSON - In judging the effects of mixed species on water depletion you must look at the system as a whole. For example, what we see in apples is that ground cover has an effect on the tree root system; they penetrate deeper if grown together with grass.

CONNOR - What is the optimum combination? You could choose an herbaceous legume with a non-leguminous tree species, or vice versa. Is there any development of theory or practical information available?

RACHIE - Work on this is still very preliminary.

STEPPLER - Perhaps we should try a legume in every system until it is shown not to be advantageous.

THE INTERCROPPING OF GRAIN LEGUMES IN AGROFORESTRY SYSTEMS

*J.F. REDHEAD, *J.A. MAGHEMBE and †B.J. NDUNGURU
*Division of Forestry and †Department of Crop Science,
University of Dar es Salaam, Morogoro, Tanzania.

ABSTRACT. The loss of soil fertility due to the shortening of grass, bush or forest fallow periods in many tropical areas is becoming a serious problem. As is the shortage of fuelwood in drier regions where populations are increasing. More sustainable land use systems in which grain legumes, trees and cereals are intercropped hold out possibilities for reversing these adverse trends and meeting community needs for food and fuelwood. Potential legumes and trees for this purpose are suggested and preliminary work undertaken at Morogoro is outlined. Future research proposals in this line are also presented.

INTRODUCTION

Land fertility and fuelwood supply: two concurrent crises

In tropical regions where shifting or rotational cropping and fallow are practised and where the population is too dense, there often is insufficient land for a long enough fallow period following the cropping sequence for soil fertility to be restored. Traditional shifting cultivation was ecologically stable but, when the fallow period becomes too short, either fertilizers have to be used, or a crop rotation must be followed involving a soil improving species. As fertilizers are expensive a system of crop rotation, or intercropping, involving plants which can restore the soil's fertility has attractive possibilities.

Where there is a shortage of rainfall, as well as a high population, another shortage invariably follows; that of fuelwood. In the Tabora Region in Tanzania, for example, fuelwood is an essential raw material for producing flue-cured tobacco, so the expanding cultivation of Virginia tobacco has raised the demand for fuelwood considerably (Temu, 1979). The tobacco farmer clears a woodland area and uses the wood for both domestic purposes and for tobacco curing. The remaining bush is burnt. As an example, per capita domestic fuelwood consumption in Gambia is $2.1\,m^3yr^{-1}$ and in Tanzania $2.2\,m^3yr^{-1}$ (Openshaw, 1971). O'Kting'ati

(1980) estimates that the fuelwood demand overshadows, by far, any other use of wood in Africa. Large areas of the semiarid tropics are facing a fuel shortage which is expected to assume crisis proportions due to the high cost of alternative imported fuels, such as kerosine. The answer sounds simple: plant trees. But it is not easy to persuade a peasant farmer that trees should be planted and tended like any other crop when, traditionally, he cuts his firewood in the bush, along with house-building poles and wood for other purposes. The thought of taking farmland out of circulation to grow trees, and waiting several years for them to mature, is not attractive to the peasant farmer.

A solution using grain legumes and trees?

The grain legumes are very important food crops because of their high protein content. When effectively nodulated they can also fix nitrogen through their root nodules, and they are thus valuable soil improvers. For these two reasons grain legumes are essential components of any crop mixture, or rotation system, for the tropics.

If trees can also be brought successfully into the rotation this could change the attitude of the farmer towards growing trees. Intercropping, which has been defined as growing two or more crops simultaneously in the same field is, indeed, the main subsistence crop production system in tropical and subtropical environments (May, 1980). Substantial evidence exists to show that intercropping can result in increased yields, improved soil fertility and an improvement of the nutritional balance at harvest (Willey, 1979). Farming systems in which intercropping of grain legumes and trees could be developed and which would also include cereals, or be grown sequentially with cereals, would then meet most of the needs of the village farming community for food and fuel.

Simple trials have begun at Morogoro (Tanzania) to try out this type of intercropping. This paper examines some of the results obtained so far, and suggests future research work which could help to solve simultaneously the food and fuel problems of the tropics.

LEGUME AND TREE INTERCROP SPECIES

Grain legumes important in tropical Africa

The following are the commonest, and potentially the most important, of the many grain legumes grown in tropical Africa.

Field beans (Phaseolus vulgaris). The common bean is variously known by many different names, especially kidney beans, haricot beans or French beans, and several hundred varieties are known, both dwarf and climbing in habit. They can be eaten green in the pod but are generally harvested as the dry bean, in which condition they can be stored as a grain legume. They thrive best at altitudes from 600 to 2400 m. The crop is grown in pure stand by large-scale farmers, but it is generally intersown with maize in smallholdings. It is the most important grain legume in East Africa.

Cowpea (Vigna unguiculata). This is a dual purpose annual, grown as much for its leaves, as a green vegetable, as for the dried beans. The plant is drought resistant and is widely grown throughout the tropics at elevations up to 1500 m, usually interplanted with maize, sorghum, or yams. Provided the soil is freely draining, cowpeas are less demanding than field beans.

Groundnut (Arachis hypogea). The groundnut is better known as an oil seed than as a grain legume. It is grown all over the tropics and subtropics, especially in West Africa, India, China and the USA. Groundnut oil is a high quality cooking oil, also widely used in making margarine. The seeds are highly nutritious, contain about 30 per cent protein and are rich in vitamins B and E. They can be processed into flour and used in soups and stews, or eaten fresh. The leaves and stalks can be used as green fodder or dried for hay.

Groundnuts prefer a light, sandy soil, a rainfall of 600 to 1200 mm, and grow at altitudes up to 1500 m. The crop is ready for harvest in 14 to 20 weeks.

Pigeon pea (Cajanus cajan). Pigeon pea has been grown in the Nile valley for centuries and is widely grown in the tropics. The plant is a short-lived perennial with a deep tap root and a woody stem which can grow over 3 m in height. It is ready for harvest in 6 to 8 months after sowing and may continue producing seed for a year or longer. Pigeon pea is generally intergrown with other crops such as maize, finger millet or beans and in some places it is left as a fallow crop for 2 to 3 years, and finally used as a fuel where firewood is scarce.

Soya bean (Glycine max). Soya bean is one of the world's most important food crops, especially in Asia and the USA where it is important both as an oil seed and a grain legume. The crop is not as widely grown in Africa as in Asia but it has enormous potential and active research is being undertaken to promote its use as a high protein grain legume.

Other useful species. Other grain legumes which deserve attention are bambara groundnuts (*Voandzeia subterranea*), bonavist beans (*Lablab niger*), chickpea (*Cicer arietinum*), green and black gram (*Vigna aureus*, *V. mungo*), lima bean (*Phaseolus lunatus*), sword bean (*Canavalia ensiformis*), winged bean (*Psophocarpus tetragonolobus*) and the yam bean (*Sphenostylis stenocarpa*). An up-to-date account of the state of scientific knowledge about a number of the grain legume species is given in Summerfield and Bunting (1981).

Trees recommended for intercropping

Most experience of growing food crops with trees, either during the tree crop establishment phase ('taungya'), or permanently as part of a mixture, is from the humid tropics (King, 1968; Ball, 1977; De las Salas, 1979). There is little published factual information on the intercropping of trees and food crops in the semiarid and arid tropics except for the important *Acacia* species, *A. albida* and *A. senegal* (Felker, 1978; El Houri Ahmed, 1979). It is commonly assumed that competition for water would

prevent the successful growth of young trees amongst food crops, but experimental work at Morogoro (Maghembe and Redhead, 1982) indicates that competition for light has a more profound effect on the young trees. The growth phase of the food crop coincides with the peak of the rainy season and, as most food crops are annuals, the dead crop residues remain as a mulch after harvest. The fact that the food crops are weeded has a beneficial effect on the young trees, even more than the 'spot' weeding carried out as normal Tanzanian forest practice (Table 1).

Table 1. Height and diameter growth of 12-month-old *Eucalyptus camaldulensis* intercropped with beans and with maize, compared with trees clean weeded and spot weeded.

Treatment	Height m	Diameter mm
Intercropped maize	238	1141
Intercropped beans	247	1560
Clean weeded	254	1777
Spot weeded	191	668
LSD P=0.05	NS	640
LSD P=0.01	NS	919

NOTE: Spot weeding involves clearing a circle of one metre diameter (measured at the root collar).

Trees suitable for intercropping with food crops, where the food crop phase is not merely an establishment phase for the trees should possess one or more of the following attributes.

- Fast growth: producing fuel and housebuilding poles within a period of not more than eight years.
- The characteristic of shedding leaves during the wet (crop growing) season: for example, *Acacia albida*.
- A straight form and dominant leader growth, even when grown at wide espacement: for example *Eucalyptus* spp.
- A high value crop as well as fuel: for example *Acacia nilotica* (tannin), *Acacia senegal* (gum arabic), *Butyrospermum paradoxum* (shea butter), *Parkia clappertoniana* (locust bean) or *Uapaca kirkiana* (edible fruits).
- The capability of being repeatedly lopped for fodder: for example, *Acacia* spp. or *Leucaena leucocephala*.
- The ability to fix nitrogen: for example, *Acacia* spp., *Leucaena* sp. or *Parkia* sp.

Foresters have traditionally grown trees for timber and planted at a close espacement of 2 × 2 m or thereabouts. The reason for this is to encourage good stem form and rapid height growth; some trees would put an unwanted amount of growth into branches if widely spaced (see Cannell, p.489). Where trees are grown for their fruits or leafy fodder they should be planted at a wide espacement so that their branches can grow in full light (see Jackson, this volume). Trees with a naturally dominant

leader growth can also be grown at wide espacement and still produce a stem of reasonably good form, albeit not as perfect as in a well-thinned closely planted plantation.

Foresters have, therefore, to try and grow trees more widely apart to give more room for the production of food crops between them. Information is lacking, for different tree species, on the appropriate spacings, which will allow a good yield of food together with trees of reasonably good form if grown for poles, and for good leaf yields in the case of fodder trees. A series of trials has been established at Morogoro to obtain this information. Several tree species are being grown at a range of espacements, and intercropped with field beans and maize in comparison with traditional forestry practices.

THE MOROGORO AGROFORESTRY TRIALS

The first trial was established in 1978 and the preliminary results are described by Maghembe and Redhead (1982). *Eucalyptus melliodora* was planted at an espacement of 2.5 × 2.5 m and either intercropped with maize, sorghum, or field beans, or clean weeded or not weeded at all. The experiment was arranged as a 5 × 5 Latin square, each plot containing 5 × 5 trees of which the inner core of 3 × 3 trees were periodically measured.

The yield of maize was 1280 kg ha^{-1} in the first year and 100 kg ha^{-1} in the second. In the third year the maize did not flower. Sorghum followed a similar pattern: at 2.5 × 2.5 m espacement the trees were too close to permit sufficient light for the cereals to grow after the first year. The yield of field beans was only 100 kg ha^{-1} in the first year, when the crop was badly attacked by an unidentified fungus. In the second year the yield was still only 150 kg ha^{-1} and in the third the field beans were etiolated and, although they set pods, the yield was insignificant.

Although the grain legume grew fairly well in shade which was too dense for the cereals, it was apparent that the trees had been planted too closely.

Survival of the trees was excellent, except for the unweeded plots, and the growth of the trees interplanted with field beans was even better than that of the clean weeded trees (Table 2).

It was this interesting result that led to a series of more elaborate long-term trials being established in 1980. This time only beans and maize were intercropped and the trees were planted at a range of espacements. The object of the trials was to ascertain the most suitable crop mixtures and tree espacements which can be recommended in village afforestation schemes.

The 1980 investigation contained the following intercropping associations in separate trials.

- *Eucalyptus camaldulensis* with maize and field beans; trees for fuel and pole production.
- *Acacia albida* with maize and field beans; trees for fodder and fuel production.
- *Leucaena leucocephala* with maize and field beans; trees for fuel production.

Table 2. Mean survival, height, dbh and volume of 30-month-old *Eucalyptus melliodora* intercropped with maize, sorghum, and beans compared with clean weeded and unweeded trees.

Treatment	Survival plot mean (out of 9 trees)	Height m	dbh mm	Volume* m^3 ha^{-1}
Maize	8.4	6.9	61	12.0
Sorghum	8.2	6.4	53	8.2
Beans	7.8	8.0	71	17.6
Clean weeded	7.8	7.5	67	14.7
Unweeded	4.2	5.9	42	2.4
LSD P=0.95	0.8	0.6	6	3.5
LSD P=0.01	1.0	0.8	8	4.0

*Volume at 30 months was calculated from mean height × crosssectional area at 1.3 m × a form factor of 40 per cent. (From Maghembe and Redhead, 1982.)

- *L. leucocephala* with maize and field beans; trees for fodder production.

New trials have been laid down in 1981 which will be variations of the *L. leucocephala* food and fodder production trial testing various regimes of lopping, and a variety of weeding regimes which one could reasonably expect a peasant farmer to adopt.

The basic design for all the experiments is the same: a split plot layout in which the food crops and weeding treatments form the main plots and the tree espacements form the subplots. Each trial has four replications. The espacements vary from 3 × 3 m to 6 × 6 m and each main plot has a subplot with no trees at all in order to measure the crop yield with no tree interference.

During the first crop-growing season of the 1980 trials the maize had a striking effect on the growth of the leucaena, but intercropping with beans was similar in effect to clean weeding. By the age of 19 weeks the mean height of leucaena intercropped with maize was 194 cm compared with heights of 160 cm and 153 cm for leucaena intercropped with field beans and clean weeded, respectively. This difference was highly significant statistically. In this trial the mean yield of maize was 1645 kg ha^{-1} and that of field beans 401 kg ha^{-1}.

The leucaena was made taller by association with maize and it had a single unbranched stem and no flowers. In comparison, the leucaena in other plots showed the normal habit of producing multiple major branches close to the ground and there was copious flowering. Now (1981) the leucaena has grown for a full year and the mean heights are shown in Table 3. The height differences are no longer statistically significant but the total biomass of leafy branches is much more for the leucaena intercropped with field beans or clean weeded than it is for those intercropped with maize. Thus, if the farmer wished to grow unbranched, small sized poles he could intercrop leucaena with maize, whereas if he wanted to grow the maximum fuel or fodder he would be better

Table 3. Mean height of 12-month-old *Leucaena leucocephala* intercropped with maize and beans compared with clean weeded trees (means of all experimental trees; see text).

Treatment	Height m
Intercropped maize	3.14
Intercropped field beans	3.04
Clean weeded	3.21

The differences are not significant at P=0.05

to intercrop his trees with field beans (or a similar crop species).

These data present an example, from preliminary work, of the use of information which is being gained from these trials. Within a further two years reliable information will be provided on the most suitable espacement for *Acacia albida*, *Eucalyptus camaldulensis* and *Leucaena leucocephala* when intercropped with maize and field beans. Such information will enable the results for these crops to be applied with confidence to village afforestation projects in a similar environment to Morogoro.

SUGGESTED FURTHER RESEARCH IN INTERCROPPING FOOD CROPS WITH TREES

It is apparent that field beans, in particular, can be grown without adverse y affecting tree growth. The trees are in fact more likely to benefit from the soil enrichment by the grain legume crop (although this has yet to be precisely established).

Two lines of research are proposed. The first is to study in depth the interrelationships of the legume crop and the trees in respect to light and water, and the relative contributions of nitrogen to the system by each plant component will be assessed. The second is to apply the simple methodology of the split plot design to other ecological zones using various grain legumes and tree species, as appropriate.

This work would complement the initial Morogoro trials and provide results which could be applied over large areas of tropical Africa. Concurrently with these new trials, extension work should focus on the acceptance of these agroforestry findings in the rural areas. Such applied research to relieve the present shortages of food and fuel deserves high priority.

REFERENCES

Ball, J.B. (1977). "Taungya in Southern Nigeria". Federal Department of Forestry, Lagos, Nigeria.

De las Salas, G. (Ed.) (1979). "Agroforestry Systems in Latin America". CATIE, Turrialba, Costa Rica.

El Houri Ahmed, A. (1979). Effects of land use on soil characteristics in the Sudan. *In* "Soils Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.1-13. ICRAF, Nairobi, Kenya.

King, K.F.S. (1968). "Agro-silviculture ('The Taungya System')". Department of Forestry, University of Ibadan, Ibadan, Nigeria.

Felker, P. (1978). "State of the art: *Acacia albida* as a complementary permanent intercrop with annual crops". University of California, Riverside, California, USA.

Maghembe, J.A. and Redhead, J.F. (1982). Agroforestry: preliminary results of intercropping *Acacia*, *Eucalyptus* and *Leucaena* with maize and beans. *In* "Proc. Second Symposium on Intercropping" (B.J. Ndunguru and C.L. Keswani, eds), pp.43-49. International Development Research Centre, Ottawa, Canada.

May, K.A. (1980). Effect of planting schedule and intercropping system on the production of green gram (*Phaseolus aureus*) and bulrush millet (*Pennisetum americanum*). *In* "Proc. Second Symposium on Intercropping" (B.J. Ndunguru and C.L. Keswani, eds.), pp.66-67. International Development Research Centre, Ottawa, Canada.

O'Kting'ati, A. (1980). "Agroforestry and the economy of the smallholder farmers in developing countries. The Tanzania case." M.Sc. Dissertation, University of Michigan, USA.

Openshaw, K. (1971). "Present Consumption and Future Requirements of Wood in Tanzania". Techn. Rep. No.3, FOFS/Tan 15, FAO, Rome, Italy.

Summerfield, R.S. and Bunting, A.H. (Eds) (1981). "Advances in Legume Science". Royal Botanic Gardens, Kew, UK.

Temu, A.B. (1979). "Fuelwood Scarcity and Other Problems associated with Tobacco Production in Tabora Region, Tanzania". Record No.12, Division of Forestry, University of Dar es Salaam, Morogoro, Tanzania.

Willey, R.W. (1979). Intercropping — its importance and research needs. II. Agronomy and research approaches. *Field Crop Abstracts* 32, 73-85.

A NOTE ON THE ROLE OF AGROFORESTRY IN ANIMAL-BASED FARMING SYSTEMS IN BOTSWANA AND SWAZILAND

W. GODFREY-SAM-AGGREY
University College of Swaziland, Department of Crop Production, Luyengo, Swaziland.

ABSTRACT. In both Botswana and Swaziland, unmanaged natural bushlands and/or grasslands are set aside by law as community grazing lands for livestock, particularly cattle, which form a central and integral part of the farming systems of these countries. These grazing lands provide fodder throughout the year for the animals, as well as fuel for the rural population. The need for fodder and fuel becomes acute during the winter months. An efficient silvopastoral system, combined with controlled rotational grazing, could usefully complement the existing practices.

INTRODUCTION

In both Swaziland and Botswana legal controls have evolved to stabilize animal-based farming systems. Sixty per cent of the population are located on the Swazi National Lands/Tribal Lands, where subsistence farming is practised. There are also individual tenure or private farms, which are strictly commercial. Table 1 shows the general pattern of land use in Swaziland.

Commercial forests are privately owned, and so are improved grazing lands. For fuel, off-cuts from the forest are sold since it is an offence to harvest fuelwood from the grazing lands.

A ROLE FOR AGROFORESTRY

Figures 1 and 2 indicate the structure of the farming systems commonly found in Botswana and Swaziland, respectively. The small size of the cropping area, which averages about 3 hectares per homestead of about 10 persons in Swaziland, prevents farmers from growing their own trees and crops for fuel and fodder. During winter months, insufficient fodder becomes a serious problem and a source of fuel is a necessity. The nearest

Table 1. Typical land use patterns in Swaziland.

A. Change in areas allocated to crops, grazing and forest, 1973 to 1977.

ha × 1000

	1973	1974	1975	1976	1977
Cultivated area	171	158	170	165	153
Grazing area	1342	1324	1143	1206	1240
Commercial forest area	99	102	96	96	97

B. Details of land use categories in 1977.

ha × 1000

Land use category	Whole country	Swazi national land	Individual tenure farms
Crops	128	77	51
Fallows	25	20	5
Total crop land	153	97	56
Natural veld	1142	829	313
Improved veld	98	-	98
Total grazing land	1240	829	411
Piries	70	-	70
Others	27	-	27
Total commercial forests	97	-	97

Source: Annual Statistical Bulletin 1978, Central Statistical Office, Mbabane, Swaziland.

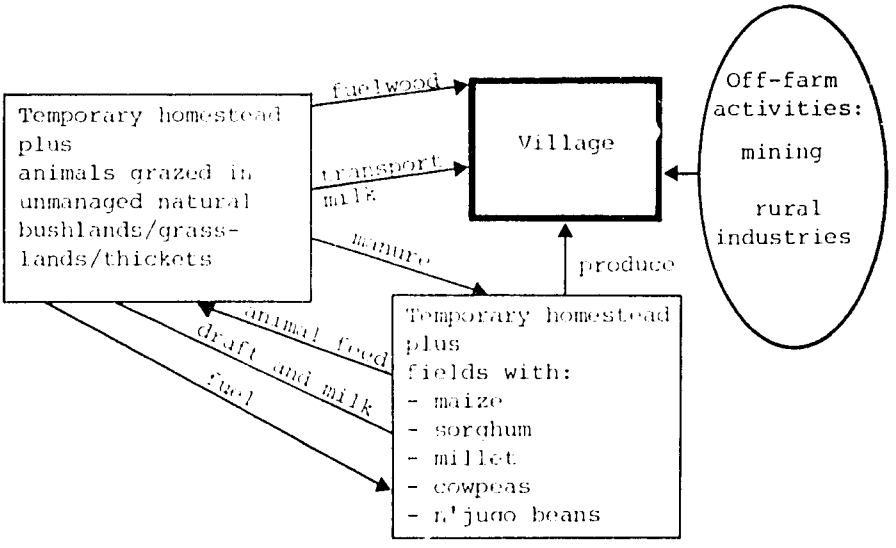


Fig. 1. Schema showing some of the interrelationships in a common village/homesteads land use system in Botswana.

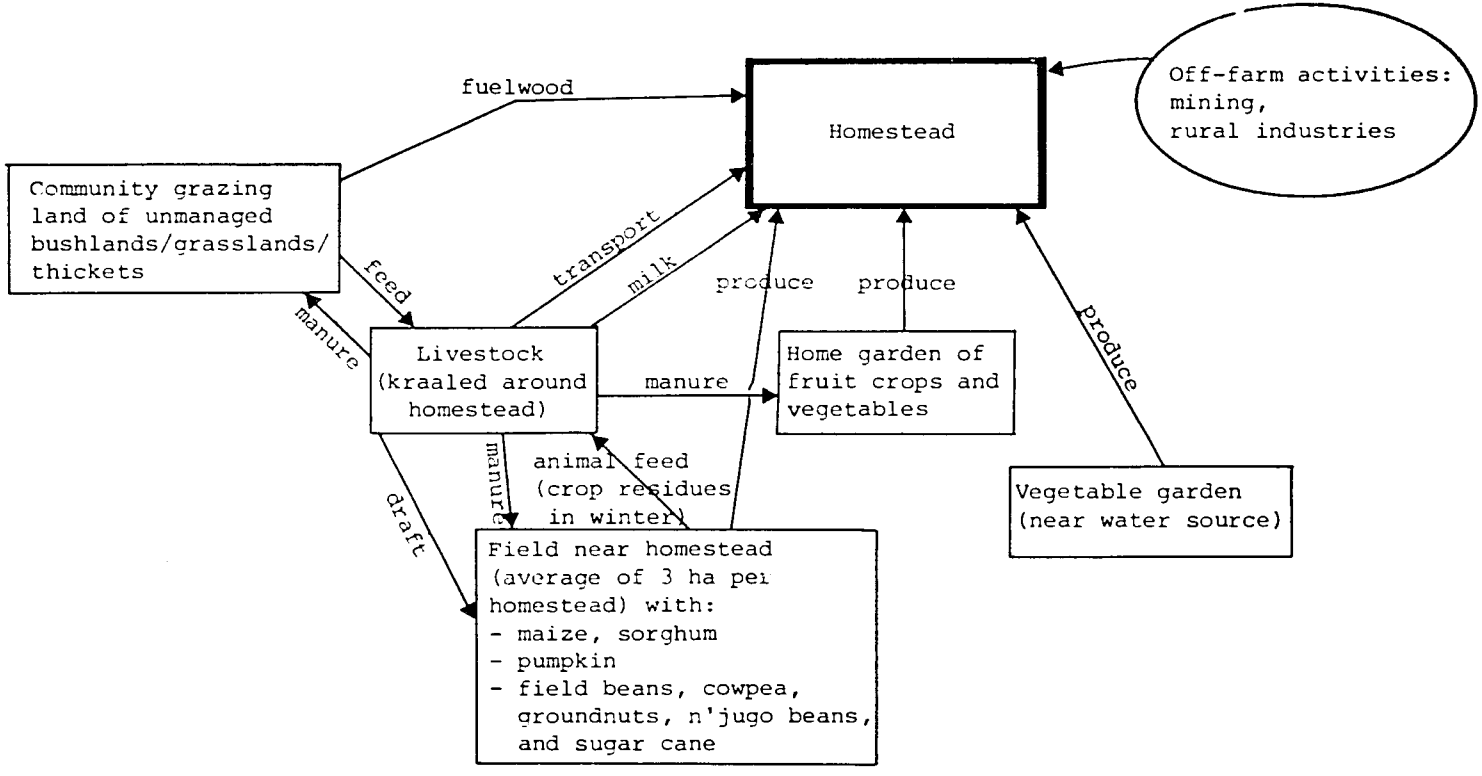


Fig. 2. Schema showing some of the interrelationships in a typical animal-based cropping system in Swaziland.

obtainable fuelwood source is becoming increasingly distant from the village or homestead, often many kilometres.

The systems of agroforestry proposed for these countries could be as follows.

Modification of grazing lands

Ten-metre wide tracts could be opened and planted with alternate rows of pine or eucalyptus (for fuel) and *Leucaena leucocephala* (for browse). This would result in a sequence of strips of mature bush and grass, fuelwood trees and browse species.

Clearing and replanting of grazing lands

A more intensive proposal is to clear the natural bush/veld vegetation and replant completely with appropriate mixtures or zones of the following species:

- Eucalyptus, pine or *Gmelina*, for fuel;
- *Leucaena leucocephala* or *Cajanus cajan* (leafy types), for browse;
- *Macroptilium atropurpureum*, *Eragrostis tef* or *E. curvula* for grazing.

Such agroforestry systems would require a higher degree of management skill than at present is commonly found. Areas should be paddocked and rotational grazing practised to enable regeneration of the grazing/browsing species to take place. An appropriate rotational harvesting scheme for the fuelwood trees would also need to be looked into.

Soil erosion, caused by overgrazing, is often a serious problem in both Swaziland and Botswana and the presence of a more continuous ground cover in the systems proposed above is at least likely to lessen soil erosive processes.

UNESCO's INTEGRATED PROJECT ON ARID LAND (IPAL): A SILVOPASTORAL APPROACH

H.F. LAMPREY
UNESCO Regional Office of Science and Technology for Africa, Nairobi, Kenya.

ABSTRACT. The Project's area, in northern Kenya, resembles large parts of the Sahel and dry northeastern Africa which are being degraded due to overgrazing and excessive tree felling. The basic ecological and socio-economic data have been collected over a number of years with the intention of formulating an integrated management plan. An understanding of the interactions between livestock and vegetation is a key factor in this, and the possibilities for an improved silvopastoral approach utilizing both indigenous and exotic woody species is being looked into.

INTRODUCTION

The Integrated Project on Arid Lands (IPAL), in principle a regional project with applications throught much of the arid zone of Africa, is administered by the United Nations Education, Scientific and Cultural Organization (UNESCO) under the Man and Biosphere (MAB) Programme. Funding for the first four years since 1976 came from UNEP and is now provided by the government of the Federal Republic of Germany.

The Project area

IPAL works on the scale of a pilot project with five specialists in the field. It has three main objectives which may be summarized as follows.

- To study the processes of desert encroachment and determine its causes.
- To provide recommendations and guidelines on the management of arid zone resources with a view to arresting desertification and promoting the rehabilitation of degraded lands.
- To establish programmes of research, resource monitoring and training in arid zone land management.

The project is situated in the subdesert country of Marsabit

District in northern Kenya, an area inhabited almost solely by nomadic pastoralists of the Samburu, Rendille and Gabbra tribes. As the mean annual rainfall over the greater part of the area is below 250 mm, and very unreliable, sustained agriculture is not feasible. The only substantial body of water, Lake Turkana, is saline, so that irrigation also appears to be impractical. The people depend for their subsistence almost entirely upon milk and some meat from their herds of camels, cattle, sheep and goats and they buy small quantities of grain food with the proceeds of selling surplus animals (Kruuk, 1980).

The problems

The Project's study area was selected partly because it bears a close resemblance to the Sahelian Zone of western Africa and is representative of large areas of dry northeastern Africa. It includes considerable areas of country which are undergoing degradation towards desert conditions through overgrazing and excessive tree felling. The basic problem is that of rising human populations (increasing at about 2 per cent annually) and the growing livestock populations necessary for their subsistence (Lamprey, 1983). However, it appears that the country would be capable of supporting these populations at their present levels, except during drought periods, if traditional nomadic practices had continued. The problems of overstocking and woodland destruction have been greatly aggravated by the recent trend towards settlement among traditionally nomadic families through the influence of several modern developments.

Village settlements have grown up around the few permanent wells and springs in the region and more particularly around recently installed boreholes. While the main incentive to settle is the presence of fresh water, the people are also attracted by several other amenities: famine relief centres, medical dispensaries, missions, schools, shops and police posts. The fear of intertribal raiding and of bandit activity constantly deters the pastoralists' families from dispersing into the large areas of grazing land away from the settlements. The concentration of people and livestock around the new villages is causing gross, but localized, overexploitation of the vegetation. Year by year, as the people are obliged to go increasing distances from the villages to obtain grazing and thorn trees for their fences, the circles of man-made desert spread outwards (Figure 1). In the Rendille tribal area two such degraded areas have coalesced to form a desert some 80 km wide.

During recurrent drought periods, such as that which occurred between 1968 and 1976 across the Sahelian Zone and northeastern Africa, the effects of the degradation of the grazing lands became most apparent. With the death of large numbers of livestock there is famine among the pastoralists which can only be relieved by emergency food supplies. Such natural balances as formerly existed through increased human mortality no longer operate and expanding human populations are being supported by land which is undergoing a steady decline in productivity and carrying capacity. Solutions to this problem, which are difficult to envisage under current economic and political circumstances, are urgently needed. They will depend upon the introduction of land reform, grazing controls and the education

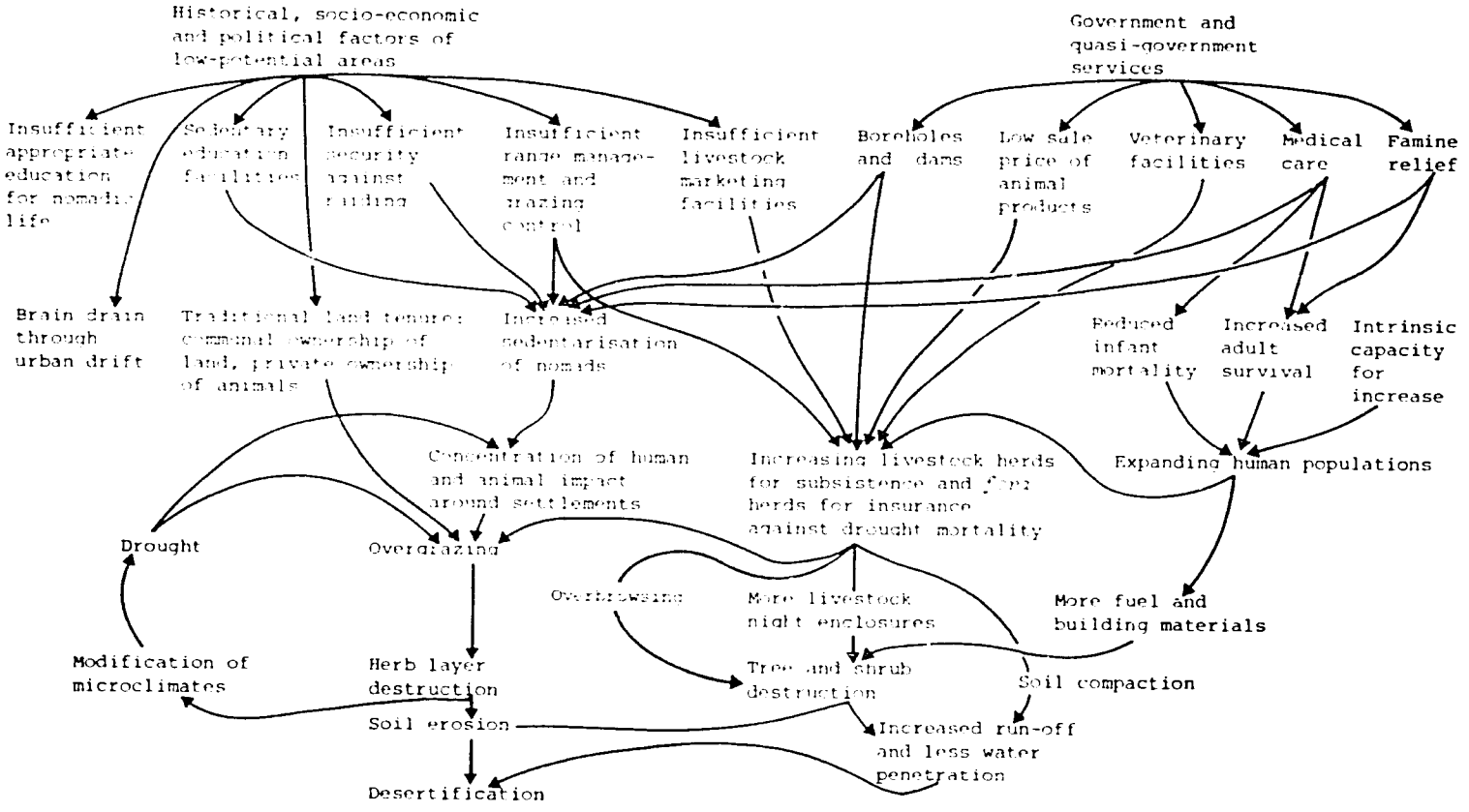


Fig. 1. Some of the factors which cause desert encroachment in northern Kenya. (Reproduced from Lamprey, 1978.)

of the people to accept considerable modifications in their economy and mode of life. While the project is looking for solutions to the ecological and sociological questions, it is also seeking alternatives to supplement the wholly livestock-based economy in order to provide livelihoods for the increasing numbers of destitute people who lack adequate subsistence herds.

THE IPAL RESEARCH PROGRAMME

To gain an understanding of the processes of desert encroachment and their causes, the project has concentrated for four years upon the ecological interactions between livestock and the vegetation of the region (Lamprey, 1978, 1981). Its main aim has been to determine carrying capacities and appropriate grazing patterns. Recently the Project has paid increasing attention to the socio-economic factors which underlie the more immediate causes of desertification and the emphasis is now shifting towards sociological studies and human ecology, with the addition of training and extension activities.

Owing to a lack of basic ecological information on the District which is relevant to desertification and to land management, much of the early research activity has been devoted to gathering baseline information on climate, soils, vegetation, wildlife and livestock. Population levels, biomass and productivity measurements in relation to fluctuating rainfall have been obtained, both for the vegetation and the animal life. The distribution and movements of people and livestock, mainly in response to the variable availability of grazing, water and security, have been mapped and the areas in which overexploitation and desert encroachment are taking place to varying degrees have been described. At the same time studies of the human economy have helped to determine the relationship between nutritional requirements of the pastoral peoples and the food resources available to them, both from within the region and imported from outside it. It is anticipated that the emphasis of the management guidelines to be prepared by the Project will be upon an integrated pattern of development activities centred on livestock and grazing rotations. Important considerations are the need for greatly improved livestock marketing facilities to enable the pastoralists to sell their surplus animals; the introduction of minor industries to diversify the economy and provide employment; and the provision of alternative means and materials for the construction of livestock fencing. The possibilities for alternative industries in Marsabit appear to be very few indeed and those which have been suggested, in some cases investigated by IPAL are mainly based upon the exploitation of indigenous vegetation, but include the planting of some exotic trees suitable for arid situations.

IPAL — INTEGRATING SILVOPASTORAL SOLUTIONS

Although IPAL operates in a region where agroforestry crop farming systems are not feasible, owing to low rainfall and the lack of fresh water, the integration of forest and woodland management with pastoralism as the main occupation, is a good example of the silvopastoral use of land. This integration has been accepted by

the Project as an important aspect of the rational development of the region and several technical reports published to date deal in part with this subject. Synnott (1979a) has fully discussed the status, importance and protection of the montane forests, stressing primarily their role in the maintenance of the very limited water catchments in the region, and also reported upon the potential for tree planting in the various ecoclimatic zones (Synnott, 1979b). The possibilities for implementing forestry programmes for local community development are described by Herlocker (1979).

A further report on the results of tree planting trials carried out by the Project between 1976 and 1980 in several altitude zones is also available (Herlocker *et al.*, 1981). Twenty-seven species, over half of which are exotic, have been tried with considerable success in the subhumid zone, but only limited success has been achieved with a few drought tolerant species in the arid zone where an initial period of watering was possible. The most successful of the introduced, drought tolerant species are *Prosopis chilensis*, *Parkinsonia aculeata*, *Melia azedarach*, *Azadirachta indica*, and *Carica papaya*. Among the indigenous species planted in arid conditions *Acacia senegal*, *A. tortilis*, and *Salvadora persica* have been the most successful although slow in their growth. An important characteristic of *Prosopis* and *Parkinsonia* is their relative unpalatability which enables them to survive in an environment where goats may prevent the growth of most small woody plants. Herlocker (1979) lists the objectives of a rural forestry programme for the arid regions of Kenya as follows.

- To provide employment for the residents of settlements.
- To provide supplies of wood products for fuel and building materials for local use.
- To establish tree species usable as cash crops, or for subsistence (including animal fodder).
- To help re-establish stabilizing vegetative cover for denuded areas.

Herlocker emphasizes that the usefulness of such a programme would be greatest if it were integrated into a broadly based district development plan covering all aspects of the economy. He envisages several aspects of woodland utilization, including the possible development of a regulated gum arabic harvest from the indigenous *Acacia senegal* trees, which are common but not abundant; a regulated collection of the indigenous *Aloe* species, needed for the pharmaceutical industry; and a strictly controlled sustained yield management of the *Acacia tortilis* and *Acacia reficiens* woodlands for firewood and charcoal and building materials. Nevertheless, he stresses the great importance of exercising the necessary control in order to avoid the kind of overexploitation which is taking place in the woodlands which are at present more accessible to towns and villages all over Kenya. One key to the success of such proposals lies in the prior achievement of land use control based upon appropriate legislation and adequate enforcement of laws and regulations. Another key to success lies in suitable education at all levels in the principles of rational land use, so that not only are people influenced to take part in the improvement of their habitats, but

they understand the reasons for the measures being adopted.

THE FUTURE

The present phase of IPAL in Kenya is being brought to a conclusion with the preparation of management guidelines for the integrated development of the Rendille tribal lands in Marsabit District. These guidelines, which have been produced in preliminary draft form will be available by July 1983. They include a summary of the background information, obtained over six years of multidisciplinary research, upon which the guidelines are based, together with a document giving management proposals for all aspects of the Rendille economy including range, woodland and livestock management. Inevitably the management of livestock and vegetation is closely integrated, since the main aim of the guidelines is to maintain a balance between stocking rates and plant production, and thus to prevent future overexploitation of the vegetation.

The next phase of the Project is proposed for early 1984, and is to take the form of an Arid Land Research Institute to be run co-operatively by the Kenya government and UNESCO. This institute will undertake training, research and monitoring and will also supervise a pilot range and livestock management project in the Rendille tribal area.

REFERENCES

Herlocker, D.J. (1979). "Implementing forestry programmes for local community development, southwestern Marsabit District, Kenya". IPAL Techn. Report D.2c. UNEP-MAB Integrated Project in Arid Lands, Nairobi, Kenya. 10 pp.

Herlocker, D.J., Barrow, E. and Peatkan, P. (1981). A preliminary report on trial plantings of woody species in arid and semi-arid northern Kenya. *In* "Proc. Kenya National Seminar on Agroforestry" (L. Buck, ed.), pp.511-577. ICRAF, Nairobi, Kenya.

Kruuk, H. (1980). "The effects of large carnivores on livestock and animal husbandry in Marsabit District, Kenya". IPAL Techn. Report E.4. UNEP-MAB Integrated Project in Arid Lands, Nairobi, Kenya. 52 pp.

Lamprey, H.F. (1978). The Integrated Project in Arid Lands (IPAL). *Nature and Resources* 14, 4-15.

Lamprey, H.F. (1981). Kenya: seeking remedies for desert encroachment. *Span* 24(2). 4 pp.

Lamprey, H.F. (1983). Pastoralism yesterday and today: the overgrazing problem. *In* "Tropical Savannas" (F. Bourlière, ed.), pp.643-666. Elsevier, Amsterdam, The Netherlands.

Synnott, T.J. (1979a). "A report on the status, importance and protection of the montane forest". IPAL Techn. Report D.2a. UNEP-MAB Integrated Project in Arid Lands, Nairobi, Kenya. 57 pp.

Synnott, T.J. (1979b). "A report on prospects, problems and proposals for tree planting". IPAL Techn. Report D.2b. UNEP-MAB Integrated Project in Arid Lands, Nairobi, Kenya. 41 pp.

PLATES illustrating this paper can be found elsewhere in this book.

DISCUSSION

CONNOR - What is the population density in the IPAL study area?

LAMPREY - One person km^{-2}. The total Project area is 22,500 km^2 and there are 500,000 people in the arid lands of Kenya.

CONNOR - Who provides the boreholes?

LAMPREY - The government and in some cases missionaries.

GETAHUN - What species are planted in the village?

LAMPREY - *Prosopis juliflora* is the most successful. It is not palatable, so it survives. *Parkinsonia*, also unpalatable, is planted as well. Twenty-seven species have been planted, but they are all protected by fences. Some information is available on the adaptability of these species, but the study is in progress.

TIESZEN - How many of these 27 species are local?

LAMPREY - About half of them are local and the rest exotic, mostly from North, Central and South America.

BRISCOE - Is *Tamarix* included?

LAMPREY - No, but there is a wild, native *Tamarix* species; it has not been studied yet.

BRISCOE - What about indigenous, salt tolerant species?

LAMPREY - They are already prolific in the area.

LEYTON - Is there sufficient water to have at least some modest irrigation?

LAMPREY - Lake Turkana has an enormous amount of water, but it is salty. Underground water is also salty. Some small fresh water springs and wells are available but insufficient for irrigation. Some missionaries have tried to use Lake Turkana water but salination prevented crop growth in the second year of irrigation. At the moment, irrigation prospects are virtually nil.

LEYTON - What about salt water irrigation?

LAMPREY - Very little possibility at present under the low economic potential of northern Kenya.

RACHIE - How secure is this border area? Are there encroachments?

LAMPREY - There are few incentives for encroachments. Raiding by brigands (shiftas) still takes place, and insecurity is always a problem in that region.

BUDOWSKI - Is there any possibility for harvesting wildlife in preference to cattle?

LAMPREY - At present, the ungulate animal population of the study area consists of 96 per cent livestock (45,000 camels, 300,000 sheep and goats, and 25,000 cattle) and 4 per cent wildlife. The wildlife species present are those representative of

the arid zone of northeastern Africa: Grant's gazelle, gerenuk, oryx, Grevy's zebra, giraffe. Wildlife numbers are suppressed by human activity and competition for grazing with livestock. The best way is to utilize the wildlife for tourism (although tourism is sometimes branded as social pollution). Giraffes might be sufficiently numerous to be harvested, but such harvesting is unlikely to be profitable or sustainable in northern Kenya.

TIESZEN - Does export of charcoal take place?

LAMPREY - Yes, but illegally.

BIOMASS PRODUCTION IN AGROFORESTRY FOR FUELS AND FOOD

*D.O. HALL and †J. COOMBS
*King's College, University of London, London, UK.
†Reading, UK.

ABSTRACT. Developments in biomass production and use are briefly reviewed and it is shown that, in many developing countries, a combination of wood and food crop production may be the only way of meeting the increasing needs for fuels and food. In many regions, the production of power alcohol (either ethanol from food crops, or methanol from trees) is not a satisfactory answer to the fuel crisis. This is due to the scale on which biomass plantations are needed in order to meet the demands of power alcohol factories, and the fact that such factories cannot, at present, operate at the local or rural level with the required degree of efficiency or economy. The possibilities of providing biomass through agroforestry are discussed. Some attention is also paid to the demands put upon the soil as a result of increased nutrient removal by biomass schemes, many of which envisage the complete removal of the entire vegetation. The possibilities of overcoming such problems through biological/microbiological means are mentioned, but the energy needs are noted. Finally, the overall requirements for technical resources are stressed, and some comments are made on development criteria for successful agroforestry schemes.

INTRODUCTION

The underlying problems

Biomass production and agroforestry, whether combined or separate, are both aimed at increasing the production of biological material for use not only as food and animal fodder, but also as fuels, building materials and chemicals. The interest in such systems has greatly increased over the last decade or so due to a series of crises related to fuel availability and price, as well as to global shortfalls in food production.

On the national scale in developed and more industrialised countries, the biomass concept has arisen from pressures due to the increased price of oil coupled with problems in terms of balance of payments and political pressures from the suppliers.

In many of these countries the choice of a biomass route to attain some degree of fuel self-sufficiency is also the result of an agricultural crisis. Not one of shortage or high cost, but quite the opposite for intensive farm methods have led, in many cases, to overproduction, depressed farm prices and movement of the population from rural regions to the towns.

Increased agricultural production of plant materials for fuels is seen as one way of overcoming such problems, and of maintaining prices to farmers. However, the number of regions where this holds true is limited. To varying degrees the gasohol programme in the USA, the Brazilian Proalcool programme, and the biomass activities in the Far East (Philippines, Thailand, etc.) fit this picture. However, this is not the case in the majority of developing countries.

In most developing countries plants have remained the major source of energy, especially in rural communities, although oil has assumed an importance as a source of energy for both transport and stationary power for purposes such as irrigation. The problem in these countries is that, although oil may represent only a small percentage (often less than 20 per cent) of their overall energy requirement, the purchase of oil or petroleum may now take a major proportion of a country's foreign currency spending power.

In order to meet an everincreasing fuel bill some countries have turned to increased sales of wood, culled from climax forests, with little thought of conservation of the system as a whole, or to the increased use of those species, or parts of the harvested trees, for which there is not an immediate export opportunity. Other ways of financing oil payments again result in widespread destruction of forest. These include the increased production of monoculture cash crops grown on a widespread plantation system, or the destruction of large areas of forest and woodland for cattle ranching. The result, in most cases, is the same. The short-term generation of foreign exchange at the long-term expense of land sustainability and the welfare of the local farmer and the country as a whole; since the spiral of increasing oil prices can only be met by yet further exploitation of the land.

The only alternative to an everincreasing fuel import bill is to direct indigenous resources to energy production. Most developing countries, especially the poorest, do not have reserves of fossil fuel, and only restricted sources of hydroelectric power may be available. The alternative solar, wind and geothermal energy sources can be significant in many countries but these cannot provide liquid fuel. For many countries the only indigenous source of such liquid transport fuel is biomass.

In some regions, due to climatic conditions, or changes in international marketing policies, there may be a surplus of food crops which can be used to produce fuel ethanol via fermentation. In other regions wood represents the only large biomass reserve. Many areas lack both sustained agricultural and forestry production. In most regions much of the biomass being produced is already being used, often at rates in excess of the renewal rate, to provide fuelwood and charcoal for rural and urban homes as well as, increasingly, for small-scale industry and agricultural

processing facilities. Thus important changes in both the production and route of utilization of biomass will have to be made in order to implement liquid fuel schemes based on wood as a raw material while, at the same time, meeting the increased, and increasing, demands for rural firewood and more food.

The technologies required

Current use of biomass in many developing countries is unsophisticated and inefficient in energy terms; but with good reason. To increase the efficiency of both production and use of biomass requires technical and capital inputs often beyond those available in the countries concerned. The recent renewed interest in biomass in developed and technically advanced regions has led to a re-evaluation of crop production systems and established conversion technologies with higher efficiencies; development of new technologies; a diversion of large amounts of money for research; and initiation of a number of national programmes and many individual commercial projects.

Associated with this resurgence of interest in biomass is much information and technology which could be of particular significance if transferred in an effective manner to the developing countries. However, there are dangers that direct extrapolation from the major power alcohol programmes (in the United States based on maize, and in Brazil on sugar cane) could generate more problems rather than solve the current fuel and food crises. Both these large power alcohol programmes are based on large-scale monocultures, and the raw materials are potential food products. Widespread land clearance for production of sugar or grain for fuel production will, of course, have the same results as clearance for the production of a cash crop, or for cattle ranching.

RAW MATERIALS AND CONVERSION SYSTEMS

The major sources of biomass and the technologies available for converting it to a variety of gas, liquid and solid fuels are shown in Figure 1. As far as raw materials are concerned a wide variety of biomass production systems has been proposed, or discussed, in the literature (Hall and Coombs, 1979; Palz *et al.*, 1981; Biomass for Energy, 1979) and some of these are indicated in Table 1. At present, and as far as the large-scale commercial production of biomass fuels is concerned, the primary raw materials are sugar, or starch crops such as sugar cane, maize and cassava (Coombs, 1980). On the other hand, the greatest volumetric consumption of biomass as a fuel will be that of wood, together with various agricultural or process residues and wastes, such as sugar cane bagasse, sawdust, straw and husks. Most of the aquatic systems based on algae or water weeds are still experimental or speculative.

Various technologies for increasing the efficiency of biomass use or upgrading it to a fuel of a higher physical and/or energy density are available. One is the production of heat or gas suitable for stationary power, or the generation of electricity, on a local basis. The processes involved include direct combustion in improved stoves or boilers, pyrolysis, thermal gasification, liquefaction by hydrogenation or catalytic means

PROCESS	PRODUCT	STATE OF ART
(*a*) *Thermal*		
Combustion	CO_2, water, ash, heat, steam, electricity	Well established
Pyrolysis	Char, oil, gas (CO, C_2H_4, H_2)	Small scale established
Gasification	Mainly CO and H_2	Large scale under development
Gasification + catalytic synthesis	Methanol, hydrocarbons	
(*b*) *Biological*		
Yeast fermentation	Ethanol + CO_2	Established
Anaerobic digestion	Methane + CO_2	Established

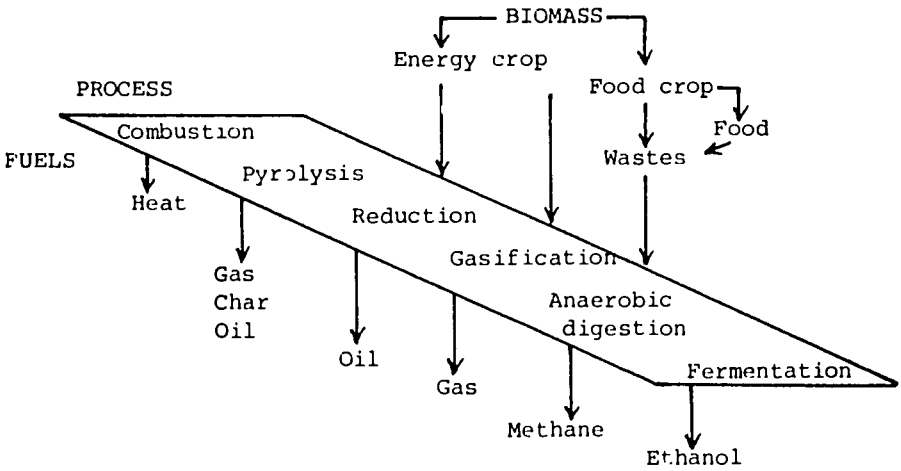


Fig. 1. Conversion techniques for producing fuels from biomass

and anaerobic digestion. Some of these systems also produce solid fuels, or by-products with fertilizer value.

Another major area of biomass conversion is that concerned with the formation of lower alcohols such as ethanol and methanol. The attraction of these products is that they may be used as fuel in internal combustion engines; either as blends with petroleum, or as a fuel in their own right. Plant oils may also be used as a liquid transport fuel in a diesel engine (Hall, 1980, 1981). At present almost all ethanol produced for fuel use is derived from either sugar cane (as juice or molasses) or starch crops. Most methanol is currently derived from natural gas, oil or coal. However, it may also be formed using wood as the raw material. Methanol in the past was obtained by destructive distillation of wood; now it is almost exclusively derived by catalytic conversion of synthesis gas (a mixture of carbon monoxide and hydrogen) which may, in theory, be derived by pyrolysis or gasification of a variety of biomass raw materials, including wood and agricultural residues. The catalytic synthesis is, of

Table 1. Biomass sources of raw materials

LAND CROPS		WASTES
Sugar crops		Manures
Beet		Slurry
Cane	AQUATIC PLANTS	Domestic
Starch crops		Sewage
Maize	Water hyacinth	Food
Cassava	Reeds	
Trees	Rushes	RESIDUES
Eucalyptus		Wood
Willow	ALGAE	Straw
Poplar		Husks
Luceana	Unicellular	Peel
Pines	Multicellular	
Firs		BY-PRODUCTS
Inulin crops		Molasses
Chicory		Whey
Artichoke		

course, well established. The problem, at present, is that no proven commercial biomass gasifier is available which provides synthesis gas of the required quality.

Power alcohol derived from wood will most likely be in the form of methanol formed via the synthesis gas route. This is due to the present problems inherent in the hydrolysis of ligno-cellulose to produce a feed material suitable for yeast fermentation. At the same time considerable research and development is at present directed towards finding a suitable procedure for the production of sugar solutions suitable for use as fermentation feed from cellulose and woody materials. The objective varies from project to project. In some the aim is to produce a substrate suitable for the production of ethanol by yeast fermentation; in others the aim is to use various bacterial and fungal systems, or enzymes, capable of degrading ligno-cellulose with the production of a variety of chemical products including ethanol, butanol, acetone and butanediol. In all cases the raw materials will need physical pretreatment to produce small particles, and this can be done by mechanical milling. The particles may then be subjected to a variety of physical, chemical or biological treatments in order to produce a number of product streams comprising cellulose, glucose, hemicellulose, pentose, and lignin, for example.

The problem with cellulose is that, in its natural state in the plant cell wall, it exists as an insoluble complex with lignin and hemicelluloses. Delignification can be achieved using reagents such as sodium hydroxide, peracetic acid, etc., as well as sulphites. Alkali treatment will swell and separate the fibres. Hydrolysis may be accomplished either by using mineral acids or enzymes (cellulases) derived from fungi such as *Trichoderma*, *Sporotrichum* and *Aspergillus*. An alternative biological approach is the use of a thermophilic bacterium such as

Clostridium thermocellum, which will grow on cellulose itself. However, at present, these methods are costly in terms of capital, process chemicals and energy inputs and, as a result, no clear commercial process has yet emerged.

Power alcohol

At present the only viable commercial process option for producing a liquid transport fuel from biomass is the production of ethanol using yeast fermentation of a sugar-containing feed stream. The major programmes are the Brazilian Proalcool, and the Gasohol programme in the USA. The objective set by the Brazilians is to produce some 12 billion litres of ethanol, mainly from sugar cane by 1985. In 1978 the production capacity of ethanol in Brazil was some 2 billion litres; in 1981 they will produce over 4 billion litres.

The short-term objective set in the USA is to produce 500 million gallons of ethanol, largely derived from maize, by the end of 1981, with a long-term objective of an overall 10 per cent substitution of all gasoline by the 1990s. In addition, a large number of countries including Thailand, the Philippines, Kenya, Zambia, Zimbabwe, Nicaragua, Paraguay, New Zealand, Australia, Fiji and others have already initiated molasses-based factories, or they have carried out feasibility studies. The implementation of such schemes depends on government initiatives, coupled with sufficient infrastructural support and a belief that such schemes are economically viable and of long-term benefit.

A number of reasons have been given for initiating a power alcohol programme. The most important of these include: self-sufficiency and the subsequent avoidance of political pressures from oil suppliers; avoidance of large balance of payment problems; the better use of internal resources such as the use of crop surpluses or wastes; and the long-term advantages of utilizing a renewable resource, rather than a finite one. Power alcohol programmes based on sugar and starch crops have reached a large scale very quickly, particularly in Brazil and the USA, for a number of reasons. Probably the most important was the fact that the raw materials were already available, the infrastructure for growth and transport of both sugar cane and maize was in existence in the countries concerned, and the technology needed for processing was already well known from the sugar, starch, brewing and distillation industries. Furthermore, since the crops concerned are annual in production, a rapid expansion of raw material production was possible once such programmes had been initiated since additional land was available. In the case of the USA this was land which had previously been taken out of production in an effort to maintain farm prices during a decade of increased yields and smaller demands. In the case of Brazil additional land was, and is being, developed for sugar cane production from previously unfarmed regions. The production of liquid transport fuels from wood will be a more complex situation to resolve; the technology is not yet proven, and the infrastructure for production, collection and transport may not exist in many countries, although it undoubtedly does exist in others.

If we assume that the major impetus for the current widespread interest in biomass-derived fuels is as a means of

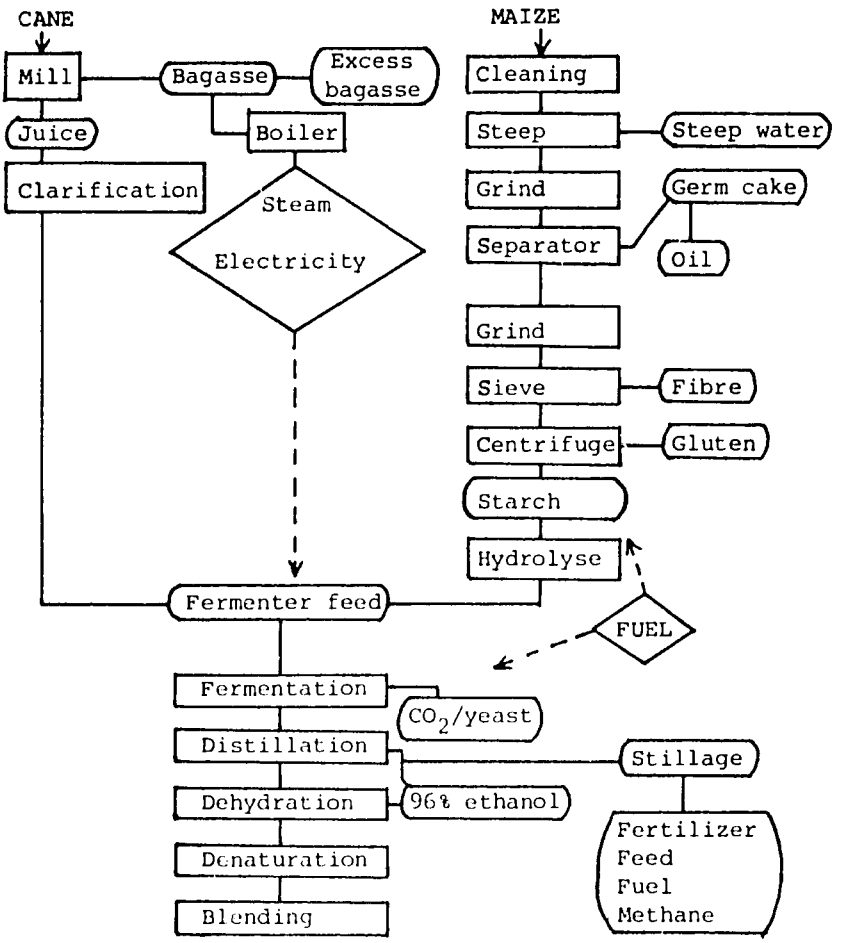


Fig. 2. Flow diagram of principal ethanol processes

reducing the high energy costs associated with the import of oil, we presuppose two things. First, that the cost of alcohol production is less than that of importing oil and, second, that the overall process does, in fact, result in a net gain of energy. The various partial processes involved in the current industrial scale distilleries typified by direct fermentation of sugar cane juice in Brazil, or the fermentation of glucose syrup derived by wet-milling of corn in the USA are shown in Figure 2.

Briefly, it is worth contrasting these two systems in relation to the fuel used for processing and the production of economically valuable by-products. In the case of the sugar cane based system all the energy for both extraction of the juice and distillation may be obtained by burning the fibrous residue of the cane (bagasse). Although the bagasse as produced from the mill contains up to 50 per cent moisture, sufficient steam may be generated by its combustion to provide the energy for the overall production of ethanol, and to leave an excess. This could be used as an energy source for processing, for example, starch to ethanol or for generating electricity, or the surplus bagasse could be used for the production of charcoal, paper or

board.

In contrast the maize based system needs an external source of fuel such as oil or natural gas. However, since the total amount of energy put into the system to produce ethanol is close to, or exceeds, the energy content of the ethanol produced this is not a viable proposition if the objective is liquid fuel substitution. On the other hand, if the maize based distillery is fuelled using coal, it represents one way of producing a liquid fuel from coal which may be both cheaper and cause less environmental pollution than thermal or chemical routes. A second benefit obtained from maize based systems lies in the by-products: oil, protein and animal feed. These have both a financial value, which may be offset against the final cost of the fuel alcohol, and an energy benefit if the overall process is taken into account. Wood may also be used as a fuel, and an integrated wood-fuelled / starch-based power alcohol plant could show a net energy gain in terms of ethanol produced.

It is generally accepted that in the sugar cane based system there is a net gain of energy. But some confusion arises due to the lack of a standard means of calculating such a gain. One way of expressing the energy gain is to divide the heat content of all the inputs required in its production (other than the agricultural raw material itself) by the heat content of the ethanol produced (not considering any other products). The resultant number is referred to as the net energy ratio. For a maize based system with current commercially used technology this ratio is less than one; for a sugar cane based system it would appear to lie between two and three.

At present the cost of producing ethanol by fermentation may, in many cases, be greater than that of imported oil. The major proportion of the final selling price (exclusive of any taxes which may be introduced by an individual government) is the feedstock. For fermentations based on sugar or starch crops, depending on the details of the processing plant and the method of finance, the raw materials may contribute between 60 and 85 per cent of the overall costs (Figure 3). A recent report, issued by the World Bank (Anon, 1980) suggests that sugar cane based ethanol production is likely to be economic at the early 1980 oil price level of US$31 per barrel of oil (f.o.b.), providing the economic cost of sugar cane at the factory gate is less than US$14 per ton. Ethanol production from molasses is likely to be economic where molasses is less than US$60 per ton. Cassava and maize based factories appear to be less attractive because of the need to purchase energy and the higher capital costs of production. To compensate for these drawbacks low cost raw materials are required; cassava at less than US$ 13 per ton and maize at less than US$1 per bushel (= 56 lbs).

Thus the problems facing power alcohol production in the form of ethanol are the costs, the competition for what are essentially food materials (Brown, 1980), and the poor energy balance if an agricultural residue is not available as a fuel. At present, if one is influenced only by economic and energy considerations the decision to proceed with the construction of a power alcohol factory might be based on the lines of argument shown in Figure 3. This makes it clear that, at present, the best systems are those based on sugar cane. However, the number

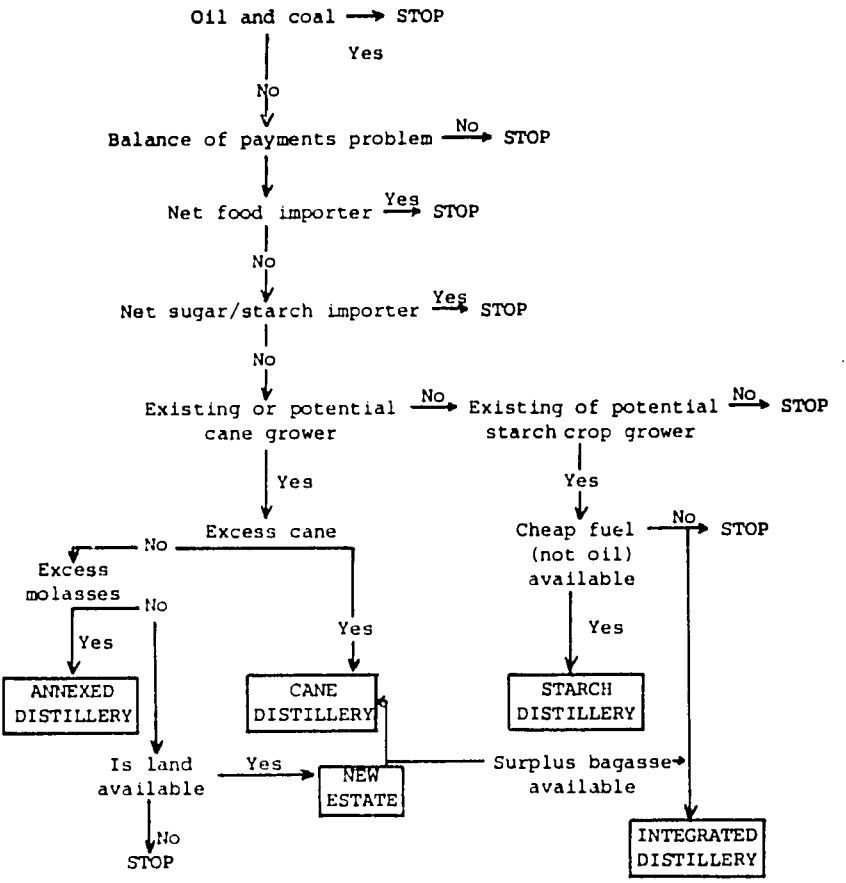


Fig. 3. Power alcohol options

of tropical countries which could initiate a power alcohol programme based on these lines is limited. Indeed the total worldwide availability of sugar and starch as food is low when compared with the present demand for oil based fuels (Table 2). As indicated in this table the only biomass resource of a magnitude comparable with that of oil is wood.

Table 2. Annual world biomass production compared with oil use

NET BIOMASS PRODUCTION	2×10^{11}	tonnes
Of which:		
Forest production	9×10^{10}	"
Cereals	1.5×10^{9}	"
as starch	1×10^{9}	"
Root crops	5.7×10^{8}	"
as starch	2.2×10^{8}	"
Sugar crops	1×10^{9}	"
as sugar	9×10^{7}	"
OIL USE	2.8×10^{9}	"

Wood as a source of liquid fuels

The most likely liquid fuel to be produced from wood for the purpose of oil substitution is methanol. As is the case with ethanol, this alcohol can be used as a blend with petroleum in existing spark engines with only small modifications, or it can be used as a fuel in its own right in new vehicles. It can also be used as a blend to 40 or 50 per cent in modified diesel engines, in modified boilers for central heating or, for the generation of electricity, in gas turbines. The technology is known, but not commercially proven, so that estimates of the cost of production are difficult. However, estimates produced in the USA vary from around 50¢ to over US$1.30 per gallon. Because the calorific value of methanol is only about half that of petroleum the cost may be as much as US$3 per gallon equivalent for the same mileage. Studies carried out by the Department of Energy (ETSU) in the United Kingdom indicate production costs of between £150 and £250 per ton, depending on the process of synthesis gas formation. Again, considerably higher, on an energy content basis, than the present cost of oil.

The problems of the actual availability of wood as raw material for fuel production, in particular where developing countries are concerned (Smith, 1981), closely parallel those of ethanol production from food crops. The technology for the production of methanol from wood, although not yet commercially proven, is not likely to be a major obstacle.

Once again the major considerations will be those related to the production of raw materials and competition both in terms of availability and economics with alternative markets, both at home and through export. The World Bank, in an energy classification of developing countries, lists some 75 countries in which net oil imports account for between 75 and 100 per cent of their commercial energy demand (Anon, 1980). Of these, almost two-thirds have an actual or potential fuelwood problem. In addition export of hard woods to industrialized regions (USA, 6×10^6 m³; Europe, 19×10^6 m³; Japan, 42×10^6 m³) represents a considerable source of income for those countries with tropical hardwood forests.

At the same time it would appear, from a number of estimates that the annual *per capita* demand for fuelwood in rural communities of many developing countries lies between 0.5 and 2 tons per year. Current estimates of availability of wood and the future potential production vary. However, two points are clear. First, that although there is a ready availability of wood on a *per capita* basis in some regions (notably Canada and the USSR), availibility is usually restricted in the regions with the highest demand for wood as a rural fuel source. Such regions also show the greatest rate of loss of forest and woodland, probably totalling worldwide some 10 to 25 million ha per year. Part of this loss arises from the clearing of forest to permit the growth of cash crops and cattle both for local consumption and for export so as to generate foreign exchange for the purchase of oil.

Hence, in the same way that production of ethanol would appear to be limited by conflict with food needs, the production of methanol as an indigenous liquid transport fuel from wood would appear to be limited by similar conflicts between

availability and alternative uses. The answer obviously lies in greater production. Again, constraints exist in terms of lack of capital, resources and trained manpower.

In general in the developed countries, research into the use of trees as an energy crop has been centred on short rotation coppiced plantations. A particular study has been made (Siren, 1979) of those broadleaf species most suited to growth in the peat fields of Ireland, the wetlands of Sweden and forest sites in France, Canada and the USA. Selection criteria have included rapid juvenile growth, climatic and pest resistance, high genetic variability, ease of vegetative propagation, ability to show early competitiveness in plantations, and overall yield. Physical wood properties such as hardness, colour and machinability are less important than short-term yields and energy content. The Swedish studies have included *Salix*, *Populus*, *Alnus* and *Betula*. This work has shown the importance of climatic adaptation. Only Scandinavian, Finnish, Siberian and Canadian clones were hardy enough to survive the winter. Of over 2500 *Salix* species screened only nine or ten survived screening through various conditions of drainage, soil type, pH, fertilizer regime, cutting sizes, planting conditions, and weed control. However, these 'survivors' could give good yields of 16 to 18 tonne $ha^{-1}yr^{-1}$.

Suggested spacings of about 1 m^2 to each rootstock, coupled with frequent harvesting, at cycles between 2 and 10 years, put considerable pressure on the soil in terms of nutrient removal as compared with conventional forestry with harvesting after 30 to 100 years. Studies (Steinbeck, 1981) in the USA have suggested a removal rate of around 50 kg ha^{-1} nitrogen; 10 kg P; 20 to 30 kg K; 35 to 40 kg Ca and 5 to 8 kg Mg, in such intensive systems. One of the major needs of such systems is, therefore, high inputs of fertilizer. However, even with such inputs, the net energy gain is between 12 and 25 times; with the major energy inputs being associated with the initial ground clearance and planting, rather than fertilizer application after each harvest.

The Swedish study (Siren, 1979) draws attention to the increase in employment that such energy plantations would provide. It is suggested that an area of 100 ha would produce around 1000 tonnes *per annum* and give employment to two or three people. Transferred to a national scale this figure implies employment of 20,000 to 30,000 people in a total area of one million hectares. The contribution to the domestic energy supply would be of the order of 100 TWh, resulting in a 30 per cent oil substitution.

Such large-scale energy plantations do exist in Brazil where some 40 per cent of the energy needed for the steel industry is provided from *Eucalyptus* plantations. The Brazilians have also looked at the possibility of methanol production from this species and suggest that for a 1000 tonne per day plant over 70,000 ha of trees would be needed; harvesting would be on a 7-year cutting cycle in an enterprise which would employ some 2000 people.

Although the emphasis in this section has been put on the production of methanol from trees it must be pointed out that ethanol may also be produced, without the need for wood hydrolysis, for example from sago-starch (Malaysia), or the babassu palm (Brazil).

FUEL PRODUCTION FROM THE LAND

The most important factor affecting the viability of the present or postulated power alcohol programmes is the size of the operations. A power alcohol factory producing 40,000 litres per day (about 3 million gallons per year is small). A large plant to be built in the USA will produce over 100 million gallons per year. Similarly, a methanol plant based on wood will have to be in the range of 500 to 1000 tons per day of product.

The agroforestry alternative

Neither the scale of operation nor the agricultural production systems lend themselves to agroforestry, hence, one must consider the other alternatives of pyrolysis, gasification and anaerobic digestion. Here the situation is the reverse. In spite of considerable research the large-scale industrial plant necessary to convert biomass to gas or liquid fuels have not yet been produced on a commercially viable basis. On the other hand the small-scale gasification plant suitable for generation of electricity, water pumping, etc., has been in existence for some fifty years, and although displaced by the use of diesel fuel, should now be a feasible option (Anon, 1979). The design and operation of small-scale anaerobic digesters is even better established, in particular in China, where over 7 million digesters are operating at the village level. Similarly, although large-scale charcoal production plants, capable of operating on a continuous basis, are now available, the majority of charcoal is still produced on a small-scale batch basis.

The production of biomass suitable for the small-scale gas production could well be a component of some agroforestry systems, whether the conversion be thermal or by anaerobic digestion. As with power alcohol systems it is a question of species selection and the integration of the production of the raw material with other requirements so as to optimize overall land use requirements.

Although anaerobic digestion of a wide range of organic materials, including plants, is possible in general there is a need for a significant input of animal manure, both to act as a source of suitable micro-organisms and to improve the nitrogen: carbon ratio. Anaerobic digesters produce a mixture of methane gas and CO_2 as a result of the breakdown of organic material by complex mixtures of micro-organisms. These also hydrolyse cellulose and some convert sugars to fatty acids, CO_2 and hydrogen, and thence to methane. As the required product is in the gas phase it can bubble off and no complex separation process is necessary. The possible raw materials which can be used in a digester vary greatly from agricultural wastes, spoilt crops, to wastes from processing and purpose-grown crops. Characteristically these raw materials all have a high content of cellulose (ligno-cellulose), and they often do not readily find an alternative use, or are of no commercial value. Typically the gas produced consists of 60 to 70 per cent methane, which is produced at a rate of around 0.5 $m^3 kg^{-1}$ dry volatile solids, with a residence time in the reactor (detention time) of 15 to 30 days. The actual destruction of material varies from around 20 to over 70 per cent, depending on the nature of the raw material and the

design of the plant. The residual sludge has value both as a fertilizer, where the nitrogen content may have been increased, or as an animal feed.

The largest number of biogas plants are of simple construction and small in scale. Although a number of different designs exist, in China their common feature is that they are brick-built with the gasholder and digester combined in one unit placed under ground. The volume may be 10 m^3 with no moving parts. Several tens of thousands of digesters have been built in India also. In general these are somewhat more complex, and so more expensive and prone to faults, and constructed of concrete or iron, with iron or plastic gasholders.

As far as the use of crop residues for anaerobic digestion is concerned most materials are suitable, as long as the size is small enough (some milling may be necessary) and the content of ligno-cellulose is not too high. As far as the production of a tree crop for fuel is concerned the requirements are for a wood that burns without sparks or toxic smoke, and has a high calorific value. This latter factor is influenced by the moisture content, the amount of mineral matter or ash it contains, and the density. Species which have a rapid growth rate, or regrow quickly after cutting and which do not attract goats and other wildlife are also good candidates. Other plant characteristics which have been suggested (National Academy of Sciences, 1980) as advantageous are: nitrogen fixing ability, a ready adaptation to different sites and soils, easy establishment, and a low demand for subsequent care and management. In particular, different species may have to be selected in order to grow successfully in a wide range of environments, including different altitudes, soil types, rainfall regimes, light intensities, and on various types of terrain. A careful selection of provenance is also likely to be important (Siren, 1979).

SOIL DEPLETION

In many agricultural systems a significant proportion of the net biomass produced is left in or on the soil at harvest. The problem with integrated fuel/food systems is that, since all parts of the plants can be used, all parts could be removed. Such practice cannot be permitted. The removal of mineral nutrients through harvesting forest plantations can be offset by adding inorganic fertilizers. However, this on its own is often not sufficient, particularly in the tropics where soils are generally more fragile, because a most important component in soil sustainibility is the organic matter. This serves both as a source of nutrients for various micro-organisms responsible for the release of mineral nutrients, and the fixation of atmospheric nitrogen, as well as a physical agent to improve the crumb structure of the soil and its waterholding capacity. In general, an otherwise unsupported ecosystem can afford to export only 10 to 20 per cent of the annual net dry matter increment. However, this applies in a situation where the canopy is kept closed throughout most of the year. Where soil is laid bare the rate of loss of organic matter will be increased. During rainy seasons leaching and erosion of top soil removes organic matter at a high rate, and may cause related problems due to silting of water courses.

Where soil is bare during the hot season the increased soil temperature increases the rate of microbial destruction of the organic matter. Hence, if agroforestry is to provide both fuel and food the complex of trees and field crops must be managed in such a way that the system also results in sufficient retention, or return, of organic matter.

As far as trees are concerned the annual leaf production may be comparable on a yield per unit area basis to the production of a field crop. In a deciduous forest this organic matter is returned to the soil each year. Furthermore, in many forest systems the harvest is taken once only every 30 to 100 years. The carbon balance is thus quite different from that in a system in which all leaf material is removed for food or fodder, or as material for anaerobic digestion, and then the woody material is burnt. Hence, an integrated approach is needed with an emphasis on the return of organic material to the soil. Furthermore, both free-living nitrogen fixing organisms, and symbiotic *Rhizobium*, have a high energy requirement as, indeed, does the actual reduction process of inorganic nitrogen (nitrate) to ammonia for subsequent assimilation by plants.

BIOCHEMICAL AND MICROBIOLOGICAL CONSIDERATIONS

Nitrogen assimilation and reduction

Considerable research has been carried out on the possibilities of replacing the use of nitrogenous fertilizers with biological nitrogen fixation. In legumes fixation of nitrogen from the atmosphere depends on the presence of an effective symbiotic *Rhizobium*. A number of free-living blue-green algae and bacteria, for instance *Anabaena*, *Azotobacter*, *Beijerinckia* and *Clostridium* species, are also capable of fixing atmospheric nitrogen (Granhall, 1976). Some tropical grasses have also been shown to have associated nitrogen fixing organisms such as *Spirilum lipoferum*.

For most plants nitrate is the immediate source of nitrogen (Hewitt and Cutting, 1979). Assimilation occurs as follows:

$$NO_3^- \xrightarrow{2e^-} NO_2^- \xrightarrow{6e^-} NH_4^+$$

This sequence is catalysed by two metalloproteins, nitrate and nitrite reductase. The source of electrons (indicated as e^- in the above equation) is either photosynthesis or respiration. In both cases there is either a direct, or an indirect, competition for the energy needed for carbon fixation, cellular metabolism or nitrogen reduction. Of particular significance is the fact that assimilatory nitrate reductase from most organisms has a fast turnover rate, being present in high levels only when the plants are in contact with nitrate.

Most higher plants contain a chloroplastic nitrite reductase which accepts electrons from photosynthetically reduced ferredoxin resulting in the production of ammonium ions. Traditionally it was assumed that ammonium ions were assimilated into glutamic acid in a reaction catalysed by glutamate dehydrogenase. However, an additional, more efficient pathway exists through the reactions catalysed by glutamine synthetase and glutamate synthase (Miflin and Lea, 1976). The first enzyme is localized both in the

cytoplasm and within chloroplasts, whereas the latter is situated mainly in the chloroplasts. Once again there will be competition for both energy and reductant between these enzymes and CO_2 fixation processes.

In the case of nitrogen reduction, the basic metabolic requirements are: a strong reductant; a source of energy, and low oxygen concentration. The enzyme complex known as nitrogenase catalyses the overall reaction

$$N_2 + 3XH_2 + 6ATP \longrightarrow 2NH_3 + 3X + 6ADP + P_1 .$$

This enzyme is once again a multi-subunit metal containing protein. The larger component, molybdoferredoxin, has four subunits and contains Mo, non-haem iron and sulphide, whereas the smaller contains only iron and sulphide.

The growth of legumes as a ley can be attractive as a biological source of nitrogen, as is the cultivation of N_2 fixing trees such as *Leucaena*. However, the position as far as grain legumes is concerned is more complex. During nitrogen fixation between 46 and 76 per cent of the photosynthate transported to the roots, which represents from 19 to over 40 per cent of the net photosynthesis, is lost as respired CO_2. Hence, there is significant competition between the use of carbon for growth and as an energy source for the fixation of nitrogen. This competition may become even more significant during the period of seed set and pod filling, and may result in a rapid drop in the rate of nitrogen fixation during the very period that the plant has the greatest need for nitrogen. The second problem is that the application of combined nitrogen to the soil reduces the ability of the *Rhizobium* to fix nitrogen. Hence, if inorganic fertilizers are applied to field crops grown, for example, in association with *Leucaena*, the potential benefit of nitrogen fixation may be only partially realized.

A similar decrease in the ability to fix nitrogen is seen in the free-living species such as *Azotobacter* when treated with combined nitrogen. However, effects of such organisms on plant growth cannot be associated with nitrogen fixation alone. In part the effect of these soil organisms may also be attributed to the production of chemical compounds with 'growth-substance-like' activities. In addition, there is evidence that compounds produced by *Azotobacter* via association with root surfaces are antagonistic to the growth of pathogenic fungi. Hence, in addition to contributing to the nitrogen economy of a given ecosystem, such bacteria may improve growth by suppressing deleterious fungi. And, at the same time, the stimulated growth due to the plant growth hormones can strengthen the plants making them, in some cases, less susceptable to infection. There is also the possibility that such bacteria assist in the mobilization of phosphate although, in general, such activity is of more importance when associated with the mycorrhizal fungi.

Mycorrhizae:

Most plant species, and trees in particular, are dependent to varying extents on their association with mycorrhiza, which assist the plant in the assimilation of phosphorus, potassium and other essential nutrients. Again, there is evidence that

these fungi can protect the host plants from attack by disease organisms.

The problem in understanding their actual contribution is similar to that with the nitrogen fixing bacteria. In the absence of applied fertilizer, improved plant growth is seen upon inoculation of sterile soils with such bacteria. However, application of phosphate, for instance, reduces the ability of these fungi to assimilate this nutrient. Again, in similarity to nitrogen fixation by symbiotic *Rhizobium*, the symbiotic fungi do exact a toll from the hosts by diverting carbon compounds to their own use. In some cases over 50 per cent of the carbon diverted to the roots may be used by the fungus, which in turn may decrease the extent of plant root growth.

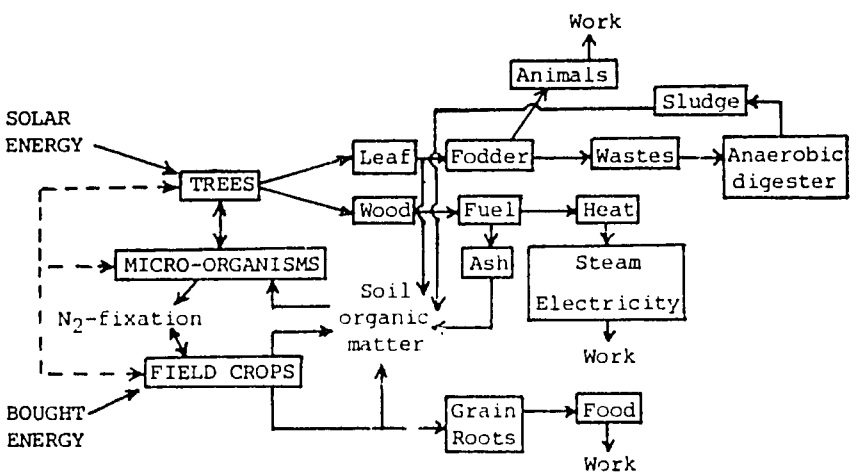


Fig. 4. Notional integrated agroforestry system for producing food, fuel and fodder.

INTEGRATED SYSTEMS

Some aspects of an integrated agroforestry scheme for food, fuel and fodder are given as an example in Figure 4. A certain amount of energy will be trapped by the system, which may be removed, and subsequently released and used for work (mechanical, human or animal), with the resultant eventual release of carbon dioxide. The amount of material which can be harvested from the system will depend on the amount of non-solar energy inputs, in terms of chemicals or tractors, for example. In the absence of such inputs the total amount of material which can be removed from the system is limited to only a percentage of the total annual biomass increment. The problem is that such systems are complex, and skills and training needed to understand them diverse. Relevant information is poorly documented and widely spread. What is needed are detailed studies of the energy and material flows in such systems. Obviously information concerning the physiological aspects of the plants in such systems is of particular value. But of equal importance are considerations of the demand which may be put upon such a production system in terms of the energy

and materials required by any given country or region, so that resources and demands may be wisely integrated.

At the physiological level the particular areas of research peculiar to agroforestry must be those resulting from the interaction (mainly chemical in nature) between the three living components: trees, field crops and rhizosphere. Such interactions are poorly understood, even in relation to single species of higher plants and specific genera of micro-organisms. The complex nature of the agroforestry ecosystem increases such problems. However, a parallel may be drawn between agroforestry and the 'organic farmer' in developed countries. In general, studies on soil nutritional status in such systems indicate a deficiency of nitrogen, potassium and phosphate. In particular, the required nitrogen input is not met unless the farmer also produces animals, such as chickens, which are fed on a protein-rich diet imported onto the farm. The status of such nutrients within agroforestry systems would appear to be a key research issue.

IMPLEMENTATION

The need for trained scientists

On the basis of our experience in organizing and running UNESCO-sponsored training courses in 'Bioproductivity and Photosynthesis' several problems emerge in relation to plant physiological research in the developing countries. In general, the provision of the basic tools and instrumentation for field and laboratory work does not seem to be a problem. The trouble lies with having a sufficient number of people who understand how it works, how it may be calibrated, and what to do if it goes wrong. In many areas the emphasis quite often appears to be misdirected, in as much as attempts are made to repeat fundamental research aimed at primary reactions, often using plants which are not native to the area, and which are grown with difficulty in controlled environments. Furthermore, such is the respect for the existing literature that very significant differences in the behaviour of tropical plants and micro-organisms are often overlooked in an attempt to repeat published work. Hence it is not enough just to define the problems in agroforestry, attention must also be given to attracting a greater number of suitable, trained people to such vitally important work.

Underlying problems

It is one thing to propose development schemes for biomass energy and agroforestry, but another to finance and implement them. Very often there are known technical options for solving problems, or at least some knowledge of how they could be solved, but what is lacking is the manpower and infrastructure to accomplish the tasks. Only a sustained effort plus adequate funding by both national and international organisations can overcome this situation.

Some points made in another context (Hall, 1982) seem worth repeating here since they are especially relevant in the present context.

Prestige. A top-level commitment on the part of those involved

has to be obtained in order to ensure any success in the long term. A major problem here is that agriculturalists, foresters, and even regional developers, often have a relatively low prestige and recourse to only limited facilities in many countries. It can be difficult, therefore, to persuade people of adequate calibre to make their main commitment to implementing regional energy or agroforestry schemes. This requires a change in attitudes at the highest level.

Incentives. A problem that regional developers often have is that their appointments are considered 'hardship' posts, and therefore undesirable. They are very often lower paid, with fewer privileges to go with the job. The opposite is required and support in the form of housing, schooling and, especially, adequate transport is mandatory.

Training. What is needed here are not so many high-level scientists but rather an adequate number of extension workers, engineers, agriculturalists, and foresters who are brought together to work in a practical way as a multidisciplinary team. Such people are needed immediately as well as for long-term developments so that training must be taken into account as a prime requirement for development. A continuing commitment to training, both prior to service and in service is required. Besides the regular educational and technical establishments, philanthropic and community organisations should be used to the fullest extent, since they often have useful local expertise and knowledge which can help.

Infrastructure. An adequate infrastructure is essential for the proper development of renewable energy resources, including agroforestry applications. An adequate number of full-time career positions is a prerequisite for attracting the required quality of people in all types of relevant jobs. This is especially important where the returns, in terms of productive effort, can take five to ten years.

Monitoring and feedback. During the implementation phase of a project it is essential that monitoring of progress, and the attitudes of the people and their local leaders, are continuously assessed. Immediate feedback should be available to the regional planners and others involved in implementing the schemes who can then adapt to changing circumstances. Such feedback should be part of any project from the outset.

Demonstrations and timing. In such schemes the most difficult stages are the first few years, because governments and development agencies usually want immediate answers, and these are not always available. Therefore provision of demonstration exercises and a realistic timing should be built into any scheme from the outset, and the expectations should not be too great. Those involved should have employment, and possibly some other form of income during the initial stages. Schemes which are well integrated into the local patterns of work and social habits will obviously be most acceptable and, in the end, most fruitful.

Implementation requirements. When the foregoing points are recognized, and can be met, the main requirements of successful implementation are:

- Involvement of local people, local expertise and artisans, entrepreneurs, creditors and leaders.
- Political, public, law, bureaucratic and media involvement and co-operation.
- A continuing commitment by leaders at international, national, regional and local levels.
- Incentives such as credit, guaranteed purchase and salaries, especially in the initial stages.

Only if these conditions are met is it likely that renewable energy/agroforestry schemes can be brought to a successful conclusion.

REFERENCES

Anon. (1979). "A Survey of Biomass Gasification." Vol.1. "Synopsis and Executive Summary." SERI, Golden, Colo., USA.

Anon. (1980a). Alcohol production from biomass in the developing countries. *World Bank Paper*, Washington D.C., USA.

Anon. (1980b). Energy in the developing countries. *World Bank Paper*, Washington D.C., USA.

Biomass for Energy (1979). Conference (C-20). UK section, The International Solar Energy Society (UK-ISES), London, UK.

Brown, L.R. (1980). Food or fuel: new competition for the world's cropland. *Worldwatch Paper* 35. Worldwatch Institute, Washington D.C., USA.

Coombs, J. (1980). Renewable sources of energy (carbohydrates). *Outlook on Agric.* 10, 235-245.

Grenhall, U. (Ed.)(1976). Environmental role of nitrogen fixing blue-green algae and asymbiotic bacteria. *Ecol. Bull.* No.26. Natural Science Research Council, Uppsala, Sweden.

Hall, D.O. (1980). Renewable resources (hydrocarbons). *Outlook on Agric.* 10, 246-254.

Hall, D.O. (1981). Put a sunflower in your tank. *New Scientist* 89, 524-526.

Hall, D.O. (1982). Regional development assisted through local renewable energy resources. *In* "Natural Resources and Regional Development: The Semi-arid Regions Case" (E. Campos-Lopez, ed.) Westview Press, Boulder, Colo., USA. (In press.)

Hall, D.O. and Coombs, J. (1979). The prospect of a biological-photochemical approach for the utilisation of solar energy. *The Watt Committee on Energy Report* No.5, pp.2-15. London, UK.

Hewitt, E.J. and Cutting, C.V. (Eds)(1979). "Nitrogen Assimilation of Plants." Proc. 6th Long Ashton Symp. Academic Press, London.

Miflin, B.J. and Lea, P.J. (1976). The pathway of nitrogen assimilation in plants. *Phytochem.* 13, 873-885.

National Academy of Sciences (1980). "Firewood Crops." National Academy of Sciences, Washington D.C., USA. 237 pp.

Palz, W., Chartier, P. and Hall, D.O. (Eds)(1981). "Energy from Biomass." Proc. 1st E.C. Conference. Applied Science Publishers Ltd, London. 982 pp.

Siren, G. (1979). Wood fuel experiments in Sweden. *In* "Biomass for Energy" pp.26-29. Conference C-20, UK-ISES, London.

Smith, N. (1981). Wood: an ancient fuel with a new future. *Wordlwatch Paper* 42. Worldwatch Institute, Washington D.C., USA.

Steinbeck, K. (1981). Short rotation forestry as a biomass source: an overview. *In* "Energy from Biomass" (W. Palz, P. Chartier and D.O. Hall, eds), pp.163-171. Applied Science Publishers Ltd, London, UK.

DISCUSSION

BRISCOE - Is there any promise for alcohol production from starch or sugar using a 'low' temperature method; for example solar power?

COOMBS - On a large scale, commercially, we need to make the process energy-efficient. Which means efficient use of fuel by, say, generating steam to turn a turbine to make electricity which drives the rollers to crush sugar cane, and also provides the low temperature process steam. On a small scale it is possible to crush the cane using wooden rollers using oxen, then ferment and use a solar still, but the yields of alcohol will be low and the energy efficiency very low.

LOOMIS - The overall energy requirement for ethanol processing is roughly equal to the energy available in the ethanol.

HUXLEY - Agroforestry systems involve complex mixtures of plants. Can we really apply management techniques which are aimed at diverting crop growth and development into particularly efficient *biochemical* pathways?

COOMBS - We should at least keep these opportunities in mind, especially where the crop is limited by nutrients. For example, with starch as the plants' end product more of the gross photosynthate is recovered than for protein synthesis.

LOOMIS - There may be two other approaches which can be made: (a) oil crops for diesel fuel, and (2) pyrolysis on a small scale. But in the former the problem is low yield per hectare, and in the latter the inefficiency of the process when done on a small scale.

COOMBS - There certainly is a place for small pyrolysis units, for example to provide fuel for internal combustion engines.

RAINTREE - How much evaluation has been done to substitute tree crops for starchy agricultural crops in alcohol production, for example by using *Prosopis* spp.?

COOMBS - There has been a study of *Ceratonia* (carob) in the Mediterranean region. The fruits contain 15 to 20 per cent sugars which can be extracted for food and/or confectionary uses, and could be used for alcohol. The problem can be the economics of harvesting tree fruits (pods) when these do not fall off, and the trees may be widely spaced or on inaccessible slopes, for example.

RAINTREE - Some stands of particular *Prosopis* spp. will give up to 20 mt of dropped pods per hectare.

LOOMIS - There is a problem using *optimum* figures of yields, and /or optimum efficiencies of processes. Some very unrealistic totals can accrue.

STEPPLER - You mentioned that we can get a much higher (up to 10 times) production of ethanol from sugar cane than oil from any oil crop. Can you give some actual figures you used?

COOMBS - I estimated 75 tons of sugar cane per hectare per year (close to the world average) which would give 125 GJ per hectare per year. The questions are, really:

- what is the yield?
- what is the net output?
- what is the energy ratio?

Oil crops give a good energy ratio, as we do not have to use so complicated a production process. But most systems such as sunflower, with which I am familiar, give a low yield per hectare. So that the energy gain is about 10 GJ per hectare per year. However, the oil palm system may give higher yields, but I have not looked at this in detail.

ODERA - Gasifiers and anaerobic digestors are being used in Kenya. Also, one should remember that the latter can return organic matter to the soil.

COOMBS - You have to work out the whole budget. Are you taking out carbon from the ecosystem? For example, a digester will lose carbon through carbon dioxide but the nitrogen content in the system can increase, so you may be returning nitrogen but *not* carbon to the system. Sludge is high in protein and this could be used for animal feed for meat production, then even less nitrogen is returned to the soil.

· 151

Understanding Agroforestry Systems

COMMENTS ON AGROFORESTRY CLASSIFICATIONS: WITH SPECIAL REFERENCE TO PLANT ASPECTS*

P.A. HUXLEY
International Council for Research in Agroforestry,
Nairobi, Kenya.

ABSTRACT. A structural process for designing classifications for particular purposes is suggested. Clearer conceptions of the spatial and temporal patterns involved in various forms of agroforestry land use are needed if they are to be adequately classified. The chronology of plants occupying land is related to the *sequence* of crop species and *succession*, or the occupancy of the land itself. Space utilization must take into account sole, mixed or zonal cropping systems. A standard terminology that will encompass all forms of land use is proposed.

INTRODUCTION

Commentaries on world agricultural systems (for example, Duckham and Masefield, 1970; Grigg, 1974; Ruthenberg, 1980) include detailed accounts of perennial cash crop systems and/or shifting cultivation with planted tree fallows. The role of woody perennials in many other kinds of agroforestry systems is either omitted or scarcely mentioned, however. Existing classifications of agricultural land use systems are, in any case, inadequate for agroforestry because they fail to encompass the greater dimensions of space and time needed. While forestry classifications do not offer sufficient complexity.

If we are to consider agroforestry land use systems analytically there is a need to have a clear conception of the broader spatial and temporal references involved. This becomes particularly important when considering systems analysis procedures. Furthermore, in order to compare *all* types of land use systems a common set of references is required. It must serve for tropical peasant farming where different cropping schemes may be arranged no more than tens of metres apart, as well as for plantation forestry, where the scale may in kilometres.

---

* Based on an ICRAF 'in-house' paper of August 1979 which was circulated prior to the meeting.

Similarly, any common scheme has to deal with within season cropping lasting only months, as well as with rotations of woody perennials, the individual steps of which may each take over half a century.

The ideas presented in this paper are put forward as examples of what has to be more fully explored, with some suggestions for consideration.

TOWARDS CLASSIFYING AGROFORESTRY SYSTEMS LOGICALLY AND COMPATIBLY

Classification schemes for agroforestry land use systems must be able to include the necessary wide range of temporal and spatial scales. And they have to accommodate a logical way of grouping key factors on which the primary and secondary production of such systems will depend, as well as indicating how the system is managed.

Types of classification

Sets or subsets of information, in this case descriptions and data concerning agroforestry land use systems, can be assembled in several ways to facilitate data storage, extraction, description and comparison. If data are logically hierarchical it may conveniently be assembled and stored in this form. However, such a scheme is enormously cumbersome to reorganize if a new need, requiring a new access approach to the stored data, is required. Assembling descriptive information and/or numerical data in a network form allows a greater flexibility in deciding, or changing, the ways that data items can be related to one another. A relational arrangement, in the mathematical sense, may be an excellent way of storing and retrieving data about agroforestry land use systems, but it is less likely to be helpful in classifying them for practical purposes. Simple hierarchical schemes have been proposed by Torres (1983) and a more complex combination of categories, based on sets of agroforestry techniques, by Combe and Budowski (1979), later modified by Wiersum (1980).

Generating compatible classifications

Any classification is of value only in as much as it facilitates inductive statements, or conclusions, about particular cases in relation to general laws or taxonomic concepts. To be of practical use a classification must be easily understood and readily handled. In an agroforestry or general land use systems context, the concepts dealt with must cover both biological/environmental/physical *and* social/economic/management elements. These complexities may not be comfortably assembled in just a single classification scheme, any one of which could be constructed in order to serve a different purpose. If a parallel series of classifications is to be made it could be helpful to have them originate from the same structural process (see Figure 1).

Any scheme of classification should start from the concept of the 'proto-agroforestry' land use system: a simple unit consisting of a woody perennial, an agricultural crop species (woody, herbaceous or a grass), and man. Figure 1 indicates a process whereby practical classification schemes can be assembled

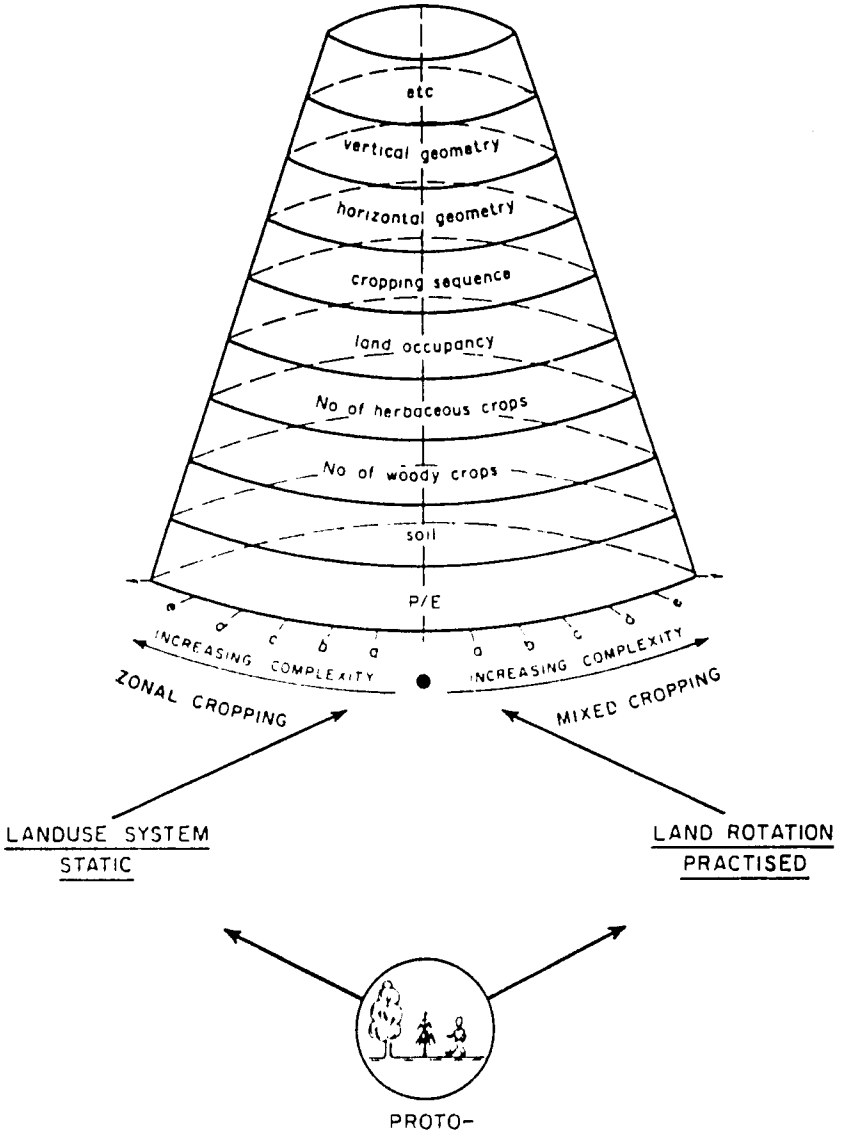


Fig. 1. Steps towards classifying agroforestry systems. From 'proto-agroforestry' (woody perennial, crop plant, man) a first major step is to specify whether land rotation is practised or not. Then, within each of these initial categories, to indicate whether the lands is managed under a mixed or zonal cropping scheme. Subsequently a hierarchy of other characteristics can be assembled (the priority ranking, from the bottom upwards, will depend on the purpose of the classification), indicating for each the level of complexity involved at the particular site, and in appropriate steps (*a*, *b*, *c*, and so on) for each characteristic. In such a way the components for a classification scheme can be grouped and compared, and their relative importance evaluated. (Amended from original 'in-house' paper, 1979.)

to suit particular purposes. For example, with an emphasis on biological components, or on management, and so on. Animals may be included as secondary producers. Two basic categories designating land use / land management have been chosen to form initial (hierarchical) steps. Three-dimensional schemes can be useful, at least to help display the alternatives (Huxley, 1972; Spedding, 1975) — this is done in Figure 1 — taking 'increasing complexity' as the third-dimensional category for each of a prioritized list of characters that need to be considered. Any specific outcome may be directed towards either an hierarchical or a network type of classification system.

In Figure 1 the two initial steps in classification are: first, whether land rotation is practised or not. For example, cropping may be followed by bush fallow, or individual cropping patterns may be rotated. Second, is a management decision one which affects the whole organization of a land unit; that is whether the spatial arrangement of crop components is zonal or mixed. Zonal arrangements can be, for example, alley cropping, strip cropping or some other geometrical arrangement whereby the crop components are separated within the unit of land being cropped, although to some extent they still interact biologically or management-wise. For example, litter or residues can be transferred from one to the other.

Thereafter biological/physical/environmental and social/economic/management characteristics can be categorized in any logical way and, within each, *in order of increasing complexity*. The arrangement of these steps will be the same in any one classification, but they could be rearranged, omitted, or added to in other classifications made for different purposes. For example, systems can be categorized according to a series of factors which relate mainly to their primary production potential. That is according to the following.

- The level (or range) of soil fertility.
- The rainfall/evaporation ratio (periodicity and probability).
- The number of woody components.
- The number of agricultural crop components.
- Land occupancy.
- The cropping sequence.
- The horizontal geometry.
- The vertical geometry.

Or, again, according to management characteristics.

- Inheritance and land tenure.
- Level of inputs in terms of labour, skill, machinery.
- Land unit size (and social/economic factors related to this).
- Access to capital.
- Need to obviate risk/uncertainties.

And so on.

Another agroforestry classification might be based on a mixtures of these. Whatever is chosen as the set of basic variables they need to be ranked, and the structure of actual systems categorized in terms of the increasing complexity involved in each.

Terminology

No set of common terms exists at present that will completely serve for all forms of land use, whether small- or large-scale, or short- or long-term. And there is probably little to be achieved by trying to establish a new set of definitions. The terms in common usage by agriculturalists and by foresters relating to area, for example, 'field', 'plot', 'block', 'zone' and so on, may suffice, although each of these can be used to mean something different under different circumstances. A glossary of terms used in agroforestry is certainly needed, with cross-referencing of all comparable terms at present in use. Many terms used for different types of crop mixtures, such as multiple, inter-, relay, and mixed cropping are, certainly, now well understood (for example, see Beets, 1978).

MAJOR CONSIDERATIONS OF TIME

In agroforestry systems the time dimensions can be particularly complex. They must relate to the life cycle or economic spans of the plant species involved, and hence the phenological events within them; to the management practices carried out from planting to final harvesting in multiple crop systems; also to the sequence of cropping on any unit of land which will involve short-term herbaceous species and long-term woody ones.

Multiple cropping schemes on the same unit of land may involve many crops a year. At the other extreme, shifting cultivators in moist, lowland tropical forest can clear previously cultivated 'forest fallow', so as to replant agricultural crops only after 30 or 40 years or so. And the cropping phase may last about four or five years before the land is allowed to revert to natural secondary forest again. Or it may be planted to a selected woody species or mixtures of species. Where agricultural rotations on whole fields are still practised, this may involve phases of up to several years with the same crop, especially with grass leys.

Cropping period

Agroforestry involves multiple cropping in which at least one woody perennial species is involved. In considering a chronological order of events, planting or sowing, and final harvesting and clearing, form natural limits. Within this will be a juvenile and a mature phase. The whole can be designated as the 'cropping period'. For perennial species this is not necessarily the same as the life span, because they are seldom left, either in agriculture or in plantation forestry, to reach an uneconomic stage. Particularly with perennials, either sequential or partial harvesting is possible. Or a significant harvest can be taken at regular or infrequent intervals, as can happen with some fruit harvesting or the lopping of fuelwood and/or building poles. Terms such as 'ratooning' or 'coppicing' are used to describe the more regular forms of harvesting for agricultural crops or trees.

Sequence and succession

In considering the chronology of plants occupying land there are

two conceptual comparisons to be made — *sequence* and *succession*. The first refers to the crop species, the second to the occupancy of land itself.

Sequence is the time course of events among crop* components utilizing the same unit of land. That is a designation of the patterns of planting, growing and harvesting with respect to each other. This can be described as 'co-incident', 'concomitant', 'overlapping' (of which the extreme case is 'relay' cropping), and 'interpolated'; as shown diagrammatically in Figure 2. Where more than two species are combined, each will stand time-wise in relation to another in one of these ways.

The other comparison is in relation to the occupancy of any unit of land, and the successive way in which it is planted or sown. A single crop species, or a sequence of different species, whatever the real time of the cropping periods involved, may occupy the same unit of land either 'intermittently' or 'continuously', depending on whether or not the land is left vacant for any reason between planting or sowing successive crops.

Continuous systems assume only that there is a virtually unbroken succession of either the same or different crops. This occurs, for agricultural or horticultural species with a short life cycle, only where there is a continuously favourable environment. For example, in the lowland humid tropics, or in partially controlled environments such as with irrigated crops and in greenhouses. Species with longer life cycles, spanning years, can more readily be planted at an appropriate season, even where there is an unfavourable climate for part of the year. That is they are planted successively, and can occupy the land continuously.

These expressions of succession refer to a characteristic of the way land is used but, because the removal of a crop canopy and exposure of bare soil can, in the tropics and subtropics, lead to extremely rapid soil degradation, it is probably better to define 'continuous' and 'intermittent' in real time, and not relative to the length of, say, the maximum cropping period involved. Figure 3 gives some examples of crop successions with different crop sequences involved.

MAJOR CONSIDERATIONS OF SPACE UTILIZATION

Crop geometry

Land can be planted or sown to a single crop (sole cropping). Or to more than one species, which can then be arranged in some form of mixture; or the species or species mixes can be clustered into zones. These zones might take the form of strips of similar or differing widths; or of some other geometric arrangement, such as a chequerboard or diamond pattern.

There are a number of integrating areas in all classifications relating to plant associations or land use, however, For example, a microzonal agricultural system, such as 'alternate row' cropping, is merely more spatially regularized than a mixed cropping one in which the individuals of different plant species are sited in an irregular fashion (but seldom spaced randomly).

---

* The term 'crop' is used here in its widest sense to incorporate forbs, grasses and woody perennial species.

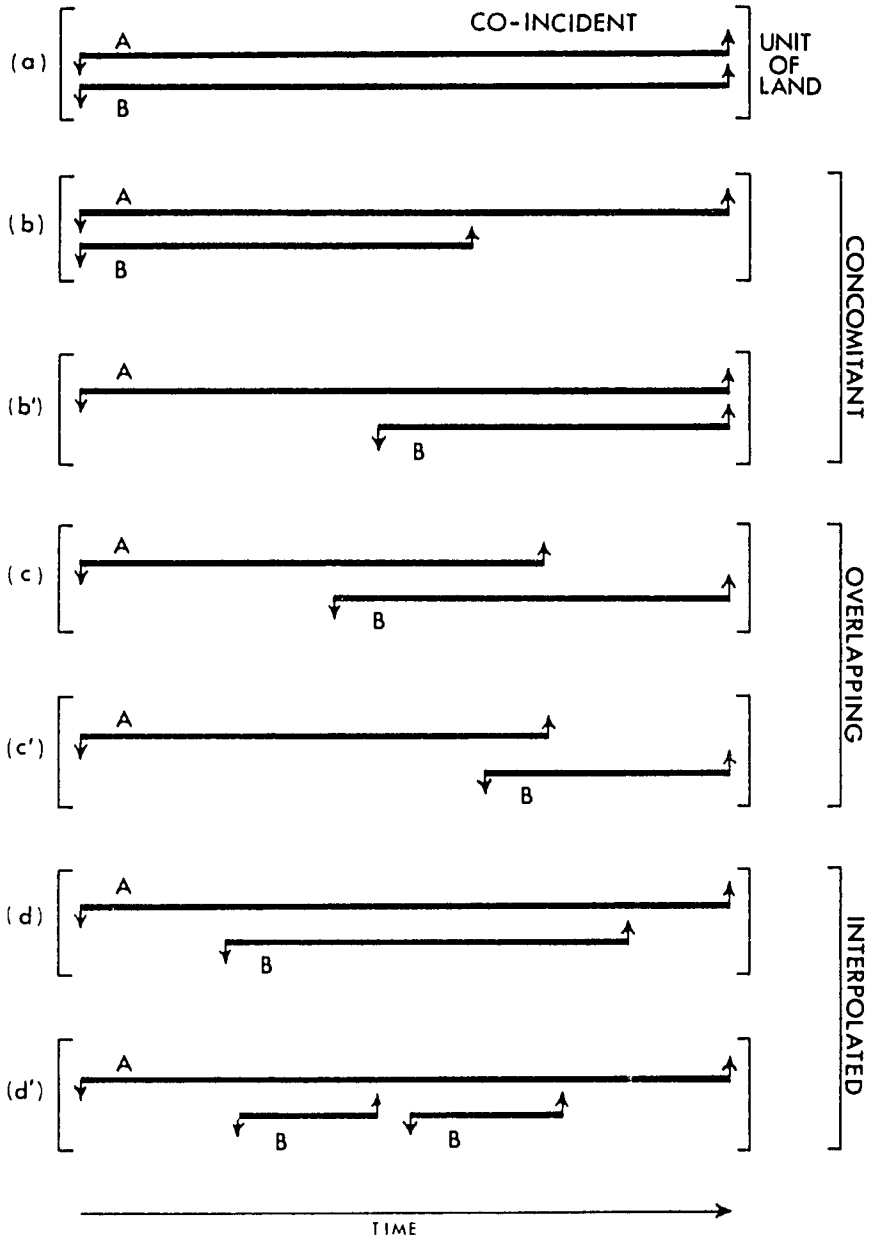


Fig. 2. Cropping sequences: (a) co-incident; (b) and (b'), forms of concomitant sequences; (c) and (c'), forms of overlapping sequences and (d) and (d'), forms of interpolated sequences. For more than two component systems the individual species making up pairs of crops relate to one another in the same way. ↓ = sowing/planting. ↑ = harvesting/clearing.

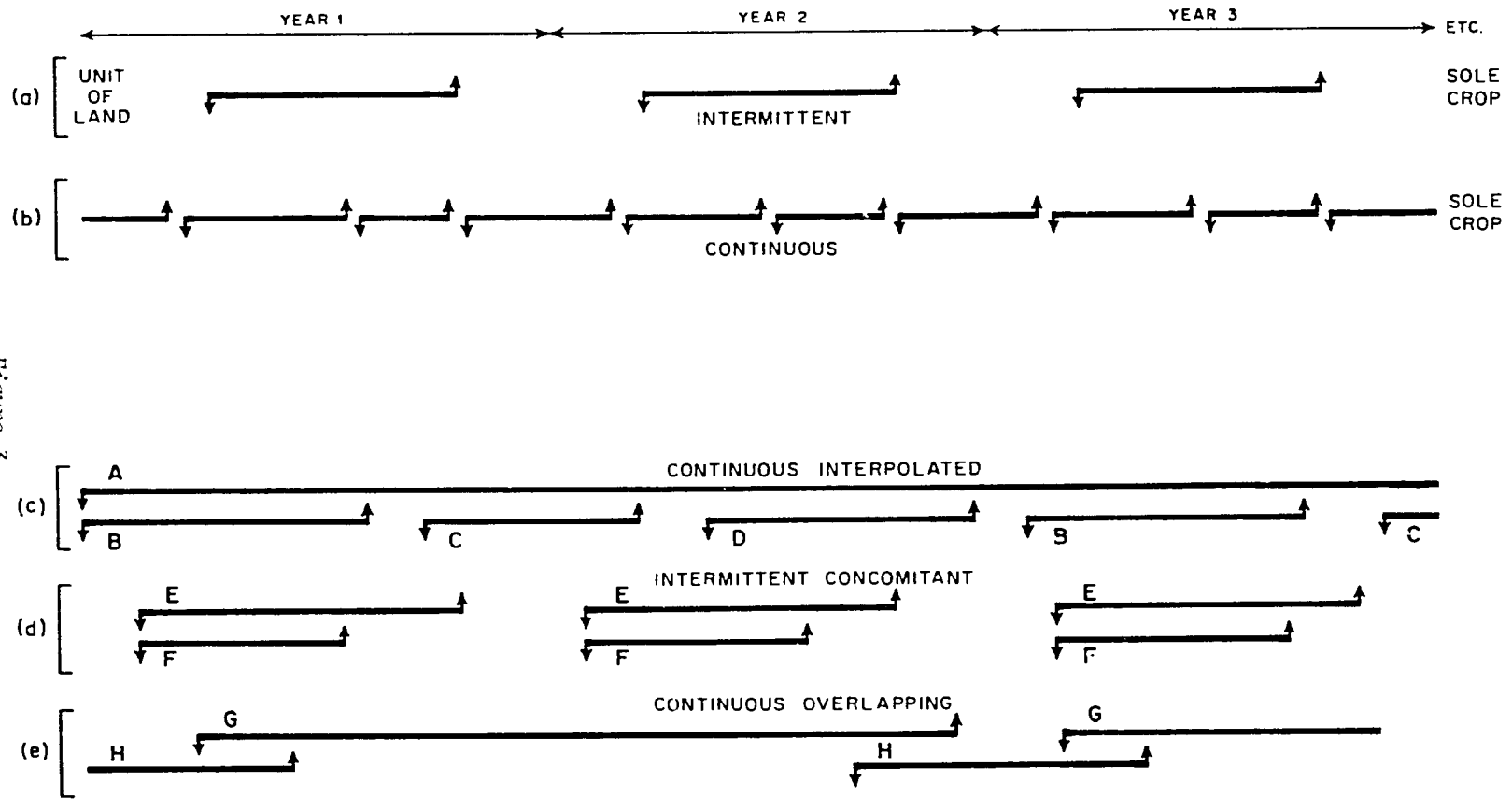

YEAR 1
YEAR 2
YEAR 3
ETC.
(a)
UNIT OF LAND
INTERMITTENT
SOLE CROP
(b)
CONTINUOUS
SOLE CROP
(c)
CONTINUOUS INTERPOLATED
A
B
C
D
B
C
(d)
INTERMITTENT CONCOMITANT
E
F
E
F
E
F
(e)
CONTINUOUS OVERLAPPING
G
H
H
G

Figure 3.

Another problem is to differentiate between macrozonal and sole cropping systems, as this depends on defining the units of land and differentiating between a 'zone', as the term is used here, and a 'field'. This raises a basic question: 'How best do we define 'area' in order to encompass the huge range of actual dimensions involved?' when considering, for example, tropical peasant farming, temperate or tropical plantation agriculture, and tropical or temperate forestry. In all these cases it is possible to define 'area' in the following way.

- In relation to the boundaries of the systems or subsystems as defined by the species or species mixture being grown *and their management*.
- In relation to the extent of the plant interactions of the species, or species mixtures involved.

Spatial units

Only three basic spatial units of area are needed. A 'primary land unit' (plot); a 'management boundary' (field) and the 'total area' (farm). The equivalent forestry designations might be 'stand' (or 'plantation'), 'compartment', and 'forest' (or 'block'). The objective is only to have meaningful divisions which will enable us to relate the parts of the systems under any one form of management to the whole, whatever the actual sizes may be. 'Regional areas' and 'ecological zones' obviously form larger divisions, but these are related to whole land use classifications, and not to units of land under individual management or control.

A fourth division is needed when looking at economic aspects because it is usual to consider common activities as an entity, or as an 'economic enterprise', whenever they are located within the farm boundary. For example, if a farmer grows a particular cereal crop the areas used may be either spatially continuous or separated within the overall confines of the total area. For economic purposes, therefore, such space used for a common purpose might be termed an 'enterprise area' usually consisting of one or more 'management boundaries' (fields).

The primary unit. In tropical subsistence agriculture, or in small-scale horticulture anywhere, this will be what is commonly called the plot. That is, a homogeneous area in which a common species or species mix, and a common form of management is being practised. For zonal systems in agroforestry, however, plots or zones might better be defined as 'those regular shaped

Fig. 3 (Opposite) Crop succession, or land occupancy cycles. Showing basic (a) intermittent and (b) continuous forms (upper part of diagram). Continuous succession will have not more than a few weeks' gap between harvesting/clearing and sowing/planting. Examples (lower part of diagram) have different numbers of plant components in the systems. Examples (c), from agroforestry, could be a tree species A interplanted with a succession of herbaceous agricultural crops B,C,D, B,C,D, and so on. Examples (d) and (e), from agriculture, could be respectively, maize (E), interplanted with cowpea (F), and cassava (G) relay planted with sweet potatoes (H).

areas between which, at any one time, the population of plants of different species, including at least one herbaceous and one woody one, interact in some way' and/or 'between the boundaries of which man or animals can readily move primarily produced materials'. The second part of the definition is needed to cover macrozonal systems in which the tree/shrub components are used for browse or woody mulch. For example, rows or plots of trees between which plots of agricultural crops, or grasses, are grown as in alley or strip cropping systems.

The management boundary. Individual 'management boundaries', which need to be ecologically homogeneous, will be the 'field' in agriculture or extensive horticulture. In intensive horticulture a greenhouse or a common set of greenhouses, or a single piece of land within a common boundary but devoted to growing one crop (or crop mix). In forestry, it can be a 'compartment' with any divisions into 'stands' or 'subcompartments', for example by firebreaks or paths, being the 'primary units' mentioned above. Any single 'management boundary' (or field) is not continuously or intimately management-related in any way with an adjacent area; although this does not preclude the transference of material on occasion. For example, dung or straw, as in older temperate mixed farming systems. 'Fields', as larger units, can thus be considered largely self-contained, whereas agroforestry 'zones', as smaller ones, will regularly interact with their neighbours in some way.

In much of forestry, as in large-scale temperate sole crop, or tropical plantation crop, agriculture the 'primary unit' or plot, is not fundamentally required; but it may be in existence as a convenient division for management purposes. For example, for organizing pruning or lopping, spraying, or for fertilizing more efficiently.

Total area. This is the largest unit referring to the whole farm or forest system being considered. It will be the total of all the smaller divisions ('fields' or 'blocks'), which may or may not be divided into primary units: 'plots' or 'zones' and it is the sum of the various enterprises. Clearly, there are cases where, for example, with some form of agricultural or horticultural co-operatives, or with certain types of state farming, whole farm groups interact or are directly managed in a unified way. Such larger conglomerates are readily designated without misunderstanding in an appropriate way related to their management or oganization, as are the 'regions' and 'ecological zones' mentioned above.

In describing individual systems, more substance and precision can be given to *any* definition by providing actual spatial dimensions. From what has been said above, however, it can be seen that no unified classification of the plant aspects of land use systems covering temperate and tropical agriculture, horticulture, forestry *and* agroforestry can be satisfied by simple, absolute, or even relative, dimensional statements. Boundaries of common management, cropping periods and their relations to one another and, in some cases, the dimensions of the interactions between different plant species must be taken into account.

In agroforestry the extent of the differences between these interactions in various systems is considerable because we can be concerned with a very wide range indeed of both herbaceous and woody perennial species being grown together.

REFERENCES

Beets, W. (1978). Multiple cropping research. *Span* 21, 114-116.

Combe, J. and Budowski, G. (1979). Classification of agroforestry techniques. *In* "Proc. UNA/CATIE Workshop on Agroforestry Systems in Latin America", pp.17-47. CATIE, Turrialba.

Duckham, A.N. and Masefield, G.B. (1970). "Farming Systems of the World". Chatto & Windus, London.

Grigg, D.B. (1974). "The Agricultural Systems of the World: An Evolutionary Approach". Cambridge University Press, Cambridge, UK.

Huxley, P.A. (1972). Appraising natural resources: a systems approach. *Span* 15, 8-10.

Ruthenberg, H. (1980). "Farming Systems in the Tropics" (3rd edn). Clarendon Press, Oxford, UK.

Spedding, C.R.W. (1975). "The Biology of Agricultural Systems". Academic Press, London.

Torres, F. (1983). Agroforestry: concepts and practices. *In* "Agroforesty Systems for Small-scale Farmers" (D.A. Hoekstra and F.M. Kuguru, eds), pp.27-42. ICRAF, Nairobi, Kenya.

Wiersum, K.F. (1980). Classification of agroforestry techniques. *In* "Outlines of the Agroforestry Concept", pp.14-16. Dept. of Tropical Sylviculture, Wageningen, Netherlands. Mimeographed.

173

14

THE DESIGN OF ECOLOGICALLY SOUND AGROFORESTS

R.A.A. OLDEMAN
Landbouwhogeschool, Wageningen, Netherlands.

ABSTRACT. The survival of all living systems requires cyclic change, and size is limited by the need to maintain organisation. A concept useful in agroforestry is to consider eco-units in this way and to attempt to understand the structure and dynamics of natural eco-units, through their successional stages, in order to rationalize the design and management of man-made 'agroforests'. Similarities between population structure and dynamic changes can establish an analogue between natural and artificial systems, and transformations can be effected by substituting more productive species for wild ones.

Using diagrams, design stages are noted and suggestions given for some examples in tropical humid climates which include complex mosaics of very small eco-units, such as the multistorey village forest and home gardens found in Indonesia. In dry or degraded tropical environments similar principles can be used in designing productive and sustainable vegetation units, but the extent of cyclic change is more restricted and successional patterns are less well known.

INTRODUCTION

Guidelines for the drafting of project proposals in the sphere of forestry and agroforestry nearly always refer to aspects of ecology; and in two principal ways. The first is the avoidance of undesirable side effects caused by natural forces such as inundation, erosion and pests. The second is the creation of possibilities to produce outputs with a lower-than-food priority such as fuelwood or the so-called minor forest products. However, no distinction is generally made between tree plantation and forest establishment, which are quite different things, and a hypothesis, implicit in many such guidelines, is that once 'solved' ecological problems do not exist any more. In the following pages we are going to try and make a more complete, and operational diagnosis of tropical forests and agroforests.

The ecological approach

The features of such ecosystems, which are sought after by human users of all categories, are the following ones. They should be durable, the economical term being 'a system with sustained yield'. They also should have buffering characteristics towards perturbation factors from outside. Furthermore, they should be perfectly adapted to local soil and climate and, finally, their production has to show a certain degree of diversity which will depend on their use.

In many instances the perfect example of a stable, well-buffered, adapted and diversified system is the local natural ecosystem; be it a forest, a tree savanna , a prairie or a tundra. All these vegetation types are living systems, adapted to specific sites and climates, as are the plants and animals functioning as elements within them. All living systems have a common dilemma. On the one hand their survival demands *stability*: the most enduring system does not change at all. But on the other hand, no system that lives does so without growth, that is, *change*. The biological answer to this dilemma is, of course, *cyclic* change. The nearer perfection a biological cycle the more lasting will be the living system which displays it. This lesson has been learnt by all successful agriculturists and foresters. Sustained yield, in an ecological sense, can only be obtained when the planting - to - harvesting cycles are perfect. Degraded

Fig. 1 (Opposite) Scale of the living systems, 'trees' and 'forests'. (*a*) Organs (leaf, axis). (*b*) Organ complexes (left to right: seedling, axis bearing leaves and flowers, unbranched palm). (*c*) Branched complex, each branch being an organ complex (left to right: Troll's model, eg. guava; each of Rauh's models, eg. mahogany; Massart's model, eg. nutmeg); these models* are hereditary and mostly express themselves well in saplings. (*d*) Reiterated complex, each spoon-like symbol represents a model-conform structure, trunk and branches; left to right: reiteration on curved trunk, as a replacement after damage, as watershoots, in crown expansion, and as root suckering, respectively. (*e*) First collective scale, the rejuvenation (= forest regeneration) unit: this small patch of forest is even-aged and started developing on the same surface. (*f*) Second collective scale: the age mosaic; this surface is covered by all developmental or age classes of one successional sere: A - seedling phase; B, C - sapling phases; D - transitional phase; E - mature phase (note roles of strongly reiterated dominating trees and shrubs against suppressed 'saplings', drawn as model-conform); F - decaying phase with underlying new rejuvenation unit. (*g*) Third collective scale: successional mosaic, including all age classes of all successional seres: I - pioneer trees; II - late pioneer (half-shadow); III - later successional stage, sometimes called 'climax'. From scales (*a*) to (*g*) systems always become more complex and have a tendency to become bigger and longer lived. A successional mosaic is sometimes larger than the site unit and then occurs in fragments throughout the landscape. Later successional seres always show smaller rejuvenation units. Figure very schematic, from Oldeman (1981).

* All tree models referred to are described by Hallé *et al.* (1978).

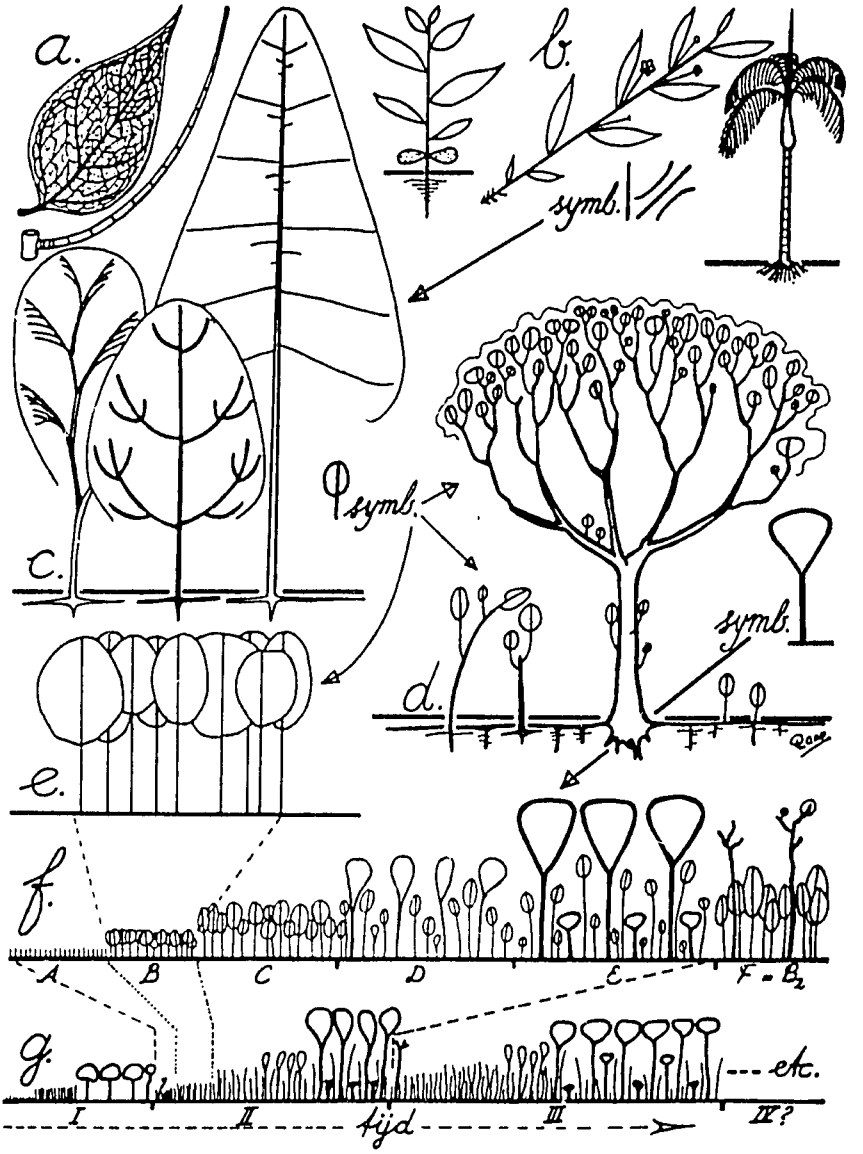


Figure 1.

agrosystems, tree plantations, forests or agroforests are the results of an ill-conceived or faulty cycle.

A second dilemma in any living system is that of organization versus size. Any particular biological growth programme can sustain, with population differences, only a limited amount of biomass. That is, the universal solution is division of biomass in adequate amounts, each to be managed by some specific set of biological instructions. This process is known as replication on the genetic level, as cell division in cytology, as multiplication in organisms, as reiteration in large trees, and as regeneration or rejuvenation in vegetation. These mechanisms are the basis of the universal existence of populations: as cells, tissues, organs, herbs, treelets, or trees. None of these exist alone as unique individuals.

Vegetation eco-units

The same can be said, although it seldom is, about vegetation units. A one-hectare field of eucalypts is not a unique phenomenon. It is a member of a population of such fields. They may be older or younger, or slightly smaller or bigger; just as one *Eucalyptus globulus* tree is part of a population of *E. globulus* the members of which have varying ages and dimensions. The term used is 'rejuvenation unit' or 'eco-unit', defined as *the unit of vegetation which started its development at the same moment and on the same surface*. Eco-units exist in numerous kinds, for instance a patch of forest growing where a single tree has fallen (a 'chablis'), a Caribbean pine stand, or a maize field. In natural ecosystems it is not always easy to delimitate eco-units from neighbouring eco-units, because of the existence of gradients between them (see Florence, 1981 for examples of chablis in Gabon). On the contrary, in artificial ecosystems, eco-units generally, are well separated by man-made limits. In the following pages eco-units are represented by graphical means; that is, by scale drawings, or by schematical diagrams derived from scale drawings. In the same way, populations of forest types, populations of successional stages (each including a population of eco-units), populations of 'climaxes' can be used for analytical purposes.

Figure 1 gives an outline of this reasoning, as described by Oldeman (1981). For instance, the organs (Fig. 1a) can be considered as 'integrated populations' within organ complexes (Fig. 1b). These organ complexes can live in their turn as free populations or as populations integrated within an organism of a higher order: the branched tree (Fig. 1c). At this level, trees branch according to a strict programme called the architectural model (see Hallé *et al.*, 1978). Model-conform trees may constitute free living populations, for example, young coffee plantations before they are pruned back. But model-conform tree-like structures may also form an integrated population originating from meristems within an organism of a still higher order, the large tree with model-conform crownlets (Fig. 1d). This is the largest individual organism. All living systems of higher orders are *collectivities* (a term used by Leibundgut) of different plants and animals, each of which is part of such an ecosystem, neither quite free because they are not built to survive outside, nor quite integrated because of movement and

seeding strategies.

The smallest ecosystem is an even-aged patch of vegetation, which started its development on some cleared, or partially cleared spot (Fig. 1e); it has already been defined as an 'eco-unit'. Such an eco-unit starts small and becomes big while developing its structure: a population of eco-units in different development phases is represented in Figure 1f. This kind of ecosystem is essential for agriculture, silviculture and agroforestry: their eco-units are fields or silvicultural stands, and the developmental series differs, according to its economical application, in duration, size and complexity. Now in the successional series, the eco-unit is different in successional Stages I, II, III ... etc. (Fig. 1g). The figure having been made for forestry purposes no eco-unit before Stage I has been indicated here. These preforest stages do exist and are herbaceous (a 'forb stage', Fig. 5): they are comparable to agricultural fields. Stage I contains fast growing treelets, lianes and some herbs, as analyzed in West Africa by Kahn (1981) and the authors he worked with (Guillaumet, 1978; de Namur, 1978; de Rouw, 1979, and others). Stage II is 'late pioneer' or 'pre-climax' forest which may live longer than a century. Stage III often is the last possible one in temperate regions. It can exist for several centuries.

This third successional stage, long-lived and often stable, is at the root of the original 'climax' concept, developed in North America by Clements and his school. However, there are sound indications that, in the humid tropics, more stages exist: Stage IV and, probably, a Stage V. From the herbaceous stages through Stage I, and up to Stage III, the eco-unit becomes progressively smaller. Herbaceous eco-units can be large-scale features of the landscape, Stage III eco-units start in forest gaps (chablis: see Oldeman, 1978a), caused by the fall of one or two trees. The minimum size for an eco-unit to develop is a one-tree chablis (one-tree gap). It is thought that differences between eco-units in Stages IV and V are determined not by the size, but by the shape or architecture of the gap. Wide, funnel shaped chablis stimulate another development, with different species, as compared with narrow, chimney shaped ones (see data in Florence, 1981).

The use of eco-units

Each different eco-unit invites human beings to use it differently. Herbaceous units grow up by means of plant species out of which agricultural crops have been selected. Pioneer forest yields fast growing trees, and some fruit producing species which are needed for forestry and fruit orchards, respectively. Later successional stages contain some fruit trees, but also many other species providing other products. These often are wrongly called 'minor forest products', from the viewpoint of wood-oriented human communities. For local populations, the wood may be rather less important than things like fibres from lianes (for example, rattans), medicinal products (many tree barks and roots), fruits and meat (game). According to van der Ent (pers. comm., 1981) these products number well over 10,000 in all in the world's tropical forests. The optimal uses of different eco-units in a successional sequence are indicated in Figure 2.

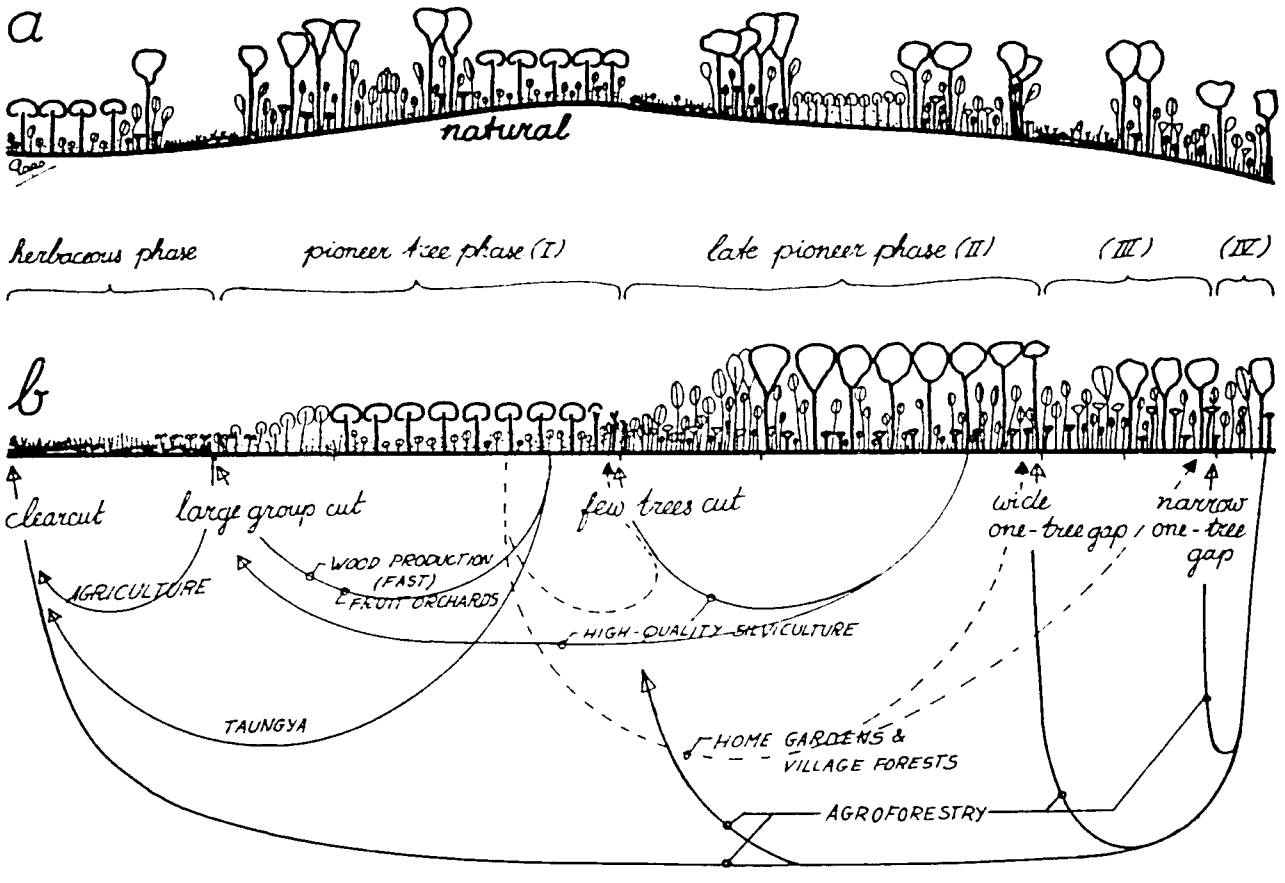

a
natural
herbaceous phase
pioneer tree phase (I)
late pioneer phase (II)
(III)
(IV)
b
clearcut
large group cut
few trees cut
wide one-tree gap
narrow one-tree gap
AGRICULTURE
WOOD PRODUCTION (FAST)
FRUIT ORCHARDS
HIGH-QUALITY SILVICULTURE
TAUNGYA
HOME GARDENS & VILLAGE FORESTS
AGROFORESTRY

Figure 2.

In reality, these eco-units do not occur according to such a sequence but are dispersed in space. They form a mosaic of different units in different growth phases, large and small, fast developing and slowly growing. In nature the dispersal of these units is mainly due to different growth and mortality rates.

The death of an eco-unit makes room for one or more eco-units to be established. In nature, dying of such units is ascribed to 'accidents' or 'disturbances'. In cultivated systems it is caused by harvesting. This is a crucial concept in establishing sound agroforests. The death of a large eco-unit generally means its fragmentation into smaller units. This is caused by the fact that such large even-aged volumes of forest (Stage I) are built by a population of even-aged trees. But the moment of death is not simultaneous in all these trees: the sound ones die later, the weak ones sooner. The difference between weak and strong may be genetic, there being either different pioneer species or different genotypes within one such species. It may also be caused by competition between trees, by abiotic factors such as the presence of rock at different depth, or by biotic factors such as parasites, diseases or the absence of certain mycorrhiza. Kahn (1981) describes how, in the Ivory Coast, on old abandoned shifting cultivation fields, some surfaces remain without trees and are covered by a blanket of lianes for long periods. Whereas other surfaces show only a light cover of lianes, under which long-lived tree species grow up. Still other patches are covered by short-lived pioneer trees rapidly building a forest architecture more or less like Stage I (Fig. 1g).

On the other hand, large surfaces of herbaceous vegetation can be recolonized first by shrubs, then by trees. This process also displays a splotchy pattern, as can be observed on the ancient meadows around Saül (French Guiana) which are now invaded by bushes of melastomaceous shrubs, in the middle of which some rare trees of bigger species are establishing themselves. The meadow in this way is being 'broken up' into smaller eco-units which, in their own time, build their own structure:

Fig. 2. (Opposite) Human use of successional seres. (*a*) Natural forest mosaic, schematic diagram; note eco-units of different sizes, with different frequency and of different architecture, the chablis (gaps) causing the mosaic to shift in a kaleidoscopic way. (*b*) Seeding - harvesting or planting - harvesting cycles in different land use systems; note the different surfaces of the harvested eco-units (compare Fig. 5), the simplicity of the 'classical' agricultural, arboricultural, silvicultural and taungya cycles, as contrasted to the composite ones in agroforestry and traditional village forestry. *Full lines*: rejuvenation, regression or 'regeneration' cutting (harvesting). *Dashed lines*: accelerated succession by anticipation, the appropriate eco-unit surface being supplemented by planting adapted plant species, a process which is stochastic in the natural forest mosaic.
The artificial character of the 'successional series' can be seen clearly; in reality every stage can succeed to every other including itself. All these natural processes together may be called sylvigenesis (Oldeman, 1974).

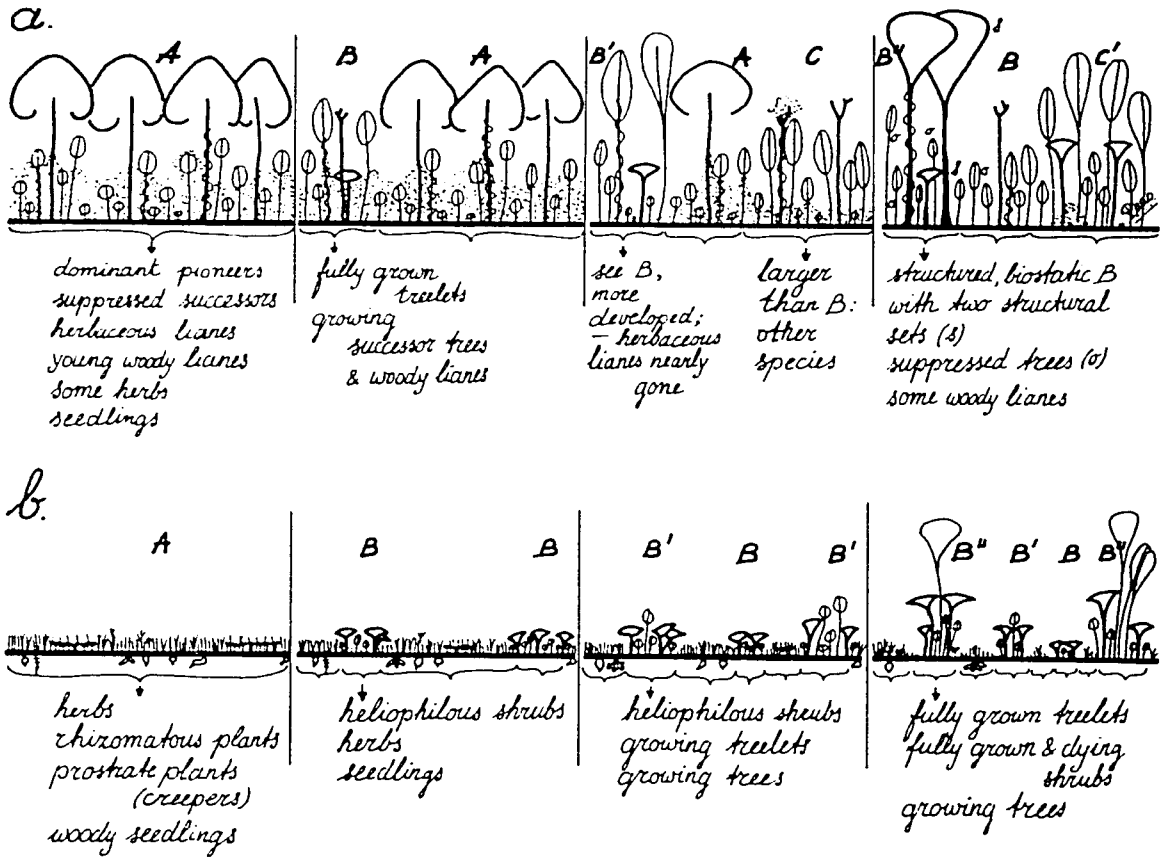

a.
A
B A
B' A C
B' B C'
dominant pioneers
suppressed successors
herbaceous lianes
young woody lianes
some herbs
seedlings
fully grown treelets
growing successor trees
& woody lianes
see B, more developed; – herbaceous lianes nearly gone
larger than B: other species
structured, biostatic B with two structural sets (s)
suppressed trees (o)
some woody lianes
b.
A
B B
B' B B'
B'' B' B B'
herbs
rhizomatous plants
prostrate plants (creepers)
woody seedlings
heliophilous shrubs
herbs
seedlings
heliophilous shrubs
growing treelets
growing trees
fully grown treelets
fully grown & dying shrubs
growing trees

Figure 3.

to be followed later by new eco-units of another kind which grow on the debris of the first ones. Both progressions — the fragmentation of monotonous early secondary forests and the patchy colonization of monotonous herbaceous vegetation by forest — lead to smaller eco-units belonging to more advanced successional stages.

Eco-unit dynamics

The death of forest patches is a perfectly natural mechanism which constitutes the motor of all vegetational dynamism. Some rules apply to the mortality factors which, most often, are operated by the fall of one or more trees.

- The older a forest the higher the risk that an accident or tree death takes place.
- Site factors, such as loose or shallow soils, exposure to wind, steepness of slopes, or earthquakes, can increase the frequency and size of eco-unit disappearance (Garwood *et al.*, 1979).
- The more chablis there are in a forest, the more tree crowns become asymmetric when growing into these gaps, and the more accident prone the trees become.
- On any site a statistically regular frequency exists of meteorological, biological and hydrological forest attacking factors on different scales, large-scale disturbance often being rarer than small-scale disturbances.

For all these reasons the resulting forest mosaic on any one site may be compared with a kaleidoscopic image: the same eco-units are always there at quite constant rates, but they are not at the same place from one year to the next.

The whole process from large-scale to small-scale eco-units has been summarized in Figure 3, with the characteristics of the plants which are needed to build each of these eco-units (see also Oldeman, 1978b, 1979a, 1979b). In general it can be said that up to Stages III or IV there is an increasing number of

Fig. 3 (Opposite) The breaking up of large-scale eco-units into small ones, in the context of the processes and structures shown in Fig. 2a. (For symbols see Figure 1.)
(*a*) Pioneer forest on rather large surface, breaking up into smaller units of later successional stages by differential dying of pioneer trees. Successor trees shown here growing with exaggerated speed so as to obtain easy visualization of differences in the fourth stage of the process. *Shadowed*: herbaceous lianes and creeping herbs. *Thick lines*: fully grown trees. *Thin lines*: trees with potential for further development. Biostatis: see Fig. 5 and text. Note potential for different plant types in different eco-units of varying ages; faunistic differences implicit. (*b*) Colonization of secondary savanna or meadow in a forest zone; for dynamics of ruderal vegetations see Ndiaye (1977). The large-scale herbaceous vegetation is broken up by the development of bush nuclei with shrubby heliophilous pioneers, among which some larger treelets and trees can develop later. Note root crop potential, existing only on unexhausted soils.

species involved in the correct functioning of the eco-unit, and that in later stages this number decreases. The peak number in a different stage depends on the specific site: Stage II may well be the richest, for instance, in less humid regions with more wind. This leads us to Figure 4, which represents the successional sequence from the most to the least hospitable environments. This may occur through climatic changes, for example, the inclusion of seasons with frost or drought, or be linked to soil changes, such as the occurrence of shallow, waterlogged, very light or very heavy soils. In any case where the environment becomes less hospitable the successional sequence is shortened; a fact which often has been observed but never completely explained. In Whittaker's terms Figure 4 would represent an ecotone, but on our figure no 'climaxes', but whole successions, are used as ecotone indicators. It is to be stressed once more that the successions in the diagrams do not exist as such, and are no more than an intellectual tool to help understand the uneven-aged, kaleidoscopic forest mosaic. Within this mosaic virtually every stage can succeed to every other stage including itself (Oldeman, 1978a).

PRINCIPLES FOR AGROFOREST DESIGN

Comparison with the local natural ecosystems can be useful for the design of new or improved agroforests aiming at higher durability and, whenever possible, also higher yields. Criteria then should be the architecture and growth dynamics of both agroforest and wild forest.

Analog and transformation methods

Recently, Hart (1980) has used this *analog* concept which depends on the use of similarities in population structure and dynamics between artificial and natural systems. More analogies constitute more reasons to think that the cultivation cycle is close to the natural cycle. The risk in this method lies in the infinite number of variables that may be considered, and their

Fig. 4. (Opposite) The successional mosaic, characterized by an abstract succession model, in increasingly inhospitable environments (top to bottom). (For symbols see Figure 1.) Note stem suckering and natural coppicing, which are forms of reiteration characteristic of less hospitable environments. Several examples checked in nature; quantitative proportions between different successional stages still remain approximative. In the lower three environments some kind of herbaceous succession has been suggested; this hypothesis should be checked (compare Descoings, 1976 p.122 ff.). *From left to right (top)*: eco-units smaller, then narrower. The disturbances which bring them into being become more frequent from left to right. Suppressed trees drawn as fine vertical lines. This schematic diagram should be worked out very precisely so as to create an ecological site reference framework, indicating what is possible in agroforest architecture and the dynamism for each ecological region. (After Oldeman, 1980a, modified).

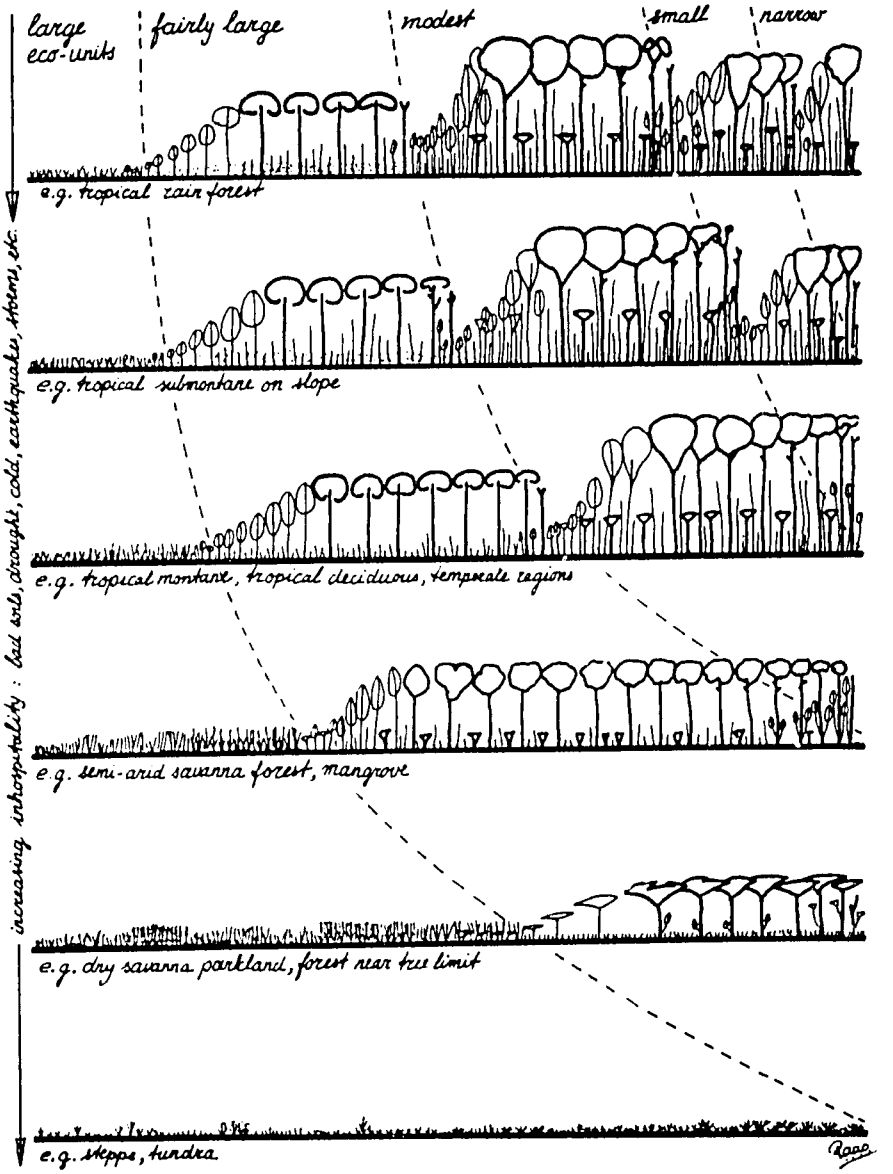

large eco-units
fairly large
modest
small
narrow
e.g. tropical rain forest
e.g. tropical submontane on slope
e.g. tropical montane, tropical deciduous, temperate regions
e.g. semi-arid savanna forest, mangrove
e.g. dry savanna parkland, forest near tree limit
e.g. steppe, tundra
increasing inhospitality: bad soils, drought, cold, earthquakes, storms, etc.

Figure 4.

frequent mutual dependence. Consideration of too few variables makes for superficial analog models. In many selective cutting systems for tropical rainforests it is, for instance, assumed that the cutting of trees over a certain diameter is analogous to their natural fall and, clearly, such an assumption will be unwarranted.

A second concept is that of *transformation*. The basis here is the structural analysis of collective units, such as the eco-units described earlier. Transformation may be effected by replacing wild species by useful species fulfilling the same functional and structural niche as their wild precedents. It can also aim at the transformation of structures while maintaining certain properties of the whole system. The risk of this method is the absence of *absolute* ecological identity between the behaviour of organisms: there always are small differences. Hence the balance of new structures has to be corrected over and over again, until it becomes self-equilibrating. Many transformed systems turn out to be unstable.

Both approaches of course are complementary as tools in the design of forests and agroforests. Agroforestry design needs both methods for different purposes.

When to use them

In regions where no natural vegetation is left, the basis for new designs can only be established by an analog model. Considering similarities between the region in question, as well as other regions with comparable abiotic environments. Successful agrosystems or agroforests from the intact region can then be imitated in the degraded one. Only afterwards can transformation analysis come into play, with a view to improving structures and species composition. On very degraded land, the only applicable analog should concern primary succession, followed by transformation to accelerate it.

On the other hand, in still intact regions, for example, where there are natural tropical rainforests, prudent transformation should be the first step, taking into account the processes and the architecture at the different scales mentioned before (Figure 1). Some transformations having been made, analog analysis becomes a useful tool to compare the result with the natural forest and with other agroforests in equivalent regions. Analogy here concerns secondary succession.

It should be noted that the succession concept used by Hart (1980) does not take into account the development of an eco-unit from young to old, as distinct from succession from early (big eco-units) to late (small eco-units) stages. In the development of a crop system, as represented in Hart's Figure 2 from beans to rubber over 50 years, a succession can be seen, but it could equally well be interpreted as the development of a single eco-unit belonging to one early successional sere, if all crop components were planted at the same time. This figure by Hart should be compared with Oldeman's Figure 2 (1979b). Taken together, they perfectly illustrate the complementary character of the two approaches.

Such a fine point may seem academic, but it should not be forgotten that ecosystem design will have to become a very refined business in order to succeed. Living systems are much

more complex than the most sophisticated industrial ones, and require a kind of biological engineering which can be compared to very advanced technological activities such as the designing of spacecraft.

AGROFORESTS FOR TROPICAL HUMID CLIMATES

Too often the humid tropics are treated as one homogeneous block with one ecosystem: *the* Tropical Rainforest! Descriptions at this level must essentially remain global and be based on averages. Rollet (1974) wrote one of the most rigorous approaches in this sense. His Figure 31 is an example. It concerns the 'total [mathematical] structures of different tropical formations', showing the 'mean pantropical curve for rainforests' of the number of stems per 100 hectares, in diameter classes of 10 cm, with its variation for different forest types: Venezuelan mangrove, Trinidad *Mora*-forest, Malaysian marsh forest, etc. Rollet uses the term 'architecture' in a statistical sense; here, on the contrary, it is used for the form complexes shown at any one moment by a living system and without the details pertaining to smaller scales (Figure 1). Holdridge *et al.*, (1971) arrive at an average image of forested landscapes by means of a statistics-based pictorial shift from 'standard forest profiles' towards 'idealized forest profiles'.

The importance of studying variability

For the design of forests or agroforests, averages are less useful than deviations from the mean. These very often indicate phenomena at scales below the one that is characterized by an average. Along a forest transect, for instance, actual forest height can be measured at every ten metres from the starting point (see Figure 2*a*). The average of these values gives a general impression of the forested landscape. However, the variation of this value shows 'the forest' to be broken up into units with different height and other properties. These units can be explained by descending towards a smaller scale (for example, from Figure 1*g* towards *f* or *e*). This smaller scale is of interest to the farmer (Figure 2*b*). As a designer, of course, one has to consider all those scales, one fitting within the next one, so as to harmonize structure and function at the level of the field, the farm and the landscape.

Figure 4 is the first step to serve in evaluating the kind of agroforest best adapted to a particular site in the humid tropics. Site analysis should be carried out carefully, with regard to all factors influencing forest dynamics, so as to estimate where a particular locality belongs on the environmental 'hospitability' scale. An example is the frequency of thunderstorms (Nieuwolt, 1977, and see his Figure 6.2). The more thunderstorms, the more chablis (gaps) in the forest and hence the younger the average successional mosaic. The mechanism implied is the loosening of soil cohesion by heavy showers, a lessening of the anchorage of trees which then fall by the influence of squalls or thunderbolts. Such a forest is in a position similar to that in Figure 4*b* or *c*. For the agroforest designer this points to the use of many fast growing pioneer tree species and fewer slow growing, accident-prone, late

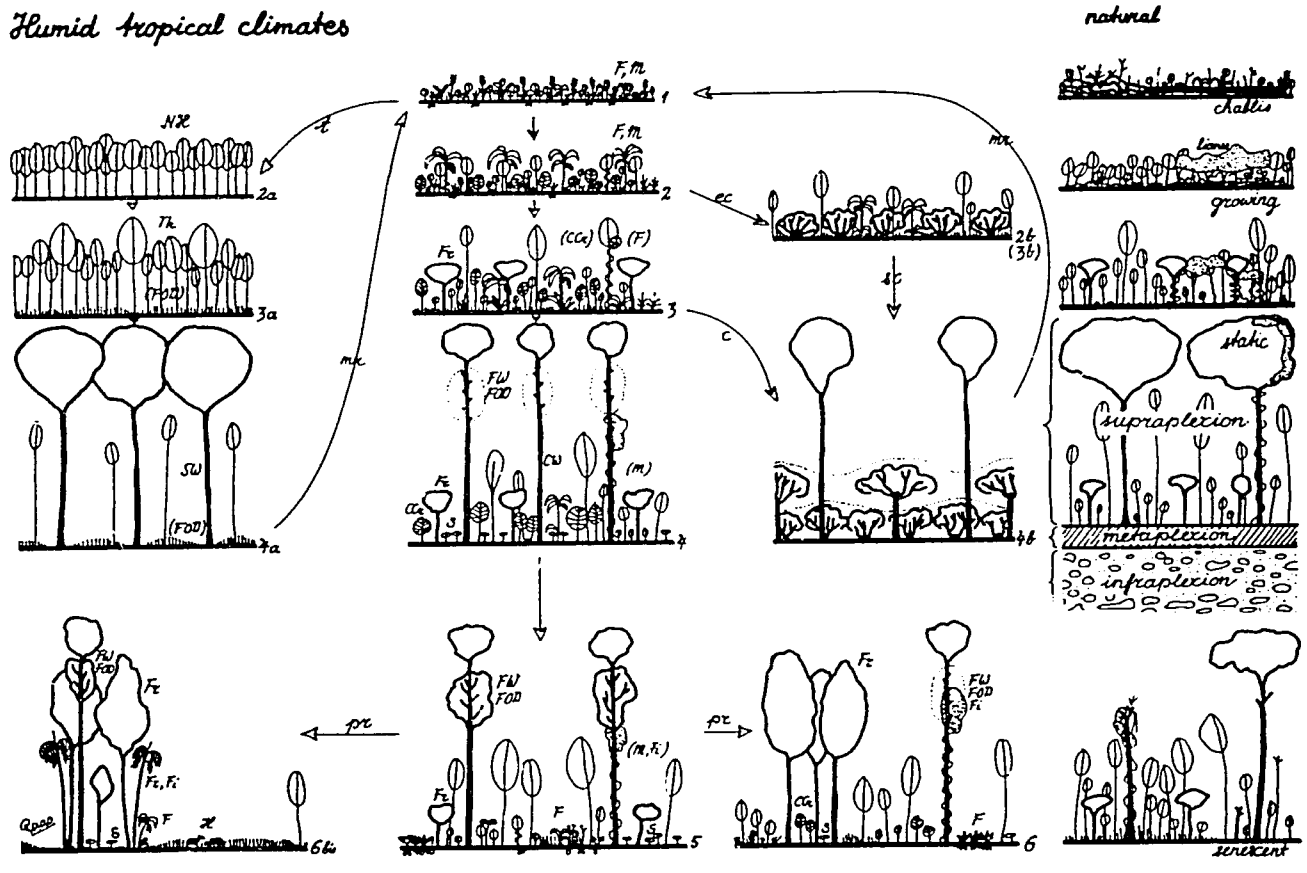

Humid tropical climates
natural
chablis
growing
static
supraplexion
metaplexion
infraplexion
senescent
F,M
NX
Th
SW
(FOD)
FW
FOD
CW
(M)
(CC)
(F)
Fz
CC
S
F
X
(M,Fz)
Fz,Fz'
Qpoo
ec
c
mr
pr
1
2
2a
2b
(3b)
3
3a
4
4b
5
6
6b

Figure 5.

successional trees.

Other important climatic factors are cyclones; the amount of precipitation beyond the physiological rainforest minimum requirements which can lead to lack of soil cohesion, soil erosion, and the leaching of minerals; cloudiness which can affect photosynthesis and the capacity to withstand short dry seasons. Is it possible, in some areas, to conceive earthquake-resistant agroforests? For example by using many young eco-units belonging to pioneer stages (see Garwood *et al.*, 1979).

Subdivision by site use

Soils and agroforestry have been treated in detail (Mongi and Huxley, 1979). They of course are among the major site factors. Natural fertility and structure, as well as soil life should be carefully assessed and used or improved. A precise regional soil map should be the basis for the agroforestry landscape (scale: Figure 1*g*), and the analysis of toposequences (see Beaudou *et al.*, 1978; Vooren, 1979) should precede farm and village design.

Low fertility and shallow soils, limited underneath by a 'root floor' where roots cannot penetrate, may not influence forest mosaic architecture overmuch. However, growth, development and the production of forests or agroforests on such soils are slowed down. Forest life is maintained by virtue of tight mineral recycling systems through co-evolved rich floras and faunas (UNESCO, 1978; and see Brunig and Sanders in this volume).

Fig. 5. (Opposite) Natural forest development (sylvigenesis) and principles of agroforest dynamics in the humid tropics, schematic diagrams. For analog basis see column 'natural' at the right, to be compared with Fig. 1*f*; basis of transdisciplinary analysis (Beaudou *et al.*, 1978; Guillaumet and Kahn, 1979) indicated in 'static' development phase (supraplexion, metaplexion, infraplexion, see text). 1. Herbaceous or forb phase, basis for all agroforests; note root crops. 2. Giant herb phase with potential trees. 3. Lower structural tree set expanded (fruit trees), some giant herbs (for example, bananas) left. 4. Biostasis: stable, perduring phase; note reiterated subcrowns under small main crown reduced by lopping in dominating trees. 5. Mosaic broken up into smaller units by selective cutting of big trees. 6. Small-scale mosaic (see Bompard *et al.*, 1980; Iskander, 1980), mainly agricultural. 6bis. Small-scale mosaic adapted to husbandry; note that this mosaic of small eco-units should not be confused with a mixture of trees and other plants. Series 2*a* to 4*a*: taungya system, main aim sawwood production after a short, preliminary stage of subsistence agriculture. Series 2*b* to 4*b* (3*b* not separated from 2*b*): coppice and pollards production; note absence of potential trees which is compelling us to clearcut and start again at Phase 1 when crop plants are ageing. Abbreviations: C, EC, SC = coppicing (early coppicing, second coppicing); CCr = commercial crops (not necessarily industrial); CW = construction wood; F = food crops; Fi = fibres; FOD = fodder; Fr = fruits; FW = firewood; H = animal husbandry; M = medicinal plants; mr = medium rotation; NH = no harvest; pr = 'permanent rotation'; S = spices; SW = sawwood; t = taungya; TH = thinnings.

These cannot be replaced by simple agricultural systems, and the use of such sites will always be very expensive because no imitation of the natural system is possible, and alternative cultural inputs are costly and could only possibly be considered for highly priced crops. Rational use of these lands therefore often implies the maintenance of wild forest, which fulfils other functions such as landscape and watershed protection.

Soil properties are closely related to toposequences. A site is more or less hospitable according to steepness of slope, valley hydrology, role of shallow root floors, or laterite shields on hill tops, and other features related to topography. At this scale the toposequence should determine the position of dwellings, the arrangements of fields with different production timetables and characteristics, and the localization of protection forest. Schematic drawings of possible spatial arrangements on toposequences have been published among others by Dubois (1979) and by Oldeman (1979b).

Designing the cultural practices

Once the landscape is rationally subdivided according to optimal site use, the cultural practices on agroforest sites have to be conceived. Whatever the design may be, it is important that its architecture and dynamics can be 'broken down' into components which can be understood easily and applied by farmers.

In this context, the transformation of eco-units will be considered first (Figure 5). Such eco-units constitute the actual *fields* or *stands* composing an agroforest; a forest farm will often include many of such units. The case of home gardens belonging to a village as common property will be treated later.

All eco-units within a new agroforest can be said to be so large as to start at the very beginning of a secondary successional sequence, sometimes called the 'forb stage' (Fig. 5.1). The surface then is occupied by herbaceous plants, sometimes lianes and most often seedlings of woody plants. During one or two growing seasons this is the equivalent of an agricultural field, whatever its subsequent use may be (see Fig. 2). It should be noted that all plant species playing some role in this field, up to Phase 4, are already present in Phase 1. Specific for this first phase are shortlived food crops, such as Gramineae (maize, dryland rice), Papilionaceae (beans), several medicinal herbs, and root crops (Araceae, Zingiberaceae). These plants most often are heliophiles, with tillering growth forms (for example, Tomlinson's model), prostrate herbaceous or lianescent architecture (Jeannoda-Robinson, 1977), swollen rhizomes, root tubers or a combination of these features (Fig. 6). Because of the preponderance of this plant form many of the essential life processes in this phase are subterranean (see Plaige, 1977; *ex* Wassink, 1977; Nair, 1980).

However, if this field is to develop into an agroforest, space should also be provided for the plant species which are going to determine the development towards Phase 4, for example, trees, shrubs and lianes. This always means that monopolization of the field by food crops is excluded in agroforestry, unless it occupies one special year, after which the perennials are planted. In general, however, yield maximization will not be possible, because part of the field has to remain unharvested

so as to prepare and improve the land for future development. Hence, spacing of different crops is of the utmost importance, and models for this have been suggested in many publications (see Fuentes Flores, 1979; Kartasubrata, 1979).

The geometrical plant spacing models most generally proposed should be considered as forerunners of more ecologically refined ones. There are, for instance, very few quantitative analyses of the occupation of root volumes by the subterranean parts of plants (for example, Bell, 1976 on Zingiberaceae; and see Huck, this volume).

Some alternative design approaches

Three alternative ways are nowadays being followed from Stage 1. These have been rigorously separated in Figure 5, as Series 1 to 4, 1 to 4*a* and 1 to 4*b*, but a variable and imaginative approach allows all kinds of combinations and transitions, so as to adapt the resulting agroforest to the site in an optimal way.

The first alternative is represented in Series 1 to 4. It follows the natural events rather closely (Fig. 5, column on the right); however, the proportion of useful species in the vegetation has been largely increased, and the plants are treated in special ways. For example, the fuelwood trees in Stage 4. Use is being made of the 'structuring from below' by the formation of layers of fully expanded crowns, which starts with such a structural layer composed of treelets or shrubs (Kahn, 1981). Among these plants there are many useful species, coffee and cacao being commercially important, and several other genera (for example, *Annona* spp. and *Psidium guajava*) yielding edible fruits. The 'commercial crops' indicated in Series 1 to 4 may therefore either be industrial or destined for local markets.

The treatment of the high trees in Phase 4, drastically reducing their crowns by lopping off most inferior branches, is a traditional way to provoke the formation of 'sub-crowns' by stem suckering on the trunk, a form of reiteration (Fig. 1*d*). It is a long-standing practice in Europe (Mayr, 1909) where it is applied when producing fodder and fuelwood. In many tropical rural regions it can be observed, for example, in Kenya (*Eucalyptus* spp.) or in Indonesia (*Albizia* spp.). Moreover, the reduction of the highest crowns modifies the vertical light gradients in lower reaches of the vegetation, so that carbon fixation can be greater near the ground.

In the column at the right of Figure 5, representing the natural situation, the equivalent of Phase 4 has been indicated as 'static'. Biostasis is the steady state of a living (= open) system with equal inputs and outputs, as distinct from homeostatis in a closed physical system. The biostatic phase has been used to illustrate some elements of the transdisciplinary analysis of whole ecosystems, as developed by a group of researchers from the Office de la Recherche Scientifique et Technique Oûtre-Mer (ORSTOM) (UNESCO-RCI, 1977; Beaudou *et al.*, 1978; Guillaumet and Kahn, 1979; Kahn, 1981). The whole system, including the inorganic parts, is divided into 'hoplexols', that is layers without any disciplinary definition, be it botanical, pedological, geographical, or other. These are each analyzed, whenever they can be found in the ecosystem. Descriptions do not use preconceived height classes, but clearly defined qualitative and

quantitative terms for the contents of each 'hoplexol'. The 'supraplexion' contains all 'hoplexols' above the ground. The 'metaplexion' includes the 'hoplexols' in the organic border zone between vegetation and mineral soil, which is neither quite vegetational, nor entirely pedological. Finally, the 'infraplexion' comprises the lower mineral 'hoplexols'. This method, and its underlying idea of one approach for the whole ecosystem, deserves careful attention. A study according to this concept, of landscapes modified by man in the southwest of Ivory Coast (UNESCO-RCI, 1977) proved the existence of several of the structures represented in Figure 5.

It should be noted that an agroforest in Phase 4 closely approaches the ideal durability as often formulated in forestry: the harvested quantities should not exceed the increment. Whenever some biomass disappears, by lopping (for fuelwood or fodder) harvesting of fruits and gathering of spices and medicinal plants, this is only an oscillation around a steady state. On the other hand some production accumulates in the trunks, to be

Fig. 6 (*Opposite*) Plant architecture in humid tropical pioneer phases and dry or degraded tropical environments. (*a*) Tomlinson's model (see our Fig. 1*e*), characteristic for many Palmae (sago palm, date palm), Musaceae (banana), Zingiberaceae (ginger), Bromeliaceae (pineapple): orthotropic axes, branching at the base, inflorescence terminal (as represented here) or lateral; definition see Hallé *et al.* (1978). (*b*) McClure's model (see our Fig. 1*e*), characteristic for many bamboos and distinct by the preformation of very differentiated shoot complexes in basal buds (see Hallé *et al.*, 1978). (*c*) *Colocasia esculenta*, dacheen, representative of many Araceous tuber crop plants (from Plaige, 1977). (*d*) *Cyperus esculentus*, a sedge with edible rhizome tubers (from Lorougnon 1971, ex Plaige, 1977). (*e*) Champagnat's model (see our Fig. 1*e*) with orthotropic mixed axes forming a sympodial tree or shrub, is representative for many woody plants in secondary bush (Torquebiau, 1981; for definition see Hallé *et al.*, 1978). (*f*) *Annona senegalensis* with its huge tap root and crown of shoots which are burnt annually (after Cesar and Menaut, 1974) is representative for many dry zone shrubs, another example being a South American *Byrsonima* species. (*g*) *Crossopteryx febrifuga* (after Cesar and Menaut, 1974) illustrates the same architecture and fire dynamics as the preceding. (*h*) *Manihot utilissima*, cassava or manioc (after Hallé, *ex* Plaige, 1977) shows Leeuwenberg's model with terminally flowering orthotropic relay axes building a sympodial tree (for definition see Hallé *et al.*, 1978); its subterranean root tubers suggest pioneer habitats; (*i*) to (*l*). Examples of graminoid growth habits taken from the classification by Descoings (1976): caespitose type with cauliphyllous and basiphyllous variants (*i*), lawn type ('type gazonnant') (*j*), rhizomatose type with two variants (*k*), and uniculm types (*l*), the last ones corresponding quite closely to the architectural tree models (Hallé *et al.*, 1978). (*m*) to (*o*). *Piliostigma thonningii*, after Cesar and Menaut (1974) as an example of a dry zone plant with preponderant subterranean survival strategy in dry tropical biomes (from the Ivory Coast).

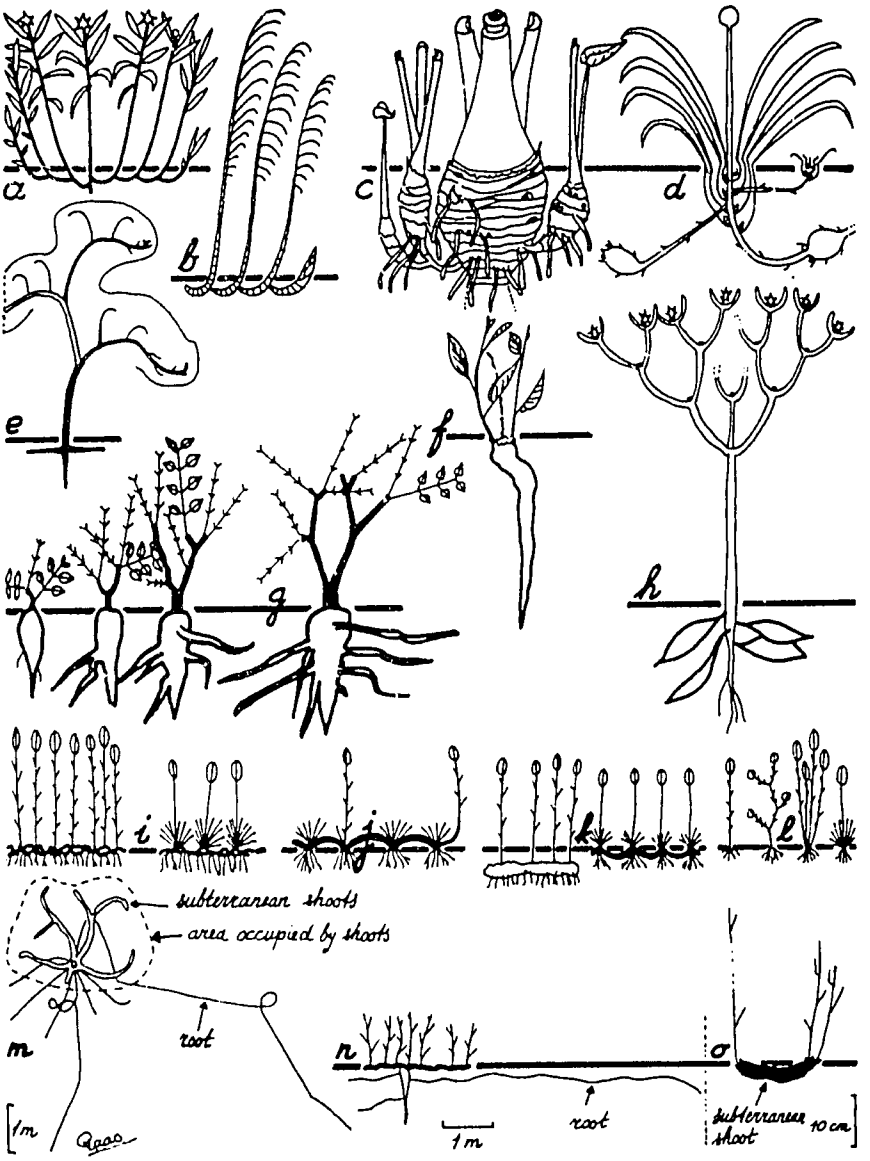

a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
subterranean shoots
area occupied by shoots
root
1m
root
1m
subterranean shoot
10 cm

Figure 6.

harvested later as construction wood or commercial wood. Yields are not maximized in this way, but they show a rather constant level from year to year, with peaks whenever a cumulated product such as wood is harvested.

The series from 1 through 2*a* to 4*a* (Fig. 5) represents an approach mainly oriented towards wood production. It is the taungya method, nearly one century and a half old, invented in Burma, and applied elsewhere under different names, such as 'système de couloirs' (corridor system) in Zaïre or 'tumpangsari' in Indonesia (Kartasubrata, 1979; Soekiman and Wahyudi, 1980).

After an initial year or two of subsistence cropping simultaneously with forest establishment, several rather extended growth phases do not show any yield immediately available to farmers. Later, some fuelwood or poles may come out of the forest in the form of thinnings and, in other cases, pasture plants may be grown under an already well-developed and thinned tree cover (Phases 3*a*, 4*a*). This is done for instance under *Pinus caribaea* plantations in Surinam, which were established by the taungya method some fifteen years ago, in combination with water melons as a marketable crop. The fact that a considerable number of cattle can be maintained in this way, wood increment scarcely suffering more than it does through competition by weeds, shows the considerable ecological potential which goes unused in the later stages of classical taungya forests.

The series from Phase 1 to Phase 4*b* are current in South and Central America, where 'coppiced' coffee and cacao treelets are grown under pollarded *Erythrina* spp. which, in turn, are overtopped by a rather open canopy of wood producing trees (see Budowski, this volume). The absence of trees and other plants with a potential for future successional development has to be noted. In ripe systems, such as Phase 4*b*, when production of the nonwood components decreases, the whole field is clearcut and started again at Phase 1 because there are no plants which can initiate any other development.

Often, the high tree layer is diversified and may yield many kinds of wood, fruits and medicines, for example in São Tomé (Groenendijk, 1979). This author also noted the probably beneficial effect on cacao of pollarding *Erythrina* twice a year, as is done in Central America but not in São Tomé. Cacao has periods when it thrives with light and others when it is best shaded: pollards produce precisely this kind of microclimatic alternation. Moreover, the pollarded *Erythrina* periodically yields fuelwood, cuttings, and a supplement of leaf fodder for cattle, whereas the leaves left in the field improve the organic matter content in the soil. As a leguminous tree *Erythrina* can also fix nitrogen.

Finally, the presence of large quantities of weeds under the lower parts of the tree components can indicate a potential biotrope for useful herbaceous plants. This space remains generally unused; sometimes herbicides are applied to keep it empty. It should be considered whether any useful, shade tolerant herbaceous plants might occupy it. For example, root crops such as the lianescent yams (*Dioscorea*) or terrestrial Araceae, or creeping, tuber forming plants (Plaige, 1977; and see Tieszen, this volume).

Such root crops do have a traditional place, which however

remains to be precisely analyzed, in the sequence from Phase 4 to some alternative phase like 6 or 6 bis. These sequences are among a multitude of possible outcomes of the interventions still currently practised in tropical villages around the world such as the recently studied kampungs in Indonesia (Bompard *et al.*, 1980; Iskander, 1980; and see paper by Michon, this volume).

The beauty of these systems is their all but unlimited elasticity. Phase 6 and 6 bis are only examples taken among the myriads of structures which can be built by the cultural measures represented in Figure 2*b* with dashed lines, and by the arrow complex indicated as 'agroforestry'. Because of the small, varying eco-units one village forest or home garden which is run along these lines can yield a large number of diverse products. One category of plants which should be kept in mind is, for instance, that of medicinal plants (Barbier and Courvoisier, 1980).

Eco-unit mosaics

One essential point should be perfectly understood when working with agroforestry in Phases 5 and 6. This is, that such phases are *not mixed cropping systems with a mixture of individual trees, but mosaics of very small eco-units*. In Figure 5, Phase 6 for instance there are, successively from right to left, one unit with growing trees and shrubs, one unit with three high fruit trees (for example, durian (*Durio zibethinus*)), useful treelets and spice plants, one unit with growing trees and fruit yielding treelets, one very small fuelwood and fodder eco-unit, and one very small root crop unit (for example, *Colocasia* sp.). The system of each of these eco-units, which includes certain plant and animal components while excluding others, has a function within the whole mosaic of such eco-units constituting a village forest or home garden. In such agroforests the eco-unit neither coincides with any economical unit ('field' or 'stand'), nor with the space occupied by one single plant.

One handicap of these complex and refined systems is that they need skill and refined work to maintain them. Foreign or uneducated farmhands are no substitute for the expertise of a traditional local farmer, who knows and understands the demands of each species and, perhaps, even of each cultivar. Much more intensive study of these systems is indispensable to our understanding of them, let alone the possibility of improving them.

There is also an absence of production data for such systems. We can state only that villages with such home gardens are fairly well supplied the whole year round with all subsistence products and more (for example, spices), but no quantitative assessment is possible as yet. Certainly, at present, we cannot calculate what the upper limits to the population density of regions where such agroforests could serve a useful purpose are. Nor can it be determined if, and to exactly what degree this production could be improved by the use of other plants, or different eco-units. As long as this information is lacking, no response can be given to the criticism concerning agroforestry formulated by Andriesse (1979).

A third subject to be investigated is the subterranean part of the eco-units. It is very possible that they interpenetrate

below the ground, and it is certain that their limits there are determined by factors other than those that determine the spread of parts above the ground. Statements promoting the association of shallow rooted herbs and deep rooting trees are often based on very inadequate information (see Jeannoda-Robinson, 1977; Ndiaye, 1977; Kahn, 1981). The difficulty of looking at roots in soil seems to have been overcome to a certain extent by the perforated soil method recently developed by van den Tweel and Schalk (1981) followed by Bosch (pers. comm.). Henceforth it will be possible to analyze root system dynamics, at least in the young stages, by the use of this cheap and simple device, consisting of a monolith built with loamy soil and horizontally pierced by numerous straight narrow holes (Ø < 1 cm). Different plants can be sown on top. Their roots traverse the perforations, possibly like equivalents of worm holes, and can be observed, counted, measured, and described by looking through the openings.

An interesting possibility with the home garden agroforest lies in its potential transfer of matter and energy towards secondary producers, concurrently with the recycling of household wastes. In phase 6, there would be a place mainly for small animals, such as poultry or fish in a pond (Soemarwoto and Soemarwoto, 1979), but in phase 6 bis, eco-units can be managed to sustain larger animals, perhaps goats. The forest eco-units then may shrink towards small tree groves, which show climatic gradients from centre to periphery and which do not display sharp limits. The minimal forest component is constituted by some isolated trees in a landscape of meadows. In this case the analysis of meadows becomes necessary. However, it is not known as yet how an herbaceous eco-unit could be defined; for example as a subsystem within stage 1. Even the data gathered by Descoings (1976) and Ndiaye (1977) are not sufficient for this purpose.

When reconsidering Figure 5, it should be borne in mind that only the sequence from Phase 1 to 6 follows some pattern comparable with succession (Fig. 2*b*). The two derived transformations, taungya (Phase 2*a* to 4*a*) and coppice - pollard - high tree systems (Phases 2*b* to 4*b*), are limited to an imitation of pioneer or late pioneer stages and their development. However, it is certainly possible to shift over from one sequence to another or to conceive agroforests combining features of more than one sequence.

Weeds can be a general problem. Their architecture and ecology should be carefully analyzed and useful plants with the same or competitive features should be sought to replace them. There also is a natural development phase which has no equivalent in agroforests: the senescent eco-unit (Fig. 5, bottom right). Farmers seldom let plants grow beyond the useful stage. Hence the dynamics of forest eco-units, which in nature are determined by trees with a potential future development ('trees of the future', Hallé *et al.*, 1978), fully expanded ('trees of the present') and decaying trees ('trees of the past') cannot be simply transposed to agroforests. Here, the dynamics are determined by trees with potential production and trees in actual production (Bompard *et al.*, 1980). Hence the same *general* pattern of development does occur within both a natural forest and an agroforest unit, but profound differences exist in other processes and properties, such as the biogeochemical cycle, or

the living conditions for small, wild animal life and their interactions with plants.

The durability of traditional agroforests in Southeast Asia has been demonstrated by their millenarian history (Wiersum, 1979). Those properties of such ecosystems as have been summarized above, confirm the idea that agroforests can be designed as custom-made systems for nearly every specific site in the humid tropics; fitting within humid tropical development frameworks such as those conceived by Poore (1976) and Webb (1977).

AGROFORESTS FOR DRY AND DEGRADED TROPICAL ENVIRONMENTS

A comparison between Figures 2 and 4 shows how biological and ecological cycles can be used in different environments. For the humid tropics, the sequence from 1 to 6 (Fig. 5) makes full use of all cycles, within cycles, within cycles ..., constituting the rich gamut of humid tropical forest dynamics. Now, from Figure 4 we should consider inhospitable environments. Here the number of available cycles strongly decreases, and their properties change.

A commonality

Budowski's rule (1965), which says that pioneer rainforest tree species occupy a large geographical area, including dryer regions, can be extended when considering Figure 4. It might be amplified as follows: *any plant which plays a pioneering role in hospitable environments shows a geographical distribution which includes some inhospitable environments*. Like Corner's rule (1949) concerning the branching of trees, Budowski's rule can be checked easily in the field, but less easily explained. This should, however, be possible by means of the classical theory of limiting factors. Pioneer plants might be viewed, in this context, as species with relatively low ecological requirements with regard to some factors or at least one factor.

It should be clearly understood that a high tolerance towards some specific form of ecological stress does not imply that such plants are tolerant to low values of most, or all factors in their environment. Drought resistant plant species, for instance, may well suffer from low soil fertility, as recently shown in Mali and other Sahelian countries (Stroosnijder, 1977; Penning de Vries *et al.*, 1982). On the left side of Figure 4 several factors are listed which may render an environment less hospitable to forests: these do not necessarily coincide with minimum factors as usually applied to species or populations, because they refer to eco-units and not to individual plants. Moreover, several factors have sometimes been lumped together into one complex, for example, 'bad soils'. An example of their joint action in Mali has been documented by Boudet (1979, p.33) where the keyword is 'erosion'.

No distinction is made in Figure 4 between natural and man-made inhospitality. The processes which are summarized in Figure 3*b*, for instance, may occur equally in dry tropical regions with a rather low soil fertility and fire hazards, or in humid tropical regions after a period of too intensive cattle keeping on artificial pastures replacing the forest. So the design of healthy agroforests for dry regions is to a large extent

identical with that for degraded regions in other, richer climatological zones.

One more reason not to separate natural and man-made inhospitality is the fact that in most semiarid and arid regions, as mapped by UNESCO (1979), there is scarcely any natural ecosystem left. Usually there has been a heavy human impact, often by pastoral nomads or by settled human populations with roving herds (for example, Gevers *et al.*, 1980). Some dry lands of Australia and South America have been less affected but, in such cases there is usually a lower insight into the causes and risks of degradation displayed by the inhabitants. Thus the design of new agrosystems, or agroforests, has to be approached very carefully.

Are agroforests for dry or degraded regions?

The question has to be raised whether agroforests do, indeed, constitute an optimal formula for dry or degraded regions. In both, the prime necessity is to upgrade environmental hospitality for plants and animals so as to increase it for humans. Upgrading through the classical means of irrigation, fertilization and the use of improved crop or pastoral plants is a slow and expensive business (Linnemann and Buhring, 1981). Traditionally, these costs are thought to be justified only when directed towards the establishment of maximum yield farms. This is done by minimizing the investment in the ecosystem while at the same time using a maximal proportion of the available means in short-term processes such as fertilization (once per season) and short cycle cropping. The input - output aspects of such farms far outweigh all features of consciously designed and inbuilt durability factors, except mechanical land management (consider the terracing and other systems described by Adams *et al.*, 1978).

On the other hand, trees are organisms with an ecological investment strategy (Oldeman and Westra, 1980). Matter and energy are immobilized in long-lived woody structures. Litter recycling functions by virtue of these structures as a long-term process with very few losses. To integrate trees into the agrosystem, that is to build an agroforest, is the equivalent of creating a decrease in immediately available productivity; an increase of accumulated production to be harvested with longer intervals; and a cheaper production method, because of its recycling virtues (see Fig. 5, sequence 1 to 4).

Successional patterns are less well known for the degraded and dry tropical environments (see Descoings, 1976, for grass savannas, and Bognetteau-Verlinden, 1980a, b, for dunes in Niger). They would be variants of the three lower levels in Figure 4. If a counterpart to Figure 2 were to be drawn for the forest or vegetation mosaic of these lower levels, there clearly would be less numerous and less varied ways in which to conceive planting-to-harvesting cycles on different scales. What follows is based mainly on documents from Cesar and Menaut (1974), Descoings (1976) and Adams *et al.*, (1978), each of whom gives a number of instant pictures of whole tree savannas, steppes, treeless savannas, deserts and the herbaceous part of savannas with some trees. FAO (1974) and Delwaulle (1979) can be used to document some practical cultivation methods.

General considerations

Savanna forests, park forests, open forests are some of the names often used for the most current vegetation types in semi-arid areas. The openness of such a vegetation is then compared with that of a forest supposedly possessing a closed cover. Thus the comparison is expressed by the degree of cover or density (of trees) per hectare. This criterion cannot serve the specific purpose which is the design of agroforests. For the description of vegetation types it is of course useful, just like other average values mentioned above for the humid tropics.

For different savanna types around Lamto in Ivory Coast, Cesar and Menaut (1974, their Figures 15, 23, 26, for example) show the 'distribution of woody plants taller than 2 m'. Using the scales represented in Figure 1, and the processes in Figure 3*b* as a starting point, it is possible to conceive a hectare of tree savanna as a mosaic of herbaceous and forest eco-units. The forest eco-units become established and maintain themselves by the dissemination pattern shown in Figure 3*b*, and the plant architectural types given in Figure 6 (*f*, *g*, *m*, *n*, *o*). The herbaceous eco-units, when made up of grasses, are often maintained through fire, or through soil compaction by cattle. The grasses can be architecturally understood following the classification made by Descoings (1976; and see our Figure 6 *i* to *l*). Other herbaceous plants have been analyzed by Jeannoda-Robinson (1977) and Ndiaye (1977).

Fire and soil compaction, and probably other mechanisms such as gradual soil exhaustion, maintain the vegetation mosaic at the lower levels of Figure 4. When protected against fire, woody eco-units soon become predominant (Cesar and Menaut, 1974). In all cases of fire hazard biological processes become more and more subterranean (pyrophyte architecture: Fig. 6).

This is also true for other limiting factors. For instance, the ratio between subterranean and above-ground volume in eco-units gradually increases when following the ecotones from Amazonia towards the Andean páramos. In arid regions roots can descend to 45 m below ground level (for example, *Acacia* spp.) and usually, the woody plant root zone is rive to ten meters deep (Adams *et al.*, 1978). If technical ways could be found to harvest the subterranean woody biomass of forest eco-units without disrupting the soil ecosystem, the value of these semi-arid eco-units could be greatly enhanced.

Besides the predominance of herbaceous eco-units and the subterranean character of many biological structures and processes, the remarkable role of large herbivores should be noted (Ricklefs, 1980, his Table 8.4). In the humid tropical forests secondary producers may well account for an important part of biomineral and bioenergetic cycling (see van Roosmalen, 1980), but their role remains discreet to the eye. On the contrary, in semiarid regions, the big herds, or sometimes groups of other animals such as kangaroos, are conspicuous. Hence the use of such regions for 'zoo forestry' (Montsma, pers. comm.) is easily conceived. These environments are the traditional domain of nomadic herdsmen whose way of life can scarcely be reconciled with sedentary agroforestry. It is now accepted that browse shrubs play a vital role in providing animal feed in these drier regions.

There is a traditional agroforestry system for dry regions, the oasis, which should be studied more closely, in the same way as the traditional Indonesian systems. It proves the point that in other times the investment of means and effort was not exclusively consecrated to short cycle agriculture but has, on the contrary, been used for the establishment of agroforests. An oasis is irrigated, its tree component is constituted by suckering palms (date palm: Fig. 6*a*), nowadays mixed with small eco-units containing one or two fuelwood trees each. Herbaceous eco-units are sometimes present (for example including millet), and lower shrub layers in forest eco-units contained useful plants like chillipepper (*Capsicum annuum*).

Designing semiarid agroforests

The design of a semiarid agroforest can follow, in principle, the same lines as the humid tropical one. In the first place, a general diagnosis of the site, by means of climatological and soil maps, should yield an impression of the overall hospitality of the environment. This should be made more precise by two methods. First, toposequence properties have to be assessed: some illustrated examples are given by Cesar and Menaut (1974) and for dryer regions by Boudet (1979). These are the site properties at the scale which is immediately relevant to the farmer. Second, a diagnosis should be established as to the degree of human interference: here, analogs with other comparable regions are the logical frame of reference.

Sites may often be situated in very variable climates where factors may be lethal one year, limiting the next and nonlimiting in the third year. Drought is such a factor. Boudet (1979) has described the site-dependent 'succession' of tree savanna to semidesert and back during and after the great Sahelian droughts

Fig. 7. (Opposite) Rough sketch of a small agroforest nucleus in semiarid or degraded environments, precise architectural elements lacking in part. Note importance of subterranean part of the ecosystem and lack of knowledge (?) of the roots in several cases. Eco-unit under *Acacia*-like Mimosaceae (A) after unpublished observations from the dry parts of Carchi (Ecuador), roots extrapolated from observed fragments along road excavation. *Tamarix* (T) after African data from Adams *et al.*, (1978). *Agave* spp. are used as aerial drought barriers (adb) in dry neotropical regions, cacti (here *Opuntia ficus-indica* with edible fruits, might serve the same purpose. Root crops, for example yams (*Dioscorea* spp.) as in Upper Volta, agriculture with millet or sorghum. Coppicing is natural to many tree and shrub species in these regions and can be used in fuelwood production or to obtain fodder. Subterranean drought protection (sdp) by deep roots reaching the water table; termites also descend to this level and take water to the surface; use of these animals in agroforest hydrology etc. should be considered and not just their role as crop parasites. The very synthetic and schematic nature of this sketch is to be stressed: many more exact data are still needed, and elements from very different geographical zones are mixed here. This figure may, however, be used as a starting point in conceiving such agroforests.

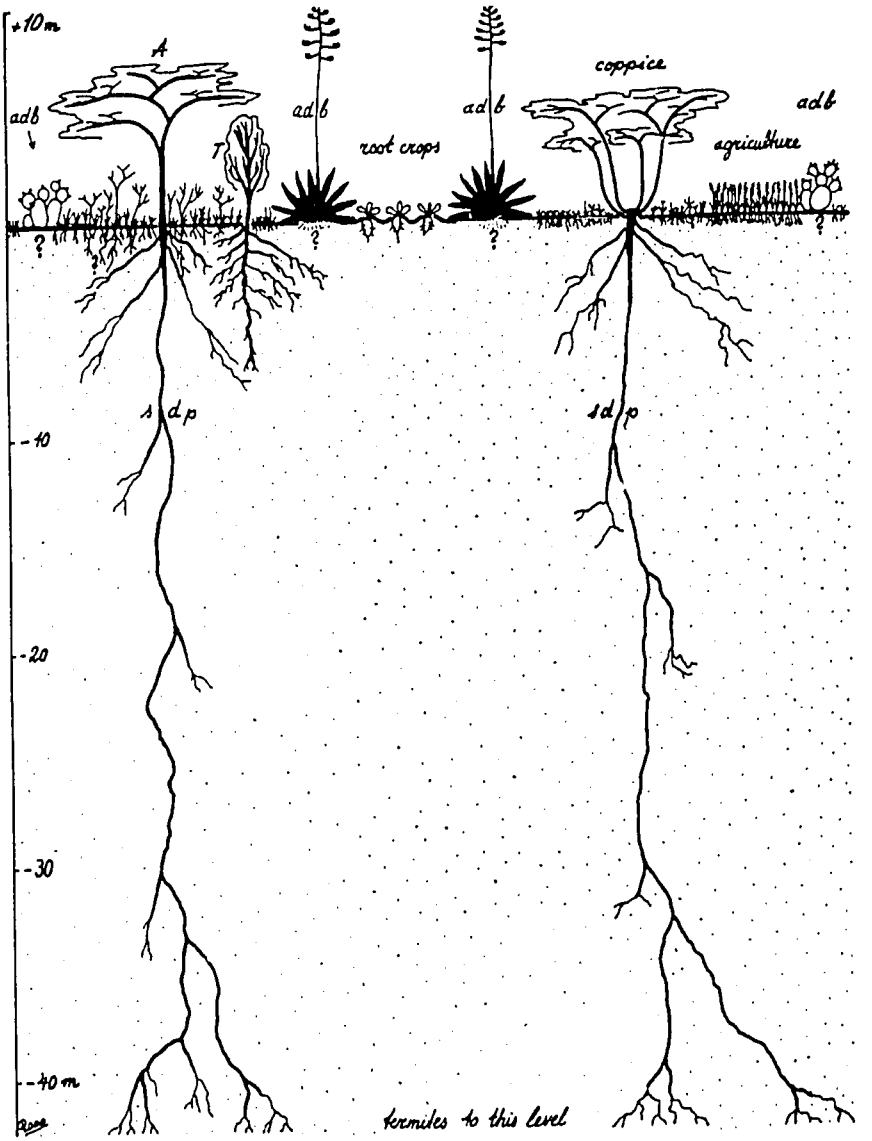

+10m
A
adb
adb
adb
root crops
coppice
adb
agriculture
s d p
s d p
-10
-20
-30
-40m
termites to this level

Figure 7.

in the years from 1970 on. Every agroforest should have some inbuilt protection against such environmental fluctuations.

Very generally, the regions in question have a potential vegetation mosaic with more natural forest eco-units than actual man-made ones. Forest eco-units, moreover, are much less variable in comparison with those in wetter countries, because they rarely represent late successional stages. This certainly is linked to the diminution of the number of species, including useful ones, from humid to dry environments. The image given by Nair (1980, Table 5) does not represent this completely, probably because in rainforest zones the majority of cultivated plant species are not 'official' crops but home-grown, and often very localized plants (see Budowski, 1978).

In the absence of adequate information on semiarid tree and ecosystem architecture, the problems inherent in the design of agroforests for such regions have been indicated just by a rough sketch in Figure 7. Self protection of such agroforests, which are conceived as nuclei in a landscape mostly dedicated to cattle husbandry in its less vulnerable parts, will repose to a great extent on the functioning of root systems: the largest part of the ecosystem is, indeed, subterranean. Root systems of the trees forming the skeleton of the agroforest should descend to the groundwater table, which is situated at a certain depth not always dependent on climate. As examples, certain *Acacia* and *Tamarix* species have been chosen. Certain neotropical cacti and *Agave* species might show enough drought resistance to be used as anti-erosive belts above the ground. The architecture of their root systems has not been analyzed as yet as far as we know. These species are used in this way in South America; moreover they yield fibres (agave) and fruits or fodder (*Opuntia*, Cactaceae). For environments with particularly long and severe droughts, other species from near neotropical deserts might be sought.

Figure 7 shows small surfaces not covered by trees and used for food crops, like those existing in the African oases. Some form of irrigation in dry regions, and fertilization when these zones are also degraded, may be necessary in order to grow agricultural crops at all. One of the advantages of agroforests is a diminishing necessity for both when developed forest eco-units start fixing nitrogen, producing litter and regulating local hydrology. Termites may well be necessary litter decomposing components of the ecosystem, and also might be used as water carriers between the phreatic level and the surface. Because these insects can also be dangerous pests, systems to put them to use must be carefully thought out, considering for instance ways of encouraging saprovorous species and of maintaining reasonable population densities.

Cattle are, of course, an almost natural element in and around these agroforests, which can become accumulation loci for their dung when the animals come into the shade of the trees (Boerboom, pers. comm.). Their access to agroforest nuclei should however be carefully regulated because cattle must never be allowed to become a degradation factor, causing soil compaction and eating seedlings. In fact no establishment of agroforests is possible unless at least a temporary and complete protection against cattle is undertaken. Perhaps this can only be achieved

economically by encouraging the existence of sedentary agricultural inhabitants in the agroforests, as a complement to the nomadic herdsmen. The use of small domestic animals and the application of organic household wastes to the land is a means of reducing the needs both for cattle and expensive fertilizers. A spectacular photograph of land protected against herds next to overgrazed land has been published by Boudet (1979).

There still persists an important lack of knowledge: most publications concerning the establishment of such agroforests in semiarid regions are based just on empirical data (FAO, 1974; Delwaulle, 1979). These are an essential asset, but they should be complemented by more fundamental research. As long as this is not available the refinement of agroforest design will be severely handicapped in the more inhospitable parts of the tropics, where many problems can only be solved by means of a very flexible approach. These problems in the first place concern the acceptability of systems to the local inhabitants, but also the optimal health and productivity of such agroforests.

CONCLUSIONS

The approach presented here allows the elaboration of very precise models or designs of forests, agroforests, zoo forests or agrosystems. This kind of analysis has by no means yet reached its potential level of precision. Much more research on vegetation architecture above and below ground, and at all integration levels or scales as defined in Figure 1 is still needed.

Architectural research can be conducted with simple instruments and yield quick results. Moreover, it can easily be included in a feedback loop coupled to practical application. The work by Bompard *et al.* (1980) and Iskander (1980) shows how existing or newly built agroforests can be followed by periodically making scale drawings. The results of analysis then can be used in the agroforestry project in the form of suggested improvements or additional observations. This does not eliminate the necessity for parallel work on natural vegetation which, for every life zone, probably represents the most durable system in existence. Feedback of the results can strengthen agroforestry design and experimentation in the same way as research on agroforests themselves.

Agroforest designs in the form of Figure 5 have another advantage. They include very precise information on a high level of abstraction. Nevertheless, they represent the agroforest in such a way that everybody can recognize it. Very little training would be necessary for local farmers to understand such drawings. For instance, it is probable that an inhabitant of rural Java, when looking at Figure 5, will react at the localization of some crop plant and either indicate an error, or mention some specific plant or cultivar. The 'green-print' approach therefore seems to enhance the chances to stimulate local participation in projects, because its visual documents are 'conversation pieces'.

The translation of such models into mathematical terms is also possible, as has been demonstrated by De Reffye (1979). For the moment, however, it does not seem to be immediately useful, particularly if contacts with local populations have priority. This situation may abruptly change whenever information of

another nature is to be linked up to an architectural model, such as data on biomass development, population dynamics, biogeochemical cycles, or energetics. This may lead to considerable simplification of observations if certain energetic, biochemical or biomass states could be linked to diagnostic indicator structures. Some current ORSTOM research in French Guiana suggests this to be possible, as does current work at Celos (Surinam). Such linking of different data can improve agroforest designs with regard to the prediction of yields, crop requirements, pest risks, and other important features of agrosystems and forests in general. The balance of the approach presented here is, therefore, that of a method which can yield fast and precise information as a starting point for design, but which is accepted as no universal solution and takes its place among other ways to solve the problems of agroforestry.

Agroforests, as with all living systems, cannot exist and survive without cyclic change, and the structures which permit this to take place. The optimal understanding of apparently simple but durable living systems changing by virtue of very refined biological cycles, remains an extraordinary challenge. It is certainly a field with exceptional scope for future development in terms of practical use in the design and management of agroforestry systems.

REFERENCES

Adams, R., Adams, M., Willens, A. and Willens, A. (1978). "Dry Lands: Man and Plants". The Architectural Press, London.

Andriesse, J.P. (1979). From shifting cultivation to agroforestry or permanent agriculture? *Royal Trop. Inst. Bull.* 303, 35-43.

Barbier, C. and Courvoisier, C. (1980). An approach of the traditional uses of medicinal plants in Java. DEA Report, University of Montpellier, France. 64 pp.

Beaudou, A.G., Blic, P. de, Chatelin, Y., Collinet, J., Filleron, J.S., Guillaumet, J.-L., Kahn, F., Zueli, K.B. and Richard, J.F. (1978). Recherche d'un langage transdisciplinaire pour l'étude du milieu naturel. [Search for a transdisciplinary language to study the natural environment.] *Travaux et Doc. ORSTOM* 91. 143 pp.

Bell, A. (1976). Computerized vegetative mobility in rhizomatous plants. *In* "Automata, Languages, Development" (A. Lindenmayer and G. Rozenberg, eds), pp.3-14. North Holland Publ. Co., Amsterdam, Netherlands.

Bognetteau-Verlinden, E. (1980a). Study on impact of windbreaks in Majjia Valley, Niger. CARE, Niger, and Agricultural University, Dept. Silviculture, Wageningen, Netherlands. 81 pp. (Also in French.)

Bognetteau-Verlinden, E. (1980b). Végétation spontanée et stabilisation des dunes. [Natural vegetation and dune stabilization.] CARE, Niger, and Agricultural University, Dept. Silviculture, Wageningen, Netherlands. 48 pp.

Bompard, J., Ducatillion, C., Hecketsweiler, Ph. and Michon, G. (1980). A traditional agricultural system: village - forest - gardens in West Java. DEA Report Terrestrial Ecology, University of Montpellier, France. 101 pp.

Boudet, G. (1979). Quelques observations sur les fluctuations du couvert végétal sahélien au Gourma Malien et leurs conséquences pour une stratégie de gestion sylvo-pastorale. [Some observations on the fluctuations of the Sahelian vegetation cover in the Gourma of Mali and their consequences for a strategy of silvo-pastoral management.] *Bois For. Trop.* 184, 31-44.

Budowski, G. (1965). Forest species in successional process. *Turrialba* 15, 40-42.

Budowski, G. (1978). Food from the forest. Eighth World For. Congress, Jakarta, paper FFF/9-0. 20 pp.

Cesar, J. and Menaut, J.C. (1974). Le peuplement végétal des savannes de Lamto (Côte d'Ivoire). [The vegetation stands of the savannas of Lamto (Ivory Coast).] *Bull. liaison chercheurs Lamto, No spécial* II. Ecole Normale Supérieure (J.C. 91), Paris, France.

Corner, E.J.H. (1949). The durian theory or the origin of the modern tree. *Ann. Bot.* (NS) 13, 367-414.

Delwaulle, J.-C. (1979). Plantations forestières en Afrique tropicale sèche. [Forestry plantations in dry tropical Africa.] *Bois For. Trop.* 184, 45-59; 185, 3-23.

Descoings, B.-M. (1976). "Approche des formations herbeuses tropicales par la structure de la végétation." [Approach to tropical herbaceous associations by the structure of the vegetation.] Dr ès Sci. Thesis, University of Montpellier, France.

Dubois, J. (1979). Aspects of agroforestry systems used in Mayombe and lower Congo (Zaire). *In* "Agroforestry Systems in Latin America" (De las Salas, ed.), pp.84-100. CATIE, Turrialba, Costa Rica.

FAO (1974). Tree planting practices in African savannas. *FAO Forestry Development Paper* 19. Rome, Italy. 185 pp.

Florence, J. (1981). "Chablis et sylvigénèse dans une forêt dense humide sempervirente du Gabon". [Windthrow and sylvigenesis in a dense, humid, evergreen forest in Gabon.] Spec. Thesis, Louis Pasteur University, Strasbourg, France.

Fuentes Flores, R. (1979). Coffee production farming systems in Mexico. *In* "Agroforestry Systems in Latin America" (De las Salas, ed.), pp.60-72. CATIE, Turrialba, Costa Rica.

Garwood, N.C., Janos, D.P. and Brokaw, N. (1979). Earthquake-caused landslides: a major disturbance to tropical forests. *Science* 205, 997-998.

Gevers, E., Ottenhof, F, and Ebregt, A. (1980). "Vee, bos en mens in Noord Tunesië (Mogods)." [Cattle, forest and man in Northern Tunesia.] Agricultural University, Dept. Silviculture, Wageningen, Netherlands. 84 pp.

Groenendijk, L. (1979). "Cacao, arvores de sombra e produtos de floresta, um sistema agro-florestal nas ilhas de São Tomé e Principe." [Cacao, shade trees and forest products, an agroforestry system in the islands of Sao Tomé and Principe.] Agricultural University, Dept. Silviculture, Wageningen, Netherlands. 55 pp.

Guillaumet, J.-L. (1978). Observations sur les premiers stades de la reconstitution de la forêt dense humide: présentation. [Observations on the first stages in the re-establishment of the dense, humid, tropical forest: introduction.] *Cahiers*

ORSTOM Sér. Biol. 13, 189-190.

Guillaumet, J.-L. and Kahn, F. (1979). Description des végétations forestières tropicales, approche morphologique et structurale. [Description of tropical forest vegetation, a morphological and structural approach.] *Candollea* 34, 109-131.

Hallé, F., Oldeman, R.A.A. and Tomlinson, P.B. (1978). "Tropical Trees and Forests: An Architectural Analysis". Springer-Verlag, Berlin.

Hart, R.D. (1980). A natural ecosystem analog approach to the design of a successional crop system for tropical forest environments. *Biotropica* 12, 73-82.

Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. and Tosi, J.A. (1971). "Forest Environments in Tropical Life Zones: A Pilot Study". Pergamon Press, Oxford, UK.

Iskander, J. (1980). "Penelitian arsitektur dan struktur tanaman pekarangan di desa Champelas Cilih Bandung". [Planning, architecture and structure of the homegarden of the village Champelas Cilih, Bandung.] Thesis, University Padjadjaran, Bandung, Indonesia.

Jeannoda-Robinson, V. (1977). "Contribution à l'étude de l'architecture des herbes". [A contribution to the study of the architecture of herbaceous plants.] Spec. Thesis, University of Montpellier, France.

Kahn, F. (1981). "La reconstitution de la forêt tropicale après culture traditionnelle (Sud-Ouest de la Côte d'Ivoire)." [The re-establishment of the tropical forest after traditional cultivation (southwestern part of the Ivory Coast).] Spec. Thesis, University of South Paris (Orsay), France.

Kartasubrata, Y. (1979). Tumpangsari method for establishment of teak plantations in Java. *Trop. Agric. Res. Series* 12, 141-152.

Linnemann, H. and Buringh, P. (1981). "De Wereldvoedselvoorziening". [World Food Supply.] Agricultural University, Wageningen, Netherlands. 22 pp.

Mongi, H.O. and Huxley, P.A. (Eds) (1979). "Soil Research in Agroforestry". ICRAF, Nairobi, Kenya.

Nair, P.K.R. (1980). "Agroforestry Species: A Crop Sheet Manual." ICRAF, Nairobi, Kenya.

Namur, C. de (1978). Quelques caractéristiques du développement d'un peuplement ligneux au course d'une succession secondaire. [Some characteristics of the development of a community of woody plants during secondary succession.] *Cahiers ORSTOM Sér. Biol.* 3, 211-222.

Ndiaye, P. (1977). "Preliminaire à l'étude architecturale des végétations herbacées." [Introduction to the architectural study of herbaceous vegetation.] DEA Report, University of Montpellier, France. 22 pp.

Nieuwolt, S. (1977). "Tropical Climatology: An Introduction to the Climates of the Low Latitudes". John Wiley & Sons, New York.

Oldeman, R.A.A. (1974). L'architecture de la forêt guyanaise. [Architecture of the Guyanan forest.] *Mém. ORSTOM* 73. 204 pp.

Oldeman, R.A.A. (1978a). Architecture and energy exchange of dicotyledonous trees in the forest. *In* "Tropical Trees as Living Systems" (P.B. Tomlinson and M.H. Zimmerman, eds), pp.535-560. Cambridge University Press, London, New York.

Oldeman, R.A.A. (1978b). Appréciation graphique de l'impact d'un déboisement ou d'un réboisement. [A graphic description of the impact of deforestation or reforestation.] Eighth World For. Congress, Jakarta, paper FQL/25-20. 6 pp.

Oldeman, R.A.A. (1979a). Quelques aspects quantifiables de l'arborigénèse et de la sylvigénèse. [Some quantifiable aspects of arborigenesis and of sylvigenesis.] *Oecol. Plant.* 14, 289-312.

Oldeman, R.A.A. (1979b). Blueprints for a new tropical agroforestry tradition. *Royal Trop. Inst. Bull.* 303, 25-34.

Oldeman, R.A.A. (1980). "Grondslagen van de Bosteelt". [Principles of Forestry.] Agricultural University, Dept. Silviculture, Wageningen, Netherlands.

Oldeman, R.A.A. (1981). Schaal, grootschaligheid and kleinschaligheid in de bosbouw. [Large-scale and small-scale forestry.] *Ned. Bosbouw Tijdschr.* 53, 71-78. (English summary.)

Oldeman, R.A.A. and Westra, J.J. (1980). De betekenis van hout in de oecologie van boom en bos. [The role of wood in tree and forest ecology.] *Ned. Bosbouw Tijdschr.* 52, 39-46. (English summary and legends.)

Penning de Vries, F.W.T., Krul, J.M. and Keulen, H. van (1982). Productivity of Sahelian rangelands in relation to the availability of nitrogen and phosphorus from the soil. *In* Proc. I.I.T.A., Ibadan, Nigeria (1978). Agricultural University, Wageningen, Netherlands.

Plaige, V. (1977). Plantes alimentaires tropicales à tubercules: une étude bibliographique. [Tuberous tropical food plants: a bibliographic study.] DEA Report Tropical Botany, University of Montpellier, France. 45 pp.

Poore, D. (1976). Ecological guidelines for development in tropical rainforests. I.U.C.N., Switzerland. 39 pp.

Reffye, Ph. de (1979). "Modelisation de l'architecture des arbres par des processus stochastiques." [Modelling tree architecture by stochastic processes.] Thesis, University of South Paris (Orsay), France.

Ricklefs, R.E. (1980). "The Economy of Nature". Chiron Press, New York.

Rollet, B. (1974). "L'architecture des forêts denses humides sempervirentes de plaine." [The architecture of dense, humid, evergreen lowland forests.] C.T.F.T., Nogent-s-Marne, France.

Roosmalen, M.G.M. van (1980). "Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* L.) in Surinam." Thesis, Agricultural University, Wageningen, Netherlands.

Rouw, A. de (1979). La culture traditionnelle dans le Sud-Ouest de la Côte d'Ivoire (Région de Taï): le système Oubi confronté aux pratiques agricoles des Baoulés immigrés. [Traditional cultivation in the southwest Ivory Coast (Taï Region): the Oubi system compared to the agricultural practices of the immigrant Baoulés.] ORSTOM, Abidjan, Ivory Coast. 41 pp.

Soekiman, A. and Wahyudi (1980). Forest management in Java in the development area. *Ned. Bosbouw Tijdschr.* 52, 153-165.

Soemarwoto, O. and Soemarwoto, I. (1979). The village homegarden: a traditional integrated system of man - plants - animals. University Padjadjaran, Bandung, Indonesia. 19 pp.

Stroosnijder, L. (1977). Aspects of soil and water in the Sahel in Mali. *In* "Proc. Intern. Symp. on Rainfed Agriculture in Semiarid Regions", pp.166-199. University of California, Riverside, California, USA.

Torquebiau, E. (1981). "Analyse architecturale de la forêt de Los Tuxtlas (Veracruz), Mexique". [Architectural analysis of the Los Tuxtlas forest (Veracruz), Mexico.] Thesis, University of Montpellier, France.

Tweel, P. van den and Schalk, B. (1981). The horizontally perforated soil system: a new root observation method. *Plant and Soil* 59, 163-165.

UNESCO (1978). "Tropical Forest Ecosystems: A State-of-Knowledge Report". UNESCO, Paris, France.

UNESCO (1979). Map of the world distribution of arid regions. MAB Techn. Notes No.7. 54 pp + map. UNESCO, Paris, France.

UNESCO - RCI (1977). Le dynamisme pionnier dans le Sud-Ouest Ivoirien, ses effets sur le milieu forestier. [Pioneer dynamism in the southwest Ivory Coast, its effects on the forest environment.] Final Report, Interdisciplinary Research Pilot Project, RCI, Abidjan, Ivory Coast. 146 pp.

Vooren, A.P. (1979). La voûte forestière et sa régénération, analyse structurelle et numérique d'une toposéquence en forêt de Taï, Cote d'Ivoire. [The forest canopy and its regeneration, a structural and quantitative analysis of a toposequence in a forest of Taï, Ivory Coast.] ORSTOM, Abidjan and Agricultural University, Dept. of Silviculture, Wageningen, Netherlands. 89 pp.

Wassink, J.T. (1977). Agroforestry, een samenspel van land- en bosbouw ten behoeve van de mens en zijn milieu. [Agroforestry, a joint venture of agriculture and forestry for man and his environment.] Supplement 67th Yearbook, Royal Trop. Inst., Amsterdam, Netherlands. 19 pp.

Webb, L.J. (1977). Ecological considerations and safeguards in the modern use of tropical lowland rainforests as a source of pulpwood: example the Madang Area Papua New Guinea. Office of Environment and Conservation, Papua New Guinea. 36 pp.

Wiersum, K.F. (1979). Possibilities for use and development of indigenous agro-forestry systems for sustained land use on Java. *In* "Tropical Ecology and Development" (J.I. Furtado, ed.), pp.515-521. Int. Soc. for Tropical Ecology, Kuala Lumpur, Malaysia.

DISCUSSION

LEYTON - Are you aware of Horn's book[1] on tree strategies; particularly with regard to the shapes of crowns? How do his ideas fit with yours?

OLDEMAN - They fit in my Figure 1. Because Horn jumps over some scales (from an 'organ', such as a leaf, to 'canopy', that is a branched complex) he needs to apply statistical procedures. I do not.

---

1. Horn, H.S. (1971). "The Adaptive Geometry of Trees". Princeton University Press, New Jersey, USA. (*Ed.*)

CONNOR - If I understand you correctly you are saying that the analysis of the spatial heterogeneity of a natural ecosystem is related to the process of replacement. And that this should be the basis for designing a stable agroforestry system which should mimic the natural system. It seems to be not only too ambitious an immediate objective but also one which is assumed and not proven. Therefore it is necessary to design simple, managed mixtures in which long-term natural vegetation is not a necessary component. Do these have parallels in nature?

OLDEMAN - For an example of an existing and demonstrated forest-like complex system you should look at Ms Michon's paper (see this volume). As to simple natural forest you need only look into Kahn's thesis on regeneration in the Ivory Coast (*see in references. Ed.*) and you will see that early secondary succession is less complex than you suggest.

CONNOR - The pattern and processes representing stages in reproduction must be known. Why should this be necessarily so in agroforestry?

OLDEMAN - We are designing ecosystems in which trees and crops have equal opportunities, each in their appropriate niche.

BUDOWSKI - With reference to your Figure 7. There may be some interesting findings. For example, in wet areas you get trees with as deep a rooting system as in dry areas. I find it undesirable to associate depth of the root with water. What kind of root systems should we aim for? And how should they be managed in wet areas?

OLDEMAN - We do not have sufficient information on root systems in most plants and, hence, generalization remains dangerous. We need to conduct a lot more research in this field.

STEPPLER - Looking at and imitating natural systems, and then continuing just to improve natural ones may not be profitable. Do you not think that there is a need to develop *new* systems rather than just mimic existing ones?

OLDEMAN - I agree. Transformations can be in larger or smaller steps leading away from the natural system. The transformation should be prudent, and small, in newly settled areas, and there is always an advantage in leaving natural checks.

STEPPLER - 'Gardening' research is often very personal (site-specific). You will realize that, with agroforestry, the problem is one of the degree of aggregation to the point of getting a definite unit to work.

OLDEMAN - 'Gardening', in its widest sense, can be used to provide technical background information for agroforestry purposes. When devising the internal technical aspects of systems, the experiences from gardening should assist in the provision of much information to be used in agroforestry design. This design should not be 'personal', but it has to appear so simple as to be 'user-friendly', whatever its inner complexities may be.

SYSTEMS ANALYSIS IN PRODUCTION ECOLOGY

R.S. LOOMIS and C.E. WHITMAN
Department of Agronomy and Range Science,
University of California, Davis, California, USA.

ABSTRACT. In the context of plant research 'systems analysis' has come to mean the analysis of cause - effect pathways, as well as the construction and use of simulation models in complex systems. Simple conceptual or process models to develop hypotheses are also valuable. Examples of simple models are given and more complex agricultural examples of the holistic cause - effect approach to problem solving are outlined. The first of these uses an analysis of the growth and development of alfalfa (*Medicago sativa*) based on research data. The second is a conjectural cause - effect model of a maize-bean intercropping system. The same type of approach will be valid for agroforestry when the information to establish quantitative budgets is available. Meanwhile even fragments of knowledge about control functions can help to formulate hypotheses for interpreting agroforestry systems and to design improvements. In considering such models agroforestry should be viewed in a continuum with other agricultural and forestry situations.

INTRODUCTION

Production ecology is concerned with the integration of physiological processes such as photosynthesis which lead to the accumulation of biomass and crop yield. Knowledge of the plant - environment interactions which are involved helps us in two ways. On the one hand, a better job of farming can be done, since we have a rational basis for diagnoses and decisions on factors such as choice of cultivar, spacing, timing and the inputs of nutrients. On the other, the information can be used for designing improvements in the farming system.

Our understanding of some production processes is very advanced. Photosynthesis, plant nutrition and microclimatology can be placed in that category. In other areas, such as plant development and temperature responses, the information is still very primitive. Weaknesses also exist in our abilities for detailed integration of the cause - effect relations which

determine yield.

New methods are gradually emerging for prediction of yield from holistic analyses of component physiological processes. These methods have been termed 'integrative physiology' (Loomis *et al.*, 1979) and are one example of the increasing importance of 'systems analysis' in agriculture. Other examples are found in nutrient cycling (Frissel, 1977), grazing studies (Innis, 1978), and pest management (Ruesink, 1976).

Systems analysis has come to have two connotations: analysis of the cause-effect pathways in a complex system (Watt, 1966); and the construction and use of simulation models of complex systems (de Wit and Goudriaan, 1974).

The importance of simulation models was stimulated by the general availability of computers and by Forrester's (1961) introduction of state-variable methods. In the state-variable approach, the real quantities of various components of the system (such as the amounts of nitrogen in soils and crops) are the variables which describe the 'state' of the system. As in the real world, the state-variables are advanced in time according to the rates of various ecological processes (e.g. nitrogen uptake by plants, residue decomposition, and mineralization of organic matter). D.J. Connor (this volume) outlines the application of this method to the analysis of crop productivity.

Other kinds of models are also useful in ecological assessments. Since systems analysis involves development of hypotheses (models) about how a system works, very simple conceptual models, simple process models, as well as large state-variable models can be employed according to one's objectives. We can examine such models here briefly. What will emerge is that systems analysis is really a way of thinking about complex systems. This is an important point since it defines systems analysis as an important methodology for agroforestry research.

SIMPLE QUALITATIVE MODELS

A classic example of a simple qualitative model is the hypothesis that heritable traits are transmitted to the next generation in units termed genes. This very simple concept proved to have profound influences in biology. It seemed to explain many observed phenomena such as segregation, and it served as the basis for an enormous increase in experimentation. The concept led to a new way of looking at plants and animals. Particularly important, the hypothesis was vulnerable to tests, and once validated, it could be applied to nearly all aspects of heredity.

Most scientific disciplines are structured around similar conceptual models. In crop ecology, for example, vegetation is examined as a 'community', 'trophic chains' exist from crop to animal to man, and the relative growth rates of plant shoots and roots are controlled by 'functional balances'.

SIMPLE QUANTITATIVE MODELS

We can sometimes extend qualitative hypotheses into simple mathematical statements. The 'limiting factor' approaches common in crop ecology provide good examples. The idea that nutrients, temperature, light and water can simultaneously, or separately,

limit crop growth leads naturally to response functions describing increases in plant growth in relation to increasing levels of the limiting factors. Mathematically, we find that rectangular hyperbolas, Mitscherlich functions, polynomials, and a host of other expressions may fit nutrient response functions.

Fick's first law of diffusion provides another example because it applies so well to flux analyses (gas exchange by leaves, ion movement to roots, and so on). That law takes the form:

$$J = -k\ (dc/dx)$$

or, flux = a conductivity gradient.

The gradient is determined by the difference in substance concentrations between source and sink, the minus sign denotes movement from regions of high concentrations to regions of lower concentration, and the conductivity term, k, describes the capacity or ease of transport. The reciprocal, 1/k, takes the form of a resistance (r) to transport so that:

$$J = -(1/r)\ (dc/dx).$$

The resistance analogy is useful in thinking about water loss from plants (stomatal resistance) and relates readily to the Ohm's Law version of the flux equation:

$$I = E/R$$

or, electrical current = potential drop/resistance.

Water use efficiency (WUE) is an example, at a higher level of organization, of a simple quantitative model applicable to vegetation. Its basic form:

$$Y = k \cdot T$$

or, yield = WUE transpiration

seems to hold well in environments with moderate evaporative demand while a modified form:

$$Y = m \cdot T/T_o$$

where T_o is potential transpiration, fits better with high evaporative demand (de Wit, 1958). These simple generalizations can be derived from more basic considerations of Fick's law fluxes of water and CO_2 exchange by leaves. In this form, they serve as very practical tools in studies of crop production.

COMPLEX MODELS

The simple models generally deal with one or two important processes at a time. Yield formation by a community of crop plants is much more complex. We must now deal simultaneously with many processes and limiting factors. At this point, it becomes very difficult to assemble all of the relevant processes and state variables without some memory aids. In addition, the dynamic nature of plant - environment interactions requires frequent iteration of the assembled model until a final result is simulated. The use of computer models solves both problems: the retention of very large amounts of information, and the process of making very large numbers of calculations.

Connor's example with wheat, in this volume, shows this clearly. It also illustrates that large models require a considerable knowledge of the system. In fact, one of the important uses of large models is the identification of missing information and this helps to establish research priorities.

SYSTEMS ANALYSIS AS A WAY OF PROBLEM SOLVING

Systems analysis is not limited to the more formal aspects of model conception and development. Returning to the idea of systems analysis as a holistic, cause-effect assessment of a complex system, we find a broad range of uses for systems analysis in the everyday efforts of agriculturalists. This is the area where systems analysis will have the most utility for agroforestry since systems thinking is particularly useful in problem-solving and in the exploration of new systems.

An example

This approach has been used by us in recent work aimed at characterizing the growth and development of alfalfa (lucerne; *Medicago sativa* L.) under Californian conditions. This perennial leguminous forage crop has been grown widely since Roman times. In California, it occupies 400,000 ha of irrigated land (4 per cent of total cropland). Yields range up to 30 mt of hay $ha^{-1}yr^{-1}$ although the average is only 12 mt.

The main issues in our research were to determine the factors affecting productivity and stand persistence over years. Our group had had relatively little experience with the crop so we adopted a two-tiered approach. At one level, we focused on specific issues such as leaf photosynthesis and root-crown anatomy which were known to be important. At the second level, we attempted an ecological description of what the crop does during regrowth after cutting. This was done through harvests at 5- to 7-day intervals in a commercial field to establish growth curves over several cutting cycles. Separation of plant parts at each harvest provided a view of photosynthate partitioning. The idea of this 'nonexperiment' was to establish a baseline picture of regrowth from which we might draw ideas regarding the controls of productivity.

Dry matter yields. The results of dry matter sampling for one of the cutting cycles are illustrated in Figure 1. The yield of oven-dry forage for this late summer cycle was 2950 kg ha^{-1}. Earlier cycles gave heavier yields while later ones were lower, following the pattern of solar radiation and the tendency for alfalfa to become dormant in the fall. Total yield for five cycles over the entire growing season was near 20 mt ha^{-1}.

In addition to stem and leaf fractions, we distinguished above- and below-ground 'crown' tissues (regrowth occurs by activity of axillary and adventitious buds on these stem and rhizomatous structures), and the central tap root. Only the upper 5 cm of the tap root was sampled; fibrous roots and nodules were not sampled. The yield was near 1500 kg ha^{-1}. This small portion of tap root totalled 1500 kg ha^{-1} so we estimate that the actual yield of the entire root system may range upwards from 3500 kg ha^{-1}.

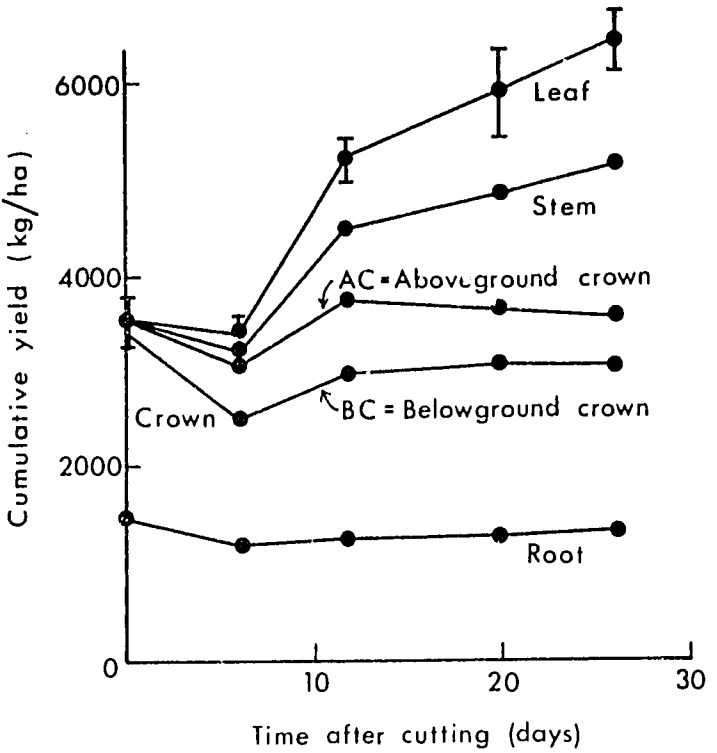


Fig. 1. The pattern of dry matter accumulation by an alfalfa (*Medicago sativa* L.) crop during a regrowth cycle. Sampling was conducted in a 3-year-old, commercial stand of a non-dormant cultivar. Each point is the mean of ten 0.1 m quadrats; standard errors were near 5 per cent of the magnitude of the means.

These rather simple results revealed a number of interesting points.

Lag period. There was no net production during the first seven days after cutting. During this first quarter of the regrowth cycle, buds were opening and cover was being re-established. The crown and root system showed negative growth. Analyses showed that this was due mainly to a decline in starch content and to the death of stem branches from which no regrowth occurred. The content of nonstructural carbohydrates in woody parts of the tap root declined from over 17 to about 12 per cent of dry weight during the first two weeks after cutting, and then returned to the original level during the last two weeks (an anatomical study is aimed at clarifying the role of the root cambium in providing new wood and bark tissues for carbohydrate storage).

Size of the perennial structures. Clearly, a very large amount of biomass is partitioned to perennial structures. Much more definition of the root system is required, and that has been given priority in current work. Since the total of perennial

structures seems to amount to 6000 or 7000 kg ha^{-1}, they represent a considerable reservoir of carbohydrates and nitrogenous materials to support regrowth. They also represent a potentially large cost in maintenance. At a relatively low maintenance requirement of 1 g glucose per 100 g root-crown material per day, as much as 70 kg photosynthate $ha^{-1}day^{-1}$ may be expended in maintenance respiration.

Peak growth rate. After the 7-day lag, crop growth rates (C; or slope of the total biomass curve) were positive, and biomass accumulated. The peak growth rate occurred during the second week and, for this cycle, reached 185 kg $ha^{-1}day^{-1}$. (Other cycles approached 300 kg $ha^{-1}day^{-1}$.)

Remarkably, this growth rate occurred with considerably less than full leaf cover. Many experiments with various crops have shown a linear relation between C and percent cover. Since cover increased from 12 per cent to only 50 per cent (0.3 to 1.9 leaf area index) during the second week, we expected C to increase above 185 kg $ha^{-1}day^{-1}$ during the third and fourth weeks as leaf area index increased to 3.7 and cover approached 100 per cent. But that did not occur. Rather, C declined to 77 kg $ha^{-1}day^{-1}$. The cumulative difference between 77 and 250 kg $ha^{-1}day^{-1}$, which might reasonably be expected during the last 15 days, is 2600 kg ha^{-1}. That behaviour seemed general for this field, and is also seen in data from other locations. However, there are other cases where yield accumulates continuously after the lag period.

Our attention quickly focused on possible explanations for the 2600 kg of 'missing yield'. This exercise in systems analysis led us to the following possibilities.

Water shortage. A growth decline of this sort could occur during drought. However, heavy irrigations were applied in the first and third weeks. Measurements of plant water status were made, but no visible signs of stress were noted and the plants used the soil moisture freely.

Nutrient shortage. Nitrogen, phosphorus and potassium are possible candidates as limiting nutrients. It is common for alfalfa forage to contain over 3 per cent N, 2 per cent K and 0.2 per cent P so the nutrient removal by a 20 mt crop can be very large. We do not expect deficiencies of K and P on this site and that was confirmed by the fact that plant analyses exceeded the critical nutrient concentrations used in the diagnoses of deficiencies.

The nitrogen analyses are presented in Figure 2. The standing crop of nitrogen and its distribution among plant parts followed a pattern very similar to that shown for dry matter. The main difference is the large proportion of nitrogen in leaves (5 per cent D.W.) at final harvest compared to stems and roots (2 per cent D.W.). The peak increase in nitrogen corresponds to peak C (second week). Here, we need data for the balance of the root systems and the nodules to establish a complete story. But it appears that the crop receives a single major contribution of about 60 kg N ha^{-1} during the second week, and very little thereafter. Whether that nitrogen is from the soil, fine roots, or nodules, is unclear. The nitrogen content of the crowns and

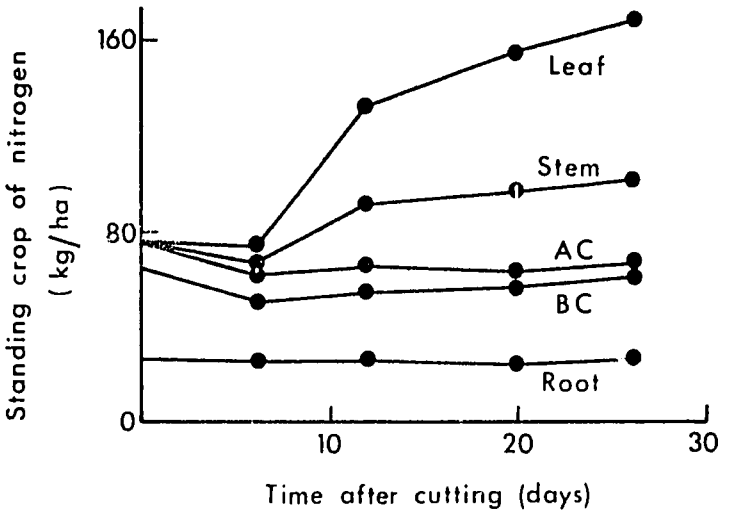


Fig. 2. Nitrogen yields for alfalfa crop presented in Figure 1.

sampled portion of the tap root declined from 2.0 to 1.8 per cent during this time. If the whole perennial structure (estimated at 7000 kg ha^{-1}) declined as much, that would account for 14 kg N ha^{-1} (0.002 × 7000). Perhaps cutting causes nodule and fibrous root decay, providing a single major release. The small gain in nitrogen during the last two weeks might reflect a re-establishment period for those structures.

Whatever the mechanisms, pulsations in nitrogen supply could account for the growth plateau seen in Figure 1 so nitrogen economy is being given a major emphasis in continuing work.

The diversion of photosynthate to replacement of nodules and to support nodule activity could contribute to the observed plateau effect in Figure 1. The actual cost of fixation, however, would not be great. The conversion of N_3 to NH_3 involves reduction of nitrogen by the addition of three electrons to each atom. Since respiration of a mole of glucose yields the equivalent of 24 moles of electrons, the ratio of assimilate use will be 3/24 mole glucose per mole NH_3 or (3 × 180) / (24 × 14) = 1.6 g glucose per g nitrogen. Thus, for the 60 kg N which appeared in this cycle, only 96 kg of photosynthate would be required. Even if we double that to account for nodule maintenance, the result is only a small fraction of the missing 2600 kg of yield. So we have to consider that fibrous root and nodule replacement as well as H_2 production by the nodules would be the major factors. Even if that accounts for the missing yield, one can still draw the interpretation that shoot growth came to be limited by nitrogen supply.

It is strange to think of a vigorous legume crop encountering a deficiency of nitrogen. This field appears to do very well in nitrogen fixation. With 20 mt of hay containing over 3 per cent N harvested each year for three years, more than 1800 kg N ha^{-1} has been removed. That amount is vastly greater than natural inputs through rainfall and dust. It also greatly exceeds the nitrogen which could be supplied from organic matter by this

desert soil. The high apparent rate of fixation, plus the oft repeated failure of agronomists to obtain alfalfa yield responses through additions of fertilizer nitrogen, leads one to be sceptical regarding nitrogen limitations. But it would appear that small amounts of inorganic nitrogen seem simply to replace an equal amount of fixation. Nodulation and fixation are both repressed in the presence of inorganic nitrogen (Evans and Barber, 1977). So, to be effective in increasing yield, considerably more than 600 kg N ha^{-1} would have to be supplied as fertilizer. Such rates have seldom been employed with alfalfa; in other words, the possibility is that the nitrogen responsiveness of alfalfa has not been tested.

Net decline in photosynthesis. Leaf photosynthesis rates sometimes decline dramatically with age. However, this seemed unlikely as an explanation for the missing yield, since alfalfa stems elongate indeterminately until slowed by heavy flowering. At final harvest, the canopy was dominated by recently expanded young leaves in the upper strata. In addition, laboratory studies revealed that the difference in maximum net photosynthesis rates of the youngest and oldest mature leaves was only 25 per cent (2.5 and 1.9 n moles CO_2 $cm^{-2}s^{-1}$, respectively).

These photosynthesis measurements were made on leaves grown at moderate light levels in glasshouses and under a high level of nutrition. If nitrogen was in short supply carbohydrates might be expected to accumulate in stems and leaves. Certainly, if that had occurred, some type of 'feedback inhibition' (Neales and Incoll, 1968) might also be expected under high light conditions in the field. An additional possibility is that photorespiration might be increased in the presence of high levels of carbohydrate (see, L. Tieszen, this volume). Both possibilities are now being investigated with plants grown under conditions with high light and restricted growth sinks.

Accumulated dry matter, as observed in Figure 1, integrates leaf net photosynthesis with respiratory activities of the whole plant. As noted earlier, maintenance respiration would be expected to increase as biomass increased and this could be a significant drain by the end of the cycle. There is also the possibility that maintenance respiration is substrate dependent, increasing as substrate supply increases. In addition, Lambers (1979) suggests that a high carbohydrate status in plant roots may induce uncoupled respiration from those tissues. In that way as with H_2 production by nodules, assimilates might be wasted away instead of contributing to dry matter production. Again, we see the need for a great deal more information about the underground structures.

APPLICATIONS OF SYSTEMS ANALYSIS TO AGROFORESTRY

The alfalfa case outlined above provides an example of a type of systems analysis which should be very useful in agroforestry research. The effort at cause-effect analysis, coupled with quantitative budgets, leads to a well-defined set of hypotheses and research objectives. Many of these can be tested further in simple field experiments so prospects for clarifying the production processes of this crop seem very good. We need similar

quantitative descriptions for agroforestry situations: what are the yields; by what pattern of events and processes do they accumulate; how do the yields compare with biological and climatic potentials?

Particular attention must be given to nutrient deficiencies and their interactive effects with light environments. The possibilities for overstorey shade to serve as a balancing mechanism for nutrient limitations are important. Greatly improved yields have been obtained with several crops when shade is reduced and nutrient supply increased. However, nutrients are often a main limitation to yield in many tropical and subtropical environments, including those where agroforestry is practised. Water will also be limiting at many sites. It is as well to examine such elementary relations before assuming that more subtle synergisms occur in mixed cropping.

An example for mixed cropping

Unfortunately we do not, as yet, have sufficient data from agroforestry systems to outline an example of the use of systems analysis in the cause - effect manner described above. We can take an agricultural mixed cropping situation, however, which will serve to elaborate the essential approach.

The maize - bean intercrop common near Nairobi, and in many other tropical regions, provides an example of nutrient limitations. Without fertilizer, grain yields on small farms may range from 1100 to 1350 kg ha^{-1} (Ackland, 1971). Since the grain has a nitrogen content of about 1.6 per cent, some 18 to 22 kg N ha^{-1} are removed with the grain; the total is increased by an additional 8 to 10 kg N ha^{-1} if the stover is removed also. If yields are to be maintained, this amount must be supplied to the soil from rain, dust, fixation by free-living bacteria, animal manures, and residues from the leguminous companion crop. Those inputs are area-dependent and small in amounts so we must allocate a relatively large soil area per plant if the maize is to grow reasonably well. Maize stands are often as low as 10,000 to 20,000 plants ha^{-1} on smallholders' plots so that each plant occupies an area of 0.5 to 1.0 m^2. With a rooting depth of 1.5 m it has a soil monolith of from 0.75 to 1.5 m^3 to exploit.

At this spacing, the maize plants have only about half the amount of nitrogen they could use but that is enough to produce a modest yield of grain. But ground cover is by no means complete and only a portion of the incoming sunlight is intercepted by the maize. In addition, full utilization of available soil water is not achieved. Thus, a companion crop could beneficially be introduced to share these resources, *but it should be noncompetitive with maize for that crop's limiting factor, nitrogen*. Hence, an understorey grain legume is a promising candidate to provide a complementary yield and a possible additional input of nitrogen.

In this kind of very simple cause - effect modelling we may wish to alter the assumptions by changing estimates of grain yield, spacing, or nitrogen inputs, but the point to be made here is that such an assessment enables us to state a hypothesis. This can then be tested by some simple field experimentation. In this case, by adding fertilizer and by replacing the space occupied by the grain legume in the mixed crop with more maize. If the arguments are correct, then in the absence of any additional

nitrogen fertilizer, the yield of the maize crop will probably decline due to the smaller input of nitrogen; but with fertilizer nitrogen maize yields should increase drastically. One should also test whether a rotation of maize and legume monocultures would perform as well or better than the intercrop. At Davis, California, with 450 mm rainfall, and with nitrogen not limiting, 10 mt of maize grain has been obtained without irrigation and over 15 mt with irrigation. But, populations near 70,000 plants ha^{-1} are required to achieve this.

Interactions and factor identification

Plant population - nutrient - water - shade interactions are also likely to be very important in agroforestry. Such interactions are studied most easily with a succession of simple, single factor or double factor experiments. Experiments with a greater number of factors become almost impossible to interpret, except by using mathematical models. It is also evident that one may need to distinguish between shade and nutrient cycling roles for the overstorey trees. Nutrient analyses, fertilizer experiments, and shade removal are useful tools for that purpose. Clearly, problems of this sort are not studied easily in small plot situations with single plants in complex mixtures. One needs relatively large, uniform plots to establish nutrient cycling, water, shade and plant population responses. The resulting principles can be applied in the interpretation of small plots. Other factors such as convenience and risk are also important considerations in subsistence farming, of course.

The word *predictive* is important. We are looking to identify the rules governing plant growth. Those rules will take various forms. 'Nitrogen is limiting; the nitrogen response function is a diminishing return.' 'Deciduous leaves from the companion leguminous tree will supply 10 kg N ha^{-1} each year, leaching is not a problem.' 'Shade lowers the harvest index of the crop.' And so on. These fragments of knowledge of control functions become the basis of our model of the agroforestry situation. We then have a foundation for monitoring and interpreting crop performance, and for designing improved systems.

CONCLUSIONS

Agroforestry is not an end in itself but a means to achieving safe, stable supplies of food, fodder, fibre, and other outputs, often from difficult environmental and economic situations. But we must be careful not to view agroforestry situations in isolation from the performance of the same plants grown in monoculture. The monocultures provide the basis for interpreting nutrient and plant population responses, and yield potentials. Mixed cropping with trees can be viewed, in a continuum with other agricultural and forestry situations, as a system designed to accommodate to some biological, environmental or social limitations. Soil problems related to nutrient cycling and supply, or erosion, will be major factors. But the situations will be more complex and less transparent to analysis than the more conventional cropping systems. They will tax our abilities for systems analysis whether in problem-solving or in formulation of simulation models.

ACKNOWLEDGEMENTS

The work with alfalfa reported here was made possible by a grant from the UC/IPM programme. Assistance in that work was provided by a large number of people including P. Meyerhof, R. Travis, D.W. Rains, L. Teuber and J. Jones.

REFERENCES

Ackland, J.D. (1971). "East African Crops." Published jointly by FAO, Rome and Longmans, London.

Evans, H.J. and Barber, L.E. (1977). Biological nitrogen fixation for food and fibre production. *Science* 197, 332-339.

Forrester, J.W. (1961). "Industrial Dynamics". M.I.T. Press, Cambridge, Massachusetts, USA.

Frissel, M.J. (Ed.) (1977). Cycling of mineral nutrients in agricultural ecosystems. *Agro-Ecosystems* 4, i-viii, 1-354.

Innis, G.S. (Ed.) (1978). "Grassland Simulation Model." Ecol. Studies Vol.26. Springer-Verlag, New York.

Lambers, J.T. (1979). "Energy Metabolism in Higher Plants in Different Environments". H. Lambers, Groningen, The Netherlands.

Loomis, R.S., Rabbinge, R. and Ng, E. (1979). Explanatory models in crop physiology. *Ann. Rev. Plant Physiology* 30, 339-367.

Neales, T.F. and Incoll, L.D. (1968). The control of leaf photosynthesis rate by the level of assimilate concentration in the leaf. A review of the hypothesis. *Bot. Rev.* 34, 107-252.

Ruesink, W.G. (1976). Status of the systems approach to pest management. *Ann. Rev. Entomol.* 21, 27-44.

Watt, K.E.F. (Ed.) (1966). "Systems Analysis in Ecology". Academic Press, New York.

Wit, C.T. de (1958). Transpiration and crop yields. *Versl. Landb. Onderz.* 64.6. 88 pp.

Wit, C.T. de and Goudriaan, J. (1974). "Simulation of Ecological Processes". Centre Agric. Publ. Doc., Wageningen, The Netherlands. 159 pp.

DISCUSSION

KOZLOWSKI - Perhaps the alfalfa plants were water stressed. Did you measure stomatal aperture?

LOOMIS - No. But alfalfa has little stomatal control. Irrigation occurred at different times in different cycles with the same result. Water used seemed to match the potential Et of 6 mm of water day^{-1}. In general, the plants were never short of water.

KOZLOWSKI - The plants may have suffered some midday water stress.

LOOMIS - I agree. We are also considering that water use could relate to respiration rate (as an explanation of the falling off in crop growth rate). Maintenance respiration can amount to a loss equal to around 1 per cent of the biomass per day, due mostly to protein increases with temperature. But the lowered soil temperature and the high rate of water use at full cover kept temperatures low and should have minimized respiration.

OLDEMAN - Does alfalfa have much cambial activity?

LOOMIS - Yes. We are in the middle of a time analysis of root anatomy. But this was mostly included in the dry matter measurements. The system did not appear to be carbohydrate limited. It could be that nitrogen deficiency, or some other limit to cambial activity resulted in feedback inhibition to photosynthesis. That is, that the system was sink limited. It is not likely to be limited by transport.

HUXLEY - Do you not need active root growth in order to produce controlling hormones?

LOOMIS - I think of hormones as being like on/off switches. I do not see that they could explain the type of result we got.

HUXLEY - The effect of cutting alfalfa may be so drastic as to perturb the whole system; including the balance of hormone regulators. With regard to the comment on transport we traced nitrogen in cowpea throughout its life cycle and found that a problem was adequate transfer of nitrogen at pod filling.

NAIR - An important part of nutrient recycling, of benefit in agroforestry systems, could be the leaching of nutrients from leaves of the upper-storey plants, which are then intercepted in the lower storey.

LOOMIS - That is true. But it is interesting that there is a lower equilibrium of soil organic matter in forest systems (and thus of organic nitrogen) than there is under grass. This may be due to a different timing or pattern of residue decay with more chance for losses.

NAIR - More nutrient cycling is involved in intensive systems of production, therefore more nutrients could be lost.

LEYTON - Did you measure the leaf area index in your lucerne community?

LOOMIS - Yes, it rose from 0.3 at one week to around 2 at two weeks, and then rose to a maximum of about 5.

JACKSON - Did you actually measure light interception?

LOOMIS - Yes, but not very well. We first tried a system using the lambda 1 m silicon cell bar, but this was not easy to place in the alfalfa canopy. We subsequently used an indirect method using the vertically projected shadow areas taken from weekly photographs.

LEYTON - Are there published figures for net CO_2 flux for lucerne?

LOOMIS - There are a few studies. Most of the available information, however, involves growth measurements of recorded sward yield at each harvest.

OLDEMAN - Does alfalfa show phasic or rhythmic growth?

LOOMIS - That should not affect these results. Flowering had just begun at final sampling and we were well away from the dormancy traits which most cultivars show in full winter conditions.

ECOSYSTEM STRUCTURE AND FUNCTIONING: SOME INTERACTIONS OF RELEVANCE TO AGROFORESTRY

E.F. BRUNIG and N. SANDER
University of Hamburg, Institute for World Forestry, Hamburg, West Germany.

ABSTRACT. The biochemical and geometrical architectural structure of tree containing mixtures of crops may be considered analogous to a genetic code which determines the functioning, performance and dynamics of the system. Except that this code itself is dynamic and continuously adapts, in an interactive manner, to variable physical, chemical and biotic environmental factors. Examples of such adaptation to site conditions in natural forest are described. Further research is necessary on the performance of crop species mixtures and alternations; on possibilities to stabilize nutrient supplies and cycles; on interactions between crop species and site climate, and its fluctuations; on soil properties, soil management and crop performance; and on the interactions between crop structure, microclimate, soil biology, soil dynamics and nutrient cycling. Especially, there is a need for research on the effects of continued cropping, either of identical or alternating cropping patterns. The development of descriptive, functional and predictive dynamic system models is essential to cope with the complexity of factors and interactions involved.

SOME FEATURES OF THE NUTRIENT CYCLE

In the system context

The nutrient cycle in natural tropical moist primary forest is closely linked to, and interacts with, the cycles of organic matter and water. The schematic diagram in Figure 1 illustrates the input, throughput and output channels and some of the store sizes of organic matter. The growing stock, that is the amount of living organic matter, naturally varies widely with the site and the developmental phase of the vegetation. Information is insufficient for a reliable estimate of global and regional total stocking and of mean stockings per hectare, but the ranges and means shown in Figure 1 give an approximate indication of

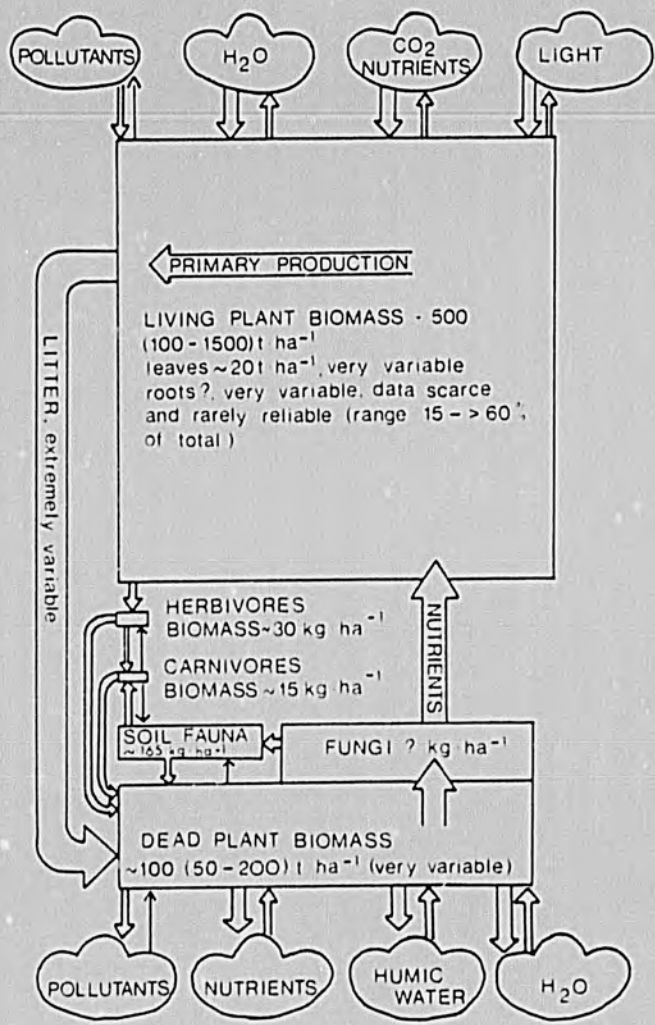


Fig. 1. Aggregated model illustrating inputs, stores and flows and outputs of some factors and elements in the biomass cycle of mature, humid, equatorial tropical, predominantly evergreen, lowland forest. The very wide range of variation of some of the stocks and flows of phytomass and the lack of information on some elements are indicated in the drawing. (From Brunig, 1982).

the vegetative growing stock in humid tropical forests, which is generally larger than in temperate forests.

The amount of organic matter in the soils of equatorial and seasonal, tropical forests is on average a little lower than in evergreen and deciduous, temperate forests. Bolin *et al.* (1979, Table 1.3, p.156) quote 8 kg m^{-2} organic matter in the whole soil profile in equatorial rainforest, 10 kg m^{-2} in tropical, seasonal forest, and 10 to 15 kg m^{-2} in temperate forests.

Table 1. Amount of material in each soil horizon on the oxisol site in the International Amazon Rainforest MAB-Project at San Carlos de Rio Negro, Venezuela (Jordan and Centro de Ecologia, 1980) (in kg ha^{-1}).

	Total mass*	Ca	K	Mg	P
Soil surface mat					
Roots+	20,207	17.8	17.3	5.6	7.4
Organic matter+	28,585	12.9	31.4	7.1	7.7
Mineral soil	21,808	0.4++	0.7++	0.1++	5.0+
Subtotal	*[illegible]*	*31.1*	*49.4*	*12.8*	*20.1*
Sand horizon					
Roots+	28,318	26.5	25.5	5.7	9.4
Organic matter+	77,005	34.1	83.5	18.9	20.5
Mineral soil	1.269,770	22.3++	41.5++	7.9++	292.2+
Subtotal	*1.375,093*	*82.9*	*150.5*	*32.5*	*322.1*
Clay					
Roots+	7,041	4.5	3.6	1.4	1.7
Total for soil organic profile	161,156	118.5	203.5	46.7	343.9

+ total ++ extractable

* From Stark and Spratt (1977), weight of the respective fraction in kg ha^{-1}).

Litter decomposition, humus formation and residence time of soil carbon vary widely with biological, physical and chemical conditions of soil and litter, and the depth of the decomposition in the soil. According to Bennema (1977) residence time at the soil surface is in the order of years, at 30 cm depth of hundreds of years. Very high values occur in tropical humus podzols and peatswamps. In Borneo, according to Anderson and Muller (1975) the age of deep peat deposits may exceed four to six thousand years.

The importance of organic matter as a nutrient store is shown by the data from San Carlos in Table 1. The organic matter fraction of 161,156 kg ha^{-1} contains most of the total soil store of Ca, K, Mg and P. The same applies to nitrogen. This feature is typical for natural humid tropical forest ecosystems.

Figure 2 shows in greater detail the compartments and processes involved for the example of the nitrogen cycle. Both diagrams in Figures 1 and 2 illustrate the tropical forest ecosystem as an open system with inputs and more or less matching outputs of energy, water, carbon, nutrients and organic matter, with the living and dead biomass acting as effective filters and sinks.

Nutrient Inputs

The most important source of nutrient input in the humid tropics is precipitation from the atmosphere of solutes and particles,

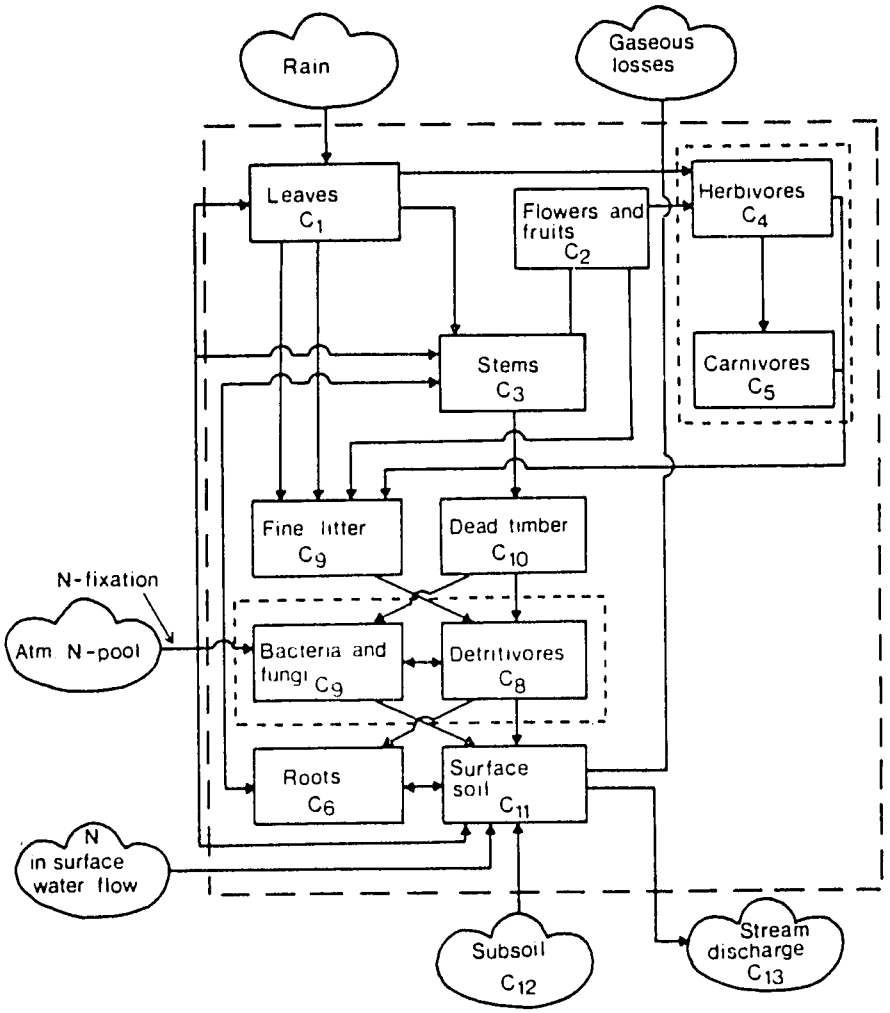


Fig. 2. Schematic model of nitrogen cycling. Rectangles represent compartments within the ecosystem, flows are represented by arrows, input sources or output sinks are represented by irregular shapes. Compartments not directly studied in the San Carlos Project but considered important as process controllers are surrounded by a small-dashed line. The long-dashed line delimitates the rainforest ecosystem toward its environment. C = compartment. (Adapted from Herrera and Jordan, 1980).

and in addition microbial fixation of nitrogen. The existing data on rainfall, water cycle and water balance, nutrient contents, throughflow and outflow in tropical natural and managed forests are neither plentiful nor very reliable but, with caution, the scale and direction of the flows may be estimated. The rainfall and its nutrient content vary with location, season, year and weather situation. A selective example of more reliable research data is reproduced in Table 2.

The nutrient content often increased when water percolates through the canopy. Such increases of nutrient contents in

Table 2. Nutrient contents of annual precipitation in six localities in perhumid and seasonal tropical climates (in kg ha^{-1}).

Place	Rainfall mm	N	P	K	Ca	Mg
Manaus, Amazon (1)	1771*	10.0	0.3	n.d.	3.7	3.0
Pasoh, Malaya (2)	2831	13.5	n.d.	6.4	4.2	0.7
Kade, Ghana (3)	1850	13.0	0.4	16.0	11.0	10.0
E. Creek, Papua New Guinea (4)	2694	n.d.	n.d.	0.8	0	0.3
Malaya (5)	2300	n.d.	n.d.	12.5	14.0	3.3
Panama (6)	1930	n.d.	1.4	9.5	29.3	4.9

*seasonal

(1) Stark and Spratt, 1977; (2) Manokaran, 1980; (3) Nye and Greenland, 1960; (4) Turvey, 1974; (5) Kenworthy, 1971; (6) Golley *et al.*, 1975. n.d. = no data available.

throughfall and stemflow in natural tropical forests have been observed in many cases. Main sources are dust particles deposited on plant surfaces, leachate from leaves and leachate from epiphytes such as lichens (Forman, 1975).

The reliability of calculations of nutrient contents and annual totals in throughfall and stemflow is rather limited, and published data exhibit considerable variation (Table 3). In the San Carlos area (Table 3(*a*)) the small differences of mineral content between the adjacent oxisol and spodosol sites are incidental but, except for potassium and nitrogen, the lower content of minerals in the throughfall on both sites appears to be significant. Similarly, differences between above canopy rain and throughfall on the ground were observed for calcium and phosphorus at six tropical locations. Calcium increased on four sites and decreased on two sites, and phosphorus on all the three sites where it was measured (Table 3(*b*)). Variation due to location, site and weather is supplemented by additional variation due to the physiological characteristics of the trees, and the nature of the differences in the epiphytic flora and fauna. Existing data for absorption in the canopy and for leaching and removal from leaves, phyllospheric vegetation and bark must therefore be treated with caution. The substantial variation in relation to tree species, species association, microsite, season and year must be considered if generalizations are made from local and/or short-term observations.

STRUCTURE - SITE - ENVIRONMENT INTERACTIONS

It is now commonly accepted that there are close and complex interactions between the floristic and geometric structures of vegetation stands, the physiognomic and biochemical properties of the plants, the climatic and edaphic site conditions and the dynamics of the ecosystem. Floristic, geometric and biochemical structures, both at plant and at vegetation system levels, can be interpreted as adaptations to the physical and chemical environment (Figure 3 and Brunig, 1970, 1971, 1976). Rather typical examples of changes in gradient of the geometric and floristic

Table 3. Mineral contents of above canopy rain and ground level throughfall.

(a)	Oxisol		Spodosol	
	Rain	Throughfall	Rain	Throughfall
Ca	27.0	3.6	28.4	6.7
K	23.4	17.1	24.6	28.9
Mg	3.4	1.3	3.5	4.0
NH_4-N	21.2	25.0	21.7	33.2
PO_4-P	24.8	10.7	24.9	5.1
SO_4-S	44.3	16.7	46.6	19.6
(b) Throughfall in kg $ha^{-1}yr^{-1}$	Calcium		Phosphorus	
Trop. montane (1)	21.8	23.9	-	-
Trop. moist (2)	29.3	37.0	1.0	0.6
Trop. rainforest (3)	0.0	23.3	-	-
Trop. rainforest (4)	14.0	28.9	-	-
Trop. rainforest (5)	27.0	3.6	24.8	10.7
Trop. rainforest (6)	28.4	6.7	24.8	5.1

(a) Amounts in kg $ha^{-1}yr^{-1}$ of nutrients in two forest associations in an Amazonian rainforest at San Carlos de Rio Negro, 1975-1976.
(b) Calcium and phosphorus in various tropical forests.
(1) Jordan, 1976, Puerto Rico. (2) Golley *et al.*, 1975, Panama.
(3) Turvey, 1974, New Guinea. (4) Kenworthy, 1971, Malaya.
(5) and (6) Jordan *et al.*, 1980, Amazonia.

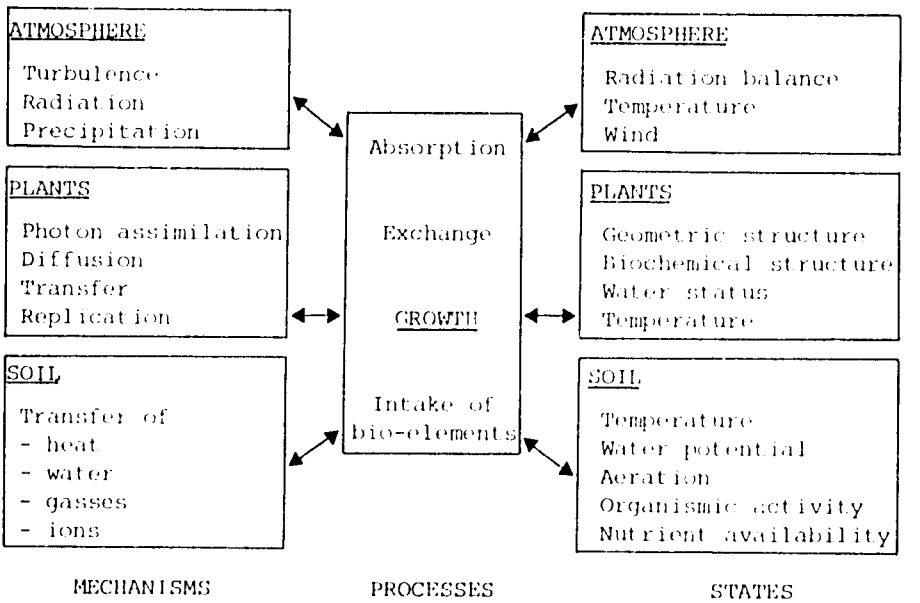


Fig. 4. Major components and interactions in an agroforestry crop which influence performance and development of the plants and the crop (adapted from Elston and Monteith, 1975).

structures of mature natural forest stands in humid evergreen tropical lowland forest in Borneo and in the Amazon basin are shown in Figure 4. The catenas of sites and soils corresponding to the changes of vegetation in Figure 4 are shown for the same ecosystem in Figure 5. The three catenas show some common features which are relevant to the subject. The more mesic and more favourable soils on the left carry tall and complex, species rich and mesophyllous vegetations with high storage levels of living phytomass, intensive turnover of phytomass, rapid and effective nutrient cycling, efficient nutrient readsorption during the decomposition phase, intensive microbial activity, high transpiration rates in relation to the rainfall rates, ranging from about 1500 to 2000 mm per year.

The more xeric, periodically rainflooded, alternatingly extremely dry, extremely oligotrophic soils on the right carry low, simple, species poor, sclerophyllous and xeromorphic vegetation. Typical are high degrees of evergreeness, low levels of biomass stocking, slow growth and turnover, slow decomposition of litter and a low speed of nutrient cycling. The aerodynamically smooth, sclerophyllous, highly reflectant canopy transpires much less than the previous types, usually less than 1000 mm per year. Low levels of micro-organismic activity are characteristic and related to the unbalanced water regime, lack of nutrients and prevalence of antibiotic polyphenolic substances. The reduced turnover rates, slow decomposition and accumulation of soil organic matter may be devices to reduce losses of essential nutrients. Typical for these forests on oligotrophic soils are high contents of polyphenols (condensed tannins) in the trees, common occurrence of mycorrhizas, dense root and raw humus matting, root growth on decaying litter and living stems (see Plate elsewhere in this book). Obviously, these aerial roots scavenge nutrients from decaying leaves, stemflow and water drip.

Along the gradient of decreasing fertility, stand stature, aerodynamic roughness and species richness decrease; simultaneously, litter and raw humus accumulate and humic hard pans are formed. High levels of humic substances on and in the soils improve the water regime and the living conditions for microorganisms. Improvement of nitrogen and phosphorus availability by humic substances in many acid soils is well documented and a common practical experience. But there is also evidence of direct effects of humic substances on the performance of plants (see below).

SOME NUTRIENT PROCURING AND PRESERVING MECHANISMS

On the more mesic soils where the nutrient supply is better, we find a combination of larger leaves, a greater tendency to deciduousness, an aerodynamically rougher canopy, and consequently greater aerial turbulence from free and forced convection, a reduced atmospheric diffusion resistance to heat and vapour fluxes, more intensive fluxes of sensible and latent heat, high rates of daily and annual transpiration and a rapid organic matter turnover. These features combined contribute to the successful scavenging, fixing and preserving of nutrients through high levels of biological activity and, consequently, a rapid and efficient nutrient cycling.

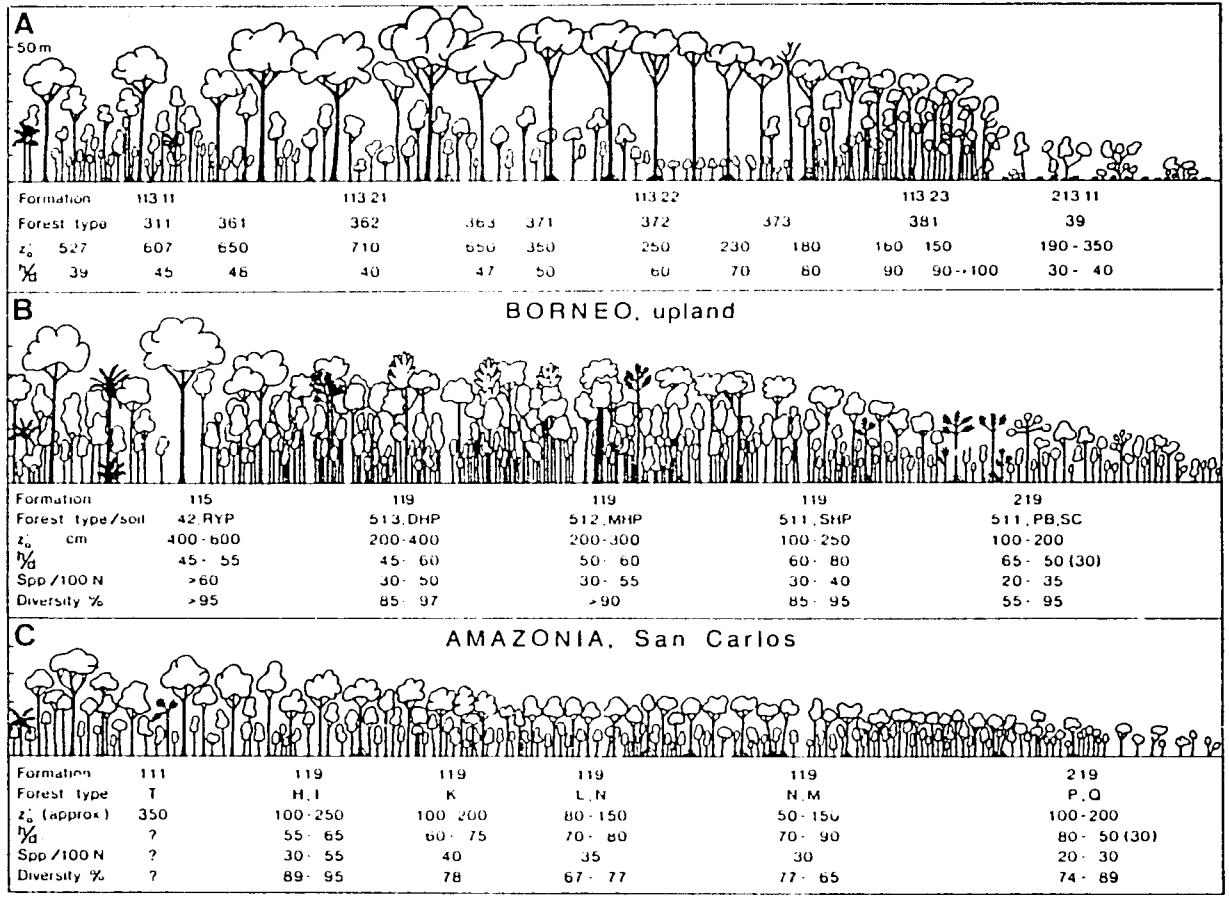

A
50m
Formation 113.11 113.21 113.22 113.23 213.11
Forest type 311 361 362 363 371 372 373 381 39
z_0 527 607 650 710 650 350 250 230 180 160 150 190-350
h/d 39 45 46 40 47 50 60 70 60 90 90-100 30-40
B
BORNEO, upland
Formation 115 119 119 119 219
Forest type/soil 42,RYP 513,DHP 512,MHP 511,SHP 511,PB,SC
z_0 cm 400-600 200-400 200-300 100-250 100-200
h/d 45-55 45-60 50-60 60-80 65-50 (30)
Spp/100 N >60 30-50 30-55 30-40 20-35
Diversity % >95 85-97 >90 85-95 55-95
C
AMAZONIA, San Carlos
Formation 111 119 119 119 119 219
Forest type T H,I K L,N N,M P,Q
z_0 (approx) 350 100-250 100-200 80-150 50-150 100-200
h/d ? 55-65 60-75 70-80 70-90 80-50 (30)
Spp/100 N ? 30-55 40 35 30 20-30
Diversity % ? 89-95 78 67-77 77-65 74-89

Figure 4.

Fig. 4 (Opposite) Sections through mature natural forest stands along ecological gradients of the site and soil in perhumid (2000 to 4000 mm), nonseasonal or weakly seasonal, equatorial lowland climate in Borneo and the northwest Amazon basin. The sections were constructed from ecological field research plot data and aerial photo interpretation of the author (sections B and C) supplemented with published data (section A; Anderson, 1961).

Section A. Transect through a deltaic peatswamp forest from phasic community 1 (formation 113.11, forest type 311) through phasic community 2 (113.21, 361-363), phasic community 3 (113.22, 371-373), phasic community 4 (113.23, 381) to stunted, open phasic community 6 (213.11, 39). The corresponding peat dome development is shown in Figure 5, section A.

Section B. Transect from mixed dipterocarp forest (115, 42) on sandy, loamy ultisol through a sequence of types of kerangas (119, 513-511) on spodosol to stunted, closed to open kerapah and dry peat woodland (219, 511). Kerapah also can assume the structure of 512 and 511 under more favourable site conditions. The sequence corresponds to the left part of the soil catena in section B in Figure 5.

Section C. Transect through the natural forest observation area of the International Amazon Rainforest Ecosystem Project at San Carlos de Rio Negro from 'tierra firme' forest (111, T) through various association groups (119, H to M) to closed (219, P) and open (219, Q) bana woodland). The corresponding soil and site catena is shown in section C in Figure 5. The catena in this section corresponds ecologically to section B.

Explanations.

Formation: major classification unit of vegetation.

Forest type: subunits according to structural features and floristic composition.

Soil (in section B): abbreviations for red yellow podzol (ultisol); deep, medium and shallow humus podzol (spodosol); peat bog or scelettal soil.

z_0': estimator of the aerodynamic roughness parameter of canopy; indicates capacity for intake of energy and turnover of energy and matter.

h/d: mean height/diameter ratio of top canopy trees in the A and B strata, mean values of sample plots; indicates vigour and stability.

Spp./100 N: species number per 100 individual trees; species richness.

Diversity %: value of the McIntosh diversity index in per cent of the maximum possible for the given spp./100 N; expresses diversity within stand.

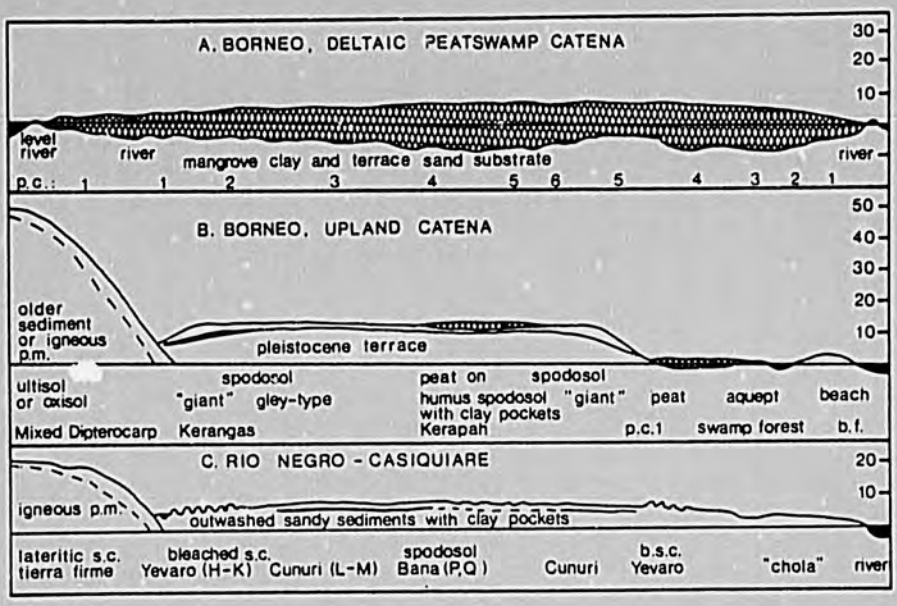


Fig. 5. Schematic sections through catenas of mesotrophic to oligotrophic soils in Borneo (A and B) and in the northwest Amazon basis (C). The sections A, B and C correspond to the sections through forest communities in Figure 4. Humic (iron) pans are drawn black, peat is shown hatched, rivers are shown black.
A. Transect through a deltaic peatswamp with forest phasic communities 1 to 6.
B. Transect through an encased pleistocene terrace; to the left a hill with mixed dipterocarp forest on loamy ultisol or oxisol soil, on the terrace the sequence of soils is from deep humus (iron) to shallow podzol or spodosol and finally to a woodland peat bog of the kerapah type. To the right follows a fringing peatswamp and a riparian freshwater swamp and finally a sandy, recent beach ridge.
C. Section through the International Amazon Ecosystem Project area at San Carlos de Rio Negro from a lateric hillock with oxisol through a sequence of spodosol soil types to the bana with shallow spodosol in the centre. Outside the project area the catena merges in riparian formations fringing the Casiquiare river.

An important link in the cycle are micro-organisms, particularly fungi. Went (1970) noted that fruiting bodies were formed by wood decomposing fungi in the Amazonian forest only if there were no tree roots close by. This suggests that diversion of nutrients, especially minerals, to the roots via mycorrhizas may inhibit fruit body formation of the fungi. Since then, evidence for the existence of direct or mycorrhizal transfer of nutrients from decaying litter into roots has been convincingly demonstrated in the International Amazon Rainforest Ecosystem Project at San Carlos de Rio Negro (Herrera, 1979).

The constraints on biological activities on the extremely oligotrophic sites with periodic drought lower the efficiency

of such mechanisms. Other adaptations are necessary, such as sclerophylly, pachyphylly, and biochemical means to reduce nutrient losses. In the almost complete absence of mineral nutrient reserves in the soil, rain is the major source of nutrients which are scavenged effectively in the canopy (Jordan *et al.*, 1980). Slowing of litter decay by antibiotic tanning compounds, accumulation of litter and raw humus, dense surface root matting and suspected longevity both of trees and leaves may act as nutrient conserving mechanisms. These mechanisms would be substitutes for the high levels of biological activity and rapid turnover rates which on the oligotrophic sites cannot be achieved.

PLANT RESPONSES AND THE NATURE OF HUMUS

The organic matter on and in the soil plays an important part in nutrient and water cycling by direct physical and chemical effects, and by maintaining favourable conditions for plant growth and microbial activity. This is particularly true for tropical soils with inherently low fertility and an unbalanced water regime. Direct and indirect physiological effects of humic substances on plant growth and health have been known for a long time (Schnitzer and Khan, 1972, pp.298-302). They include the following:

- Small concentrations of humic substances enhance root development and plant growth.
- Humic substances enter plants and affect oxidation-reduction processes.
- Humic substances in plants may alter the carbohydrate metabolism causing accumulation of reducible sugars, and increased osmotic pressures and resistance to wilting.
- Humic substances in plants may affect oxygen intake and chlorophyll synthesis, and promote translocation of iron to leaves, thus preventing chlorosis.

Nutrient availability and allelopathy: an example

In the soil humus fractions nutrients are absorbed, preserved and accumulated, which generally is beneficial. But the chemical nature of the organic matter varies with species and site. Consequently, it is possible that the status of organically bound nutrients is affected and some nutrients may become unavailable.

Under some species organic compounds may accumulate which have an allelopathic effect on other species. An illustrative example from natural peatswamp forest in Lassa Forest Reserve, Rejang delta, Sarawak, may serve to elaborate the point.

Differences in peat. In each of two forest types, 10 widely spaced peat samples were taken at 40 cm depth. The two forest types were the floristically different natural peatswamp phasic communities (p.c.) 1 = forest type 311 and p.c. 3 = forest type 372 in Figures 4 and 5, Section A. The samples were immediately airfreighted to Hamburg. A subsample of each sample was analysed by Dr Salfeld at the Institute of Soil Biochemistry, Federal Research Centre for Agriculture, Brunswick, and by Dr Waughman, University of Durham, UK. The results reported by Salfeld (pers.

comm., 1974) showed not only significant differences of total nitrogen content and correspondingly of C/N ratios (Figure 6), but also of the chemical nature of the nitrogen compounds (Table 4). The peat in p.c. 1 is much more heterogenous than the peat from p.c. 3. Both peats differ from each other in some important features. The proportion of HCl-hydrolysable N is generally higher in p.c. 1, but particularly high in a group of three adjacent samples (Table 4, p.c. 1(2)). The chemical composition of the hydrolysable N is almost identical within the samples from p.c. 1, but differs notably between p.c. 1 and p.c. 3. The latter has a considerably higher content and proportion of ammonium and amide-nitrogen and a much lower content and proportion of α-amino N.

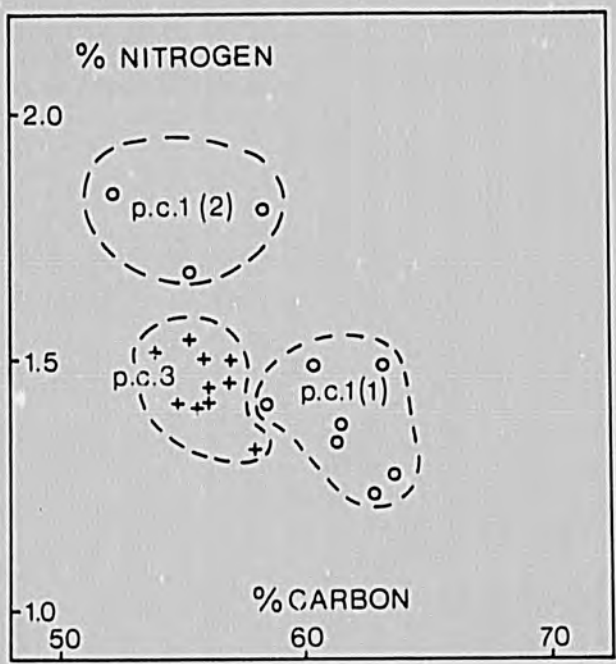


Fig. 6. C/N ratio of peat from peatswamp forest in Sarawak from phasic community (p.c.) 1 = forest type 311 (*Gonystylus - Dactylocladus - Neoscortechinia* association) (circles) and from p.c. 3 = forest type 372 (*Shorea albida* consociation) (crosses). Lassa Forest Reserve, Rejang Delta, Sarawak (from Salfeld, pers. comm., 1974). P.c. 1(1) = subgroup of seven samples, p.c. 1(2) = subgroup of the remaining three samples.

As for nitrogen, the three groups of peat samples are also distinguished by the nature of their humic fractions. These fractions show distinctly different light extinction rates at the four wavelengths 400, 500, 600 and 700 nm. The quotients of the extinction rates, that is E.Q. 400/500, 500/600 and 600/700 are shown in Figure 7 and display a marked grouping in the E.Q. 400/500 - E.Q. 600/700 co-ordinates which corresponds closely with the grouping according to the C/N ratios in Figure 6.

The major minerals (Ca, Na, Mg, K, Zn, Al, Fe, Mn, P) of the same 20 samples from p.c. 1 and 3 were determined at the

Table 4. Chemical nature of the soil nitrogen in 10 samples each of forest peat in phasic communities 1 and 2, Lassa Forest Reserve, Sarawak (Salfeld, pers. comm., 1974). Phasic community 1(1) is subgroup of seven samples; phasic community 1(2) is subgroup of remaining three samples (compare Figures 6 and 7). The positions of the phasic communities 1 and 3 along the ecological gradient is shown in Figures 4 and 5.

Phasic community	Hydrolysable	Ammonium and amide N	Hexosamin N	α-amino N
	% of total N	% of hydrolysable N		
1(1 + 2)	54.3	22.7	13.2	47.9
1(1)	60.2	22.6	13.4	49.7
1(2)	51.7	22.7	13.2	47.1
3	48.0	27.8	20.6	18.9

University of Durham. Significantly different means of the total contents were found for K, Zn, Al, Fe and P, with consistently lower values in p.c. 3 (Waughman, pers. comm.).

In conclusion we may hypothetically state that there are differences between the peats in different phasic communities with respect to the contents and the biochemical nature of nutrient minerals and of the organic compounds, and that these differences are the result of the change of floristic composition along the ecological gradient from p.c. 1 to p.c. 3. The species which is possibly mainly responsible is *Shorea albida* Sym., which is gregarious in p.c. 3, forest type 371, and excludes almost all other species (see Figure 4).

Effects on plant responses. Plants of *Gonystylus bancanus* Miq., a common and characteristic species in p.c. 1, but almost absent from p.c. 3, were grown from seed on these peats for several years from 1972. For comparison, plants were grown in quartz sand (Q-series) which simulates conditions in a sandy spodosol where *G. bancanus* occurs sporadically, and in standard potting mixture (E-series). After three years under a controlled rainforest climate in the greenhouse, the CO_2 exchange was monitored at different light intensities and temperatures. The plants growing in native peat (M-series) had medium rates of apparent gross photosynthesis and low rates of dark respiration. The plants in *Shorea albida* consociation peat (A-series) had lower rates of photosynthesis, except at 30°C, but very high rates of respiration. The plants grown in sand (Q-series) reacted similarly, but the temperature tolerance was greater. The lowest rates were shown by plants in the relatively fertile potting mixture (E-series) (Figures 8 and 9).

After four years of growth in 26°C and 60 to 90 per cent humidity the *G. bancanus* plants had significantly different mean heights in the four series. The tallest seedlings had grown in the native peat (M, h = 53.3 cm). Intermediate height growth occurred in the *Shorea albida* consociation peat (A, h = 41.1 cm) and the quartz sand (Q, h = 42.5 cm). The poorest growth occurred in the most fertile standard potting soil (E, h = 36.5 cm)

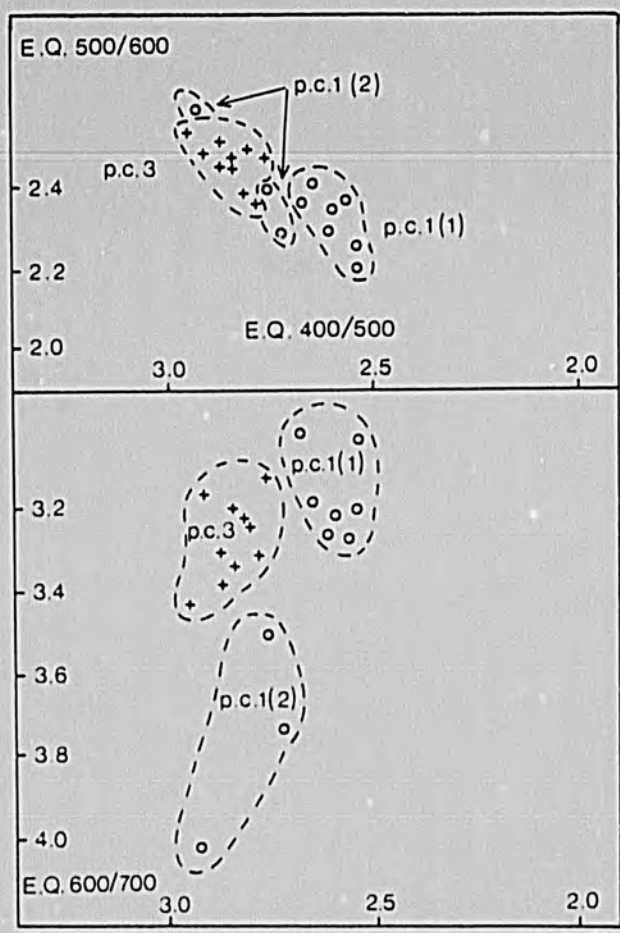


Fig. 7. Ratios of spectral extinction rates at different wavelengths by the humic fractions of samples of peat from two distinct phasic communities (p.c.) of peatswamp forest. P.c. 1 is forest type 311, mixed *Gonystylus* - *Dactylocladus* - *Neoscortechinia* association, groups (1) and (2) (circles). P.c. 2 is forest type 372, *Shorea albida* consociation (crosses). Lassa Forest Reserve, Rejang Delta, Sarawak (from Salfeld, pers. comm., 1974).

(Müllerstael and Brunig, 1976).

Some conclusions. These tentative results cannot yet be fully interpreted in physiological terms. But some important conclusions are possible. The peats in the two phasic communities differ in chemical properties and the growth of *G. bancanus* reacts to the two peats in a manner which accords with its performance and social role in the two phasic communities. Nutrients do not seem to be the decisive factors. The peat of p.c. 3 differs chemically and contains organic compounds which seem to interfere in some manner with the processes of photosynthesis and respiration. The result is that the sensitivity to high temperature and the respiration rates are significantly higher and the net productivity and growth lower in p.c. 3 than in the

native p.c. 1, habitat of *G. lancerus*.

The wider implications

Substances which can produce similar allelopathic effects are virtually universal in plants and soils. Drought conditions often intensify the allelopathic action (Whittaker, 1970). This must be kept in mind when need for humus preservation in agroforestry is considered. The expected global and local climatic changes as a result of deforestation and air pollution are

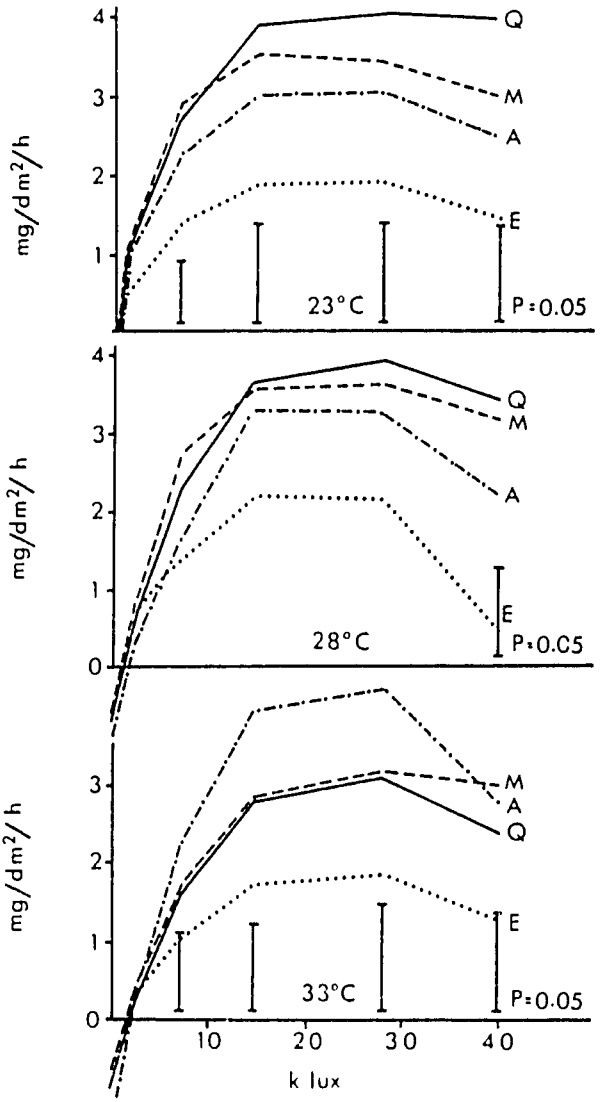


Fig. 8. Apparent gross photosynthesis (in mg CO_2 $dm^{-2}h^{-1}$) of *Gongylylus lancerus* Miq. seedlings at 10, 20, 30 and 40 k lux and 23, 28 and 33°C air temperature.
M: peat from phasic community 1. A: peat from phasic community 3. Q: quartz sand. E: standard potting mixture. Vertical bars indicate least significant differences at P = 0.05.

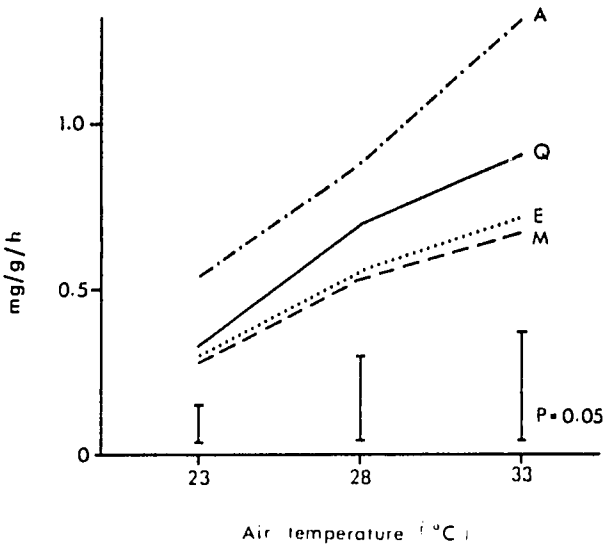


Fig. 9. Respiration of *Gonystylus bancanus* Miq. (in mg CO_2 g^{-1} leaf dry weight h^{-1}) in the same four series as in Figure 8 at 23, 28 and 33°C air temperature. (See Figure 8 for explanation).

relevant in this respect if the risk of periodical drought is increased. The interaction of allelopathy and drought may contribute to the noticeable tendency to single species dominance in natural forest stands and plantations on oligotrophic, xeric sites with unbalanced water regimes in the humid tropics. Examples are the kerangas forests in Borneo and the very similar forests on spodosols in the Rio Negro - Orinoco - Amazonas basin.

The accumulation of phytotoxic compounds is less likely in soils with high microbial activity, but there are well-known examples especially in forestry, but also in agriculture and horticulture, of phytotoxic effects occurring under certain species in spite of high microbial activity in the soil.

Hardly any information exists on the effect of understorey intercropping of tree crops with non-leguminous crop plants. Ojeniyi *et al.* (1980) analysed 240 soil samples from *Gmelina arborea* plantations grown pure and underplanted with three kinds of food crops (maize, yam and cassava). Some decrease in organic C, and some increase of N and P, were found but differences were not statistically significant. The various multipurpose tree species which are suitable for agroforestry produce different amounts of chemically diverse litter; their litter production may also vary in quantity and quality compared to that of natural forest on the same site. This will, no doubt, have profound long-term effects on the organic matter and nutrient regimes on some of the more fragile soils. In order to make appropriate choices of agroforestry crop mixtures, and to utilize them in appropriately designed systems that will be sustainable, much more information will be required about the nature and amounts of humic materials that accumulate.

PREDICTING CROP PERFORMANCE AND MODELLING AGROFORESTRY SYSTEMS

The dynamic processes within a stand, and the interaction between the stand and its environment, are probably subject to influences derived from the canopy structure (especially size and morphology), the distribution and orientation of the leaves, the leaf area index, and the aerodynamic roughness of the canopy. But available data on stand functioning are insufficient to verify this hypothesis. The great complexity and variability of the interactions between environmental factors and the crop plants and crop mixtures make it unlikely that we shall possess sufficient data in the near future for the development of abstracted mathematical models of the stand structure - function - environment interactions. This makes it particularly hazardous to try to predict performance, including the growth and yield of long-lived mixed cropping associations such as are found in agroforestry.

The quantitative assessment of the potential resistance and reaction of tropical forestry, agroforestry or agricultural ecosystems to erosion, leaching and other damaging processes requires reliable long-term statistics from long-term case studies which are just not available as yet. Particularly critical but difficult to quantify are the probabilities of extreme events such as severe drought or flooding, gales or excessively hot or cold spells. The situation is complicated by the yet uncertain effects of human activities on the climate. A further and possibly serious long-term threat to plant health and performance, soil fertility and system stability is the growing worldwide pollution of the environment, especially with sulphur.

The reaction of agroforestry and forestry crops to such impacts depends not only on specific susceptability, but also on the geometric structure and floristic mixture of the crop mixture which, in turn, influences the soil conditions and soil reactions to acidification. But again, information on structure - functions - performance interrelationships is too scanty, sectoral and isolated. As a result, assessments of future system performance and reaction will remain largely speculative.

In addition to this problem of lack of adequate data, there is the problem that few of the existing models are really adequate and operational. The problems of modelling plant - environment and crop - environment interactions have been exemplified again recently by van Keulen (1981) with the model ('PAPRAN') of the water - nitrogen interaction and its effect on growth and yield under semiarid conditions. In the example, the multitude and diversity of combinations of factors and interactions produced as many erratic deviations of predictions from reality as hits.

A further complication is the risk of error and fallacious argument by extrapolating results on physiological reactions of small plants, which were tested under laboratory conditions, to large plants in crops grown in the field. The linking of laboratory results with observed performances in natural or man-made stands under very variable field conditions is beset with problems and pitfalls. Particularly, the possibility that interactions between past and present states of long-lived crops will affect future performance adds to the problems of predictive modelling.

However, dynamic system modelling at various levels of eco-

systems, in the order of plant, crop, forest and, finally, region can be of some help to identify and demonstrate major and critical causal feedback loops which may affect the functioning and dynamics of the real ecosystem. Results of such simulation modelling can be very useful by identifying critical interactions, especially positive feedback loops. This is a useful help in designing crop types which are likely to survive better and thus promise to produce more sustained benefits than other crops. An example of such an approach in agroforestry has been described recently by Grossmann and Schneider (1980). The various models are interconnected in a hierarchical order. The models at the various levels, and the connecting interfaces and supplementary feasibility checks, have been developed over several years by an interdisciplinary group of scientists centred at Hamburg University. The general scheme of the hierarchy and the complexity of interdependencies and feedbacks are illustrated in Figure 10 which indicates the complex interactions between the natural and cultural systems which must be considered in modelling at any level for purposes of systems analysis and development forecasting and planning. A description of the structure and functions of the system model hierarchy and the applications and problems of system simulation at the various levels and scales is given in papers by Grossmann, and Brunig *et al.* in Man and Biosphere (1982).

CONCLUSIONS FOR AGROFORESTRY DESIGN

Physio-ecological considerations

The interplay of specific combinations of adaptive features of the different species in a mixed stand will determine the features of the 'niche' which is available for any of them. This is particularly true for species of lower social position in a forest, or in an agroforestry crop mix. The combined effects of competition for light, nutrients and water, and of allelopathic or symbiotic interactions will, under given specific site conditions, define the possibilities and limits for crop structural designs.

It is, therefore, extremely important to understand the physio-ecological significance of those plant features which, apparently, are adaptive to the chemical, physical and biotic environment. Particularly important is an understanding of the influence of continuous or periodical environmental constraints on plant and crop performance, especially on growth and survival (see Connor, page 401, this volume). Other contributions in this volume consider particular, relevant physio-ecological aspects. But, in a number of areas our knowledge is still sketchy. Certainly, much more research and supplementary field validation is required before efficient and adapted agroforestry cropping patterns can be confidently designed for all the different types of land use systems in which they are needed.

Crop nutrition

Interactions between structural and biochemical crop characteristics directly and indirectly influence the supplies of nutrients, especially of nitrogen and phosphorus, as well as of water

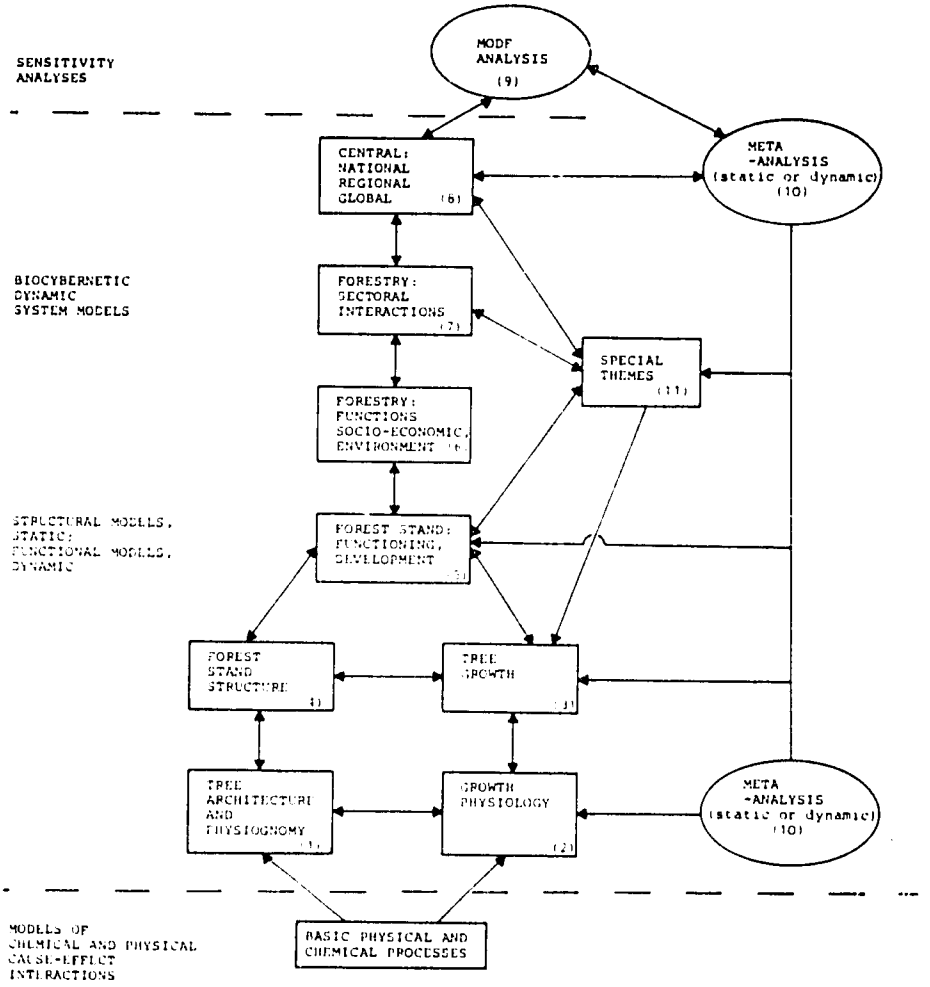


Fig. 1. Integrated hierarchy of interacting dynamic or static system models which abstract and simulate the structure, functioning, endogenous dynamics, exogenous responses and development under management of the real systems 'TREE' (1-3); 'FOREST STAND' (4-5); 'FORESTRY' (business unit or sector; 6-7) and 'CENTRAL (national to global) SYSTEM' (8). Special subjects or themes such as deforestation are being treated in the 'SPECIAL THEME' (11) model. Sensitivity analysis of the responses of the system models, especially the central and forestry models, to changes in public attitudes and preferences are done by means of the 'MODE ANALYSIS' (9); responses to change of strategy or deliberate human impact are studied by means of the 'META ANALYSIS' (10). This hierarchy and interaction concept may be applied to scientific research, land use analysis and planning and public education in the UNESCO Programme MAB (from Man and Biosphere, 1982).

and light energy to the crop plants. Nutrient and water supplies may be improved by natural or induced microbial associations. For example, Dommergues *et al.* (1979) suggested that altering the microflora to act directly through the plant is another promising possibility to increase nitrogen supplies, and thereby improve crop production and save energy. Micro-organisms and the soil organic matter are important links in the critical phosphorus cycle.

On the other hand, improving supplies by increasing inputs may create adverse side effects which must be considered in designing crop mixtures. For example, Novoa and Loomis (1981) point out that crop rotations involving alternating high yielding cultivars of di-nitrogen fixing plant species can effect a large energy saving by adding substantial amounts of nitrogen, and thus substituting for artificial N-fertilization. But additional nitrogen may increase the susceptibility of the plants to drought and hot-spell damage. Knowledge of climatic fluctuations is necessary to assess such risks and to apply adequate countermeasures in agricultural (Fischer, 1981) as well as in agroforestry and forestry crop management.

Nitrogen application usually increases leaf area in agricultural crops by increasing leaf number and/or leaf size (Novoa and Loomis, 1981). Perhaps something of this nature underlies the preliminary and puzzling result of structural analysis in the International Amazon Rainforest Ecosystem Man and Biosphere Project, where the leaf area index and the nitrogen content of the leaves vary surprisingly little between forest association groups, in spite of widely different site conditions. Natural nitrogen fixation, and efficient nutrient preservation mechanisms in these systems, may work toward a build-up of nitrogen to a more or less uniform level. The variation of nutrient stocks per unit area in these natural forests seems to be more strongly dependent on phytomass stocking density than on soil differences, as long as the nutrient cycling is not disrupted.

Agroforestry crops in the humid tropics should therefore aim at high levels of phytomass stocking and minimum disruption of nutrient cycling. Limiting the phytomass density are, above all, the amount and reliability of supply of plant available water.

The water cycle

Transpiration conveys nutrients through the system. It is therefore good management policy to design crops in such a manner that the proportion of water which passes through the plants and transpires is as large as possible. This aim of maximizing transpiration must be balanced against the aim of containing the risk of damage from lack of water during drought periods. This is particularly important in mixed agroforestry crops which include perennial plants and species of different competitive capacity under drought conditions.

However, high rates of evapotranspiration increase the risk of drought damage. A structural complexity, which involves rates of energy and water turnover which exceed the capacity of the site, create instability and loss of vigour, health and production. It is well known and documented by long-term observation in rubber plantations in the perhumid climate of Malaysia that

substantial reductions of yield occur as a result of periodic water deficiency. The situation is aggravated by the effects of declining infiltrability of the soil after extended monoculture, and by the tendency to more concentrated rainfall distribution caused by the man-made landcover changes.

Under otherwise equal conditions, greater aerodynamic canopy surface roughness will tend to increase the ratio of evapotranspiration to incident net radiation. Rough crop surfaces demand an ample water supply from rainfall and soil storage. The close correlation between rainfall pattern, soil water storage capacity and structure of mature natural forests, and of primary and secondary successional phases of forests, has been described for Borneo by the author (Brunig, 1966, 1970, 1971).

Underlying assumptions which can affect design

From what has been stated it follows that there are some generally applicable assumptions that may serve as guidelines for designing agroforestry cropping patterns. These are some of them.

- A good chance of survival, and the ability to maintain a sustained performance in extreme situations is, in long-living crop species, more important than maximizing yield.
- High levels of growth resilience and yield stability are essential and desirable characteristics under conditions of progressing soil deterioration, adverse climatic change and, perhaps, even pollution; all of which may lead to unpredictable future states and consequences.
- Water supply is a limiting and critical factor, even in a perhumid, nonseasonal, equatorial climate.
- The nutrient regime is, more directly than the water regime, open to manipulation and improvement by biological and technical means, but particularly phosphorus may be, or may become, a critically limiting factor.
- The parameters: leaf size, shape and colour, leaf distribution, aerodynamic roughness of crown and canopy, may all be regarded as acting as a structured code which regulates the partitioning and cycling of energy and matter within the ecosystem, and between it and the environment.

SUGGESTIONS FOR SOME SUITABLE DESIGNS FOR SPECIES MIXTURES

Bearing the above points in mind we can begin to assemble some practical design features; at least in so far as plant - environment factors are concerned.

- The top canopy should be formed of water-use efficient and biochemically nonagressive trees which have open crowns and yield multiple products (timber, fuel, fodder, fruit, latex, oil, and so on), in addition to maintaining favourable soil and climatic conditions.
- The aerodynamic roughness of the top canopy should be adjusted to the climatic and hydrological conditions of site,

bearing in mind the possibilities of storms, dry winds and so on, and with the objective of obtaining the highest rates of atmospheric water transfers and flux intensities sustainable on that site.

- The top canopy trees should be mechanically strong, have a low ratio of height to stem diameter, have large crowns and a favourable ratio of water transport to water transpiring tissue in order to improve vigour, health and mechanical stability.
- The top canopy trees should be relatively sclerophyllic, possibly more so than in the natural forest on the site, so as to improve light and water penetration, and to reduce risk of drought damage.
- The mid-canopy layers should be filled with a fairly dense association; it should be species-rich so that the diverse assemblage of trees, shrubs, climbers, and so on, will provide a range of products, and give effective soil protection and ample living space and food for animals. Favourable micro-organisms need to be encouraged as this layer is particularly important as a source of richly mixed litter.
- The lower under-canopy enjoys less light energy and water, and it will contribute relatively little to the production and turnover of organic matter; it is suitable for growing shrubs and treelets which yield particularly valuable substances (for example, pharmaceutical drugs or dyes).
- At ground level, annual and perennial herbaceous plants can be grown as short-lived, successive or alternating crops, in gaps or during phases of crop development which are more favourable with respect to light and water supplies. This layer needs not be species-rich and diverse, and the main objective is to produce food, condiments or special crops. Additionally, ecological benefits from nutrient fixation and preservation, a good soil cover and the maintenance of favourable micro-organisms can be achieved if this level is well managed.
- On more xeric and oligotrophic sites, greater sclerophylly and lower aerodynamic roughness and stature of the canopy will be necessary to reduce the risk of drought damage. Humus formation and nutrient preservation are important and top and mid-canopy species must be selected accordingly. Generally, species selection will be limited to fewer suitable species and symbiotic mixtures will be more difficult to achieve. The crop structure must necessarily be more simple and uniform, and the maintenance of soil fertility may require crop rotation.
- Adequate production of litter as a raw material for humus formation, and to provide energy and nutrients for micro-organisms, is important on all soils. On sites with a high capacity for rapid production and decomposition, species richness and diversity usually will have to be high to meet the needs of nutrient preservation. On less fertile, oligotrophic sites, humus preservation is essential to supplement the less efficient filtering capacity of the simpler crop,

and to maintain adequate physical soil conditions.

- The objectives of high levels of ecosystem resilience and stability will best be served by mixtures of species which are both suitable to the site and compatible with each other. Such species are capable of forming and sustaining high levels of phytomass stocking, multiple interactions between trophic levels and high levels of organization (Figure 11) with relatively low inputs of management, chemicals and energy.

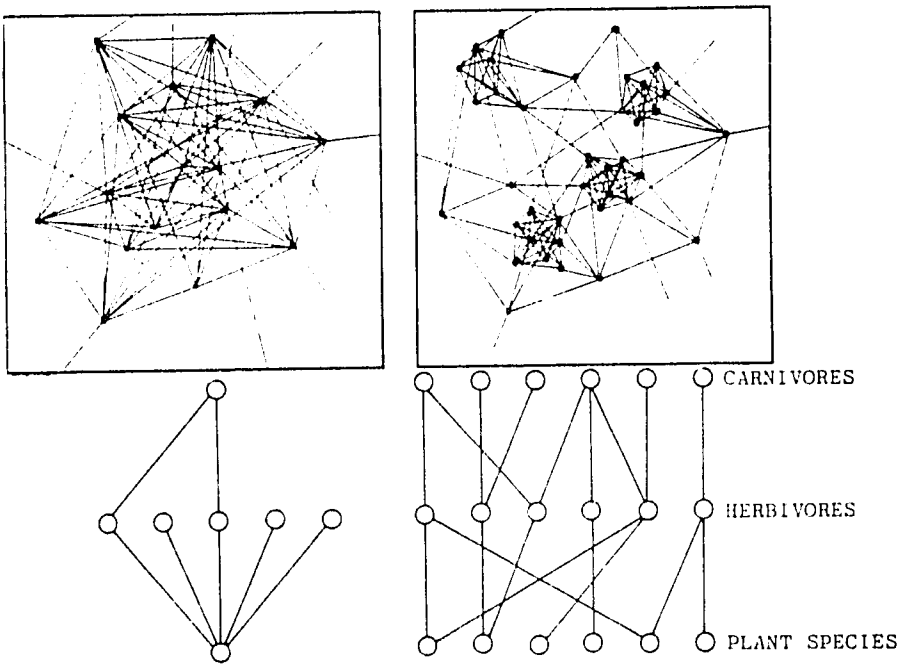


Fig. 11. Network patterns of interactive linkages in forest and agroforestry systems. *Left*: monoculture, less stable. *Middle*: complex mixed crop, more stable. *Top*: organisation patterns of the same number of linkages with higher level of organization by subunit formation in the complex, structured mixed crop which produces greater stability and resilience. *Bottom*: greater species richness and diversity of plant species (bottom line) produces more linkages and effectively regulating negative feedback loops in the food chain of herbivores (including plant pests) and carnivores (predators on pests). (Adapted from Vester, 1980.)

CONCLUSIONS

We may conclude that it is essential, in designing agroforestry crops, to consider the site specific physio-ecological significance in a system context of tree and canopy structure, species mixture, humus and hydrological conditions, nutrient cycling and preserving mechanisms, allelopathic incompatibility and symbiotic co-operation.

Lundgren (1979) stated, that 'one crucial problem in

research will be to quantify the effect that different tree crops have on the inputs and outputs of nutrients and organic matter in the system during the rotation'. The convincing success of Indonesian farmers in achieving sustained production by means of permanent tree/shrub/herb combinations even on soils of average fertility, as described by Michon (see this volume), and Wirakusumah (1978), shows what can be done by the experienced practitioner with plants and sites, both of which he knows well.

While it is very worthwhile to find out how and why these systems function in order to improve them and to learn from them, we need additional basic and experimental physio-ecological and synecological research to provide the knowledge needed to design adapted crop types with new species or genotypes which can survive and continue to be useful under changing environmental and social conditions.

A PLATE illustrating this paper can be found elsewhere in this book.

REFERENCES

Anderson, J.A.R. (1961). "The ecology and forest types of the peatswamp forests of Sarawak and Brunei in relation to their silviculture." PhD Thesis, University of Edinburgh, Edinburgh.

Anderson, J.A.R. and Muller, J. (1975). Palynological study of a holocene peat and a miocene coal deposit from NW Borneo. *Rev. Palaeobotany and Palynology* 19, 291-351.

Bennema, J. (1977). Soils. *In* "Ecophysiology of Tropical Crops" (P. de T. Alvim and T.T. Kozlowski, eds), pp.29-55. Academic Press, New York, San Francisco, London.

Bolin, S., Degens, E.T., Kempe, S. and Ketner, P. (Eds) (1979). "The Global Carbon Cycle". Scope 13. John Wiley & Sons, Chichester, New York, Brisbane, Toronto.

Brunig, E.F. (1966). "Der Heidewald von Sarawak und Brunei - eine Studie seiner Vegetation und Oekologie". [The heather-forest of Sarawak and Brunei - a study of its vegetation and ecology.] Thesis, University of Hamburg, Hamburg.

Brunig, E.F. (1970). Stand structure, physiognomy and environmental factors in some lowland forests in Sarawak. *Trop. Ecol.* 2, 26-43.

Brunig, E.F. (1971). On the ecological significance of drought in the equatorial wet evergreen (rain)forest of Sarawak (Borneo). *In* "Trans. First Aberdeen-Hull Symp. on Malaysian Ecology". University of Hull, Dept. of Geography Misc. Ser. No.11, pp.66-97.

Brunig, E.F. (1976). Tree forms in relation to environmental conditions: an ecological viewpoint. *In* "Tree Physiology and Yield Improvement" (M.G.R. Cannell and F.T. Last, eds), pp.139-156. Academic Press, London, New York.

Brunig, E.F. (1982). Some problems connected with the assessment of the role of humid tropical evergreen forest as source and sink of carbon. *Mitt. Geol.-Paläont. Inst. Hamburg, SCOPE/UNEP Special Report* No.52, pp.59-68.

Brunig, E.F., Grossmann, W.D., Kreysa, J., Sander, N. and Schneider, T.W. (1982). The testing and integration of dynamic system models by information exchange and simulation.

In "MAB Mitteilungen" No.10 (E.F. Brunig, ed.), pp.44-66. German National MAB Committee, Bonn, West Germany.

Dommergues, Y.R., Diem, H.D. and Gangri, F. (1979). The effect of soil micro-organisms on plant productivity. *In* "Soils Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.205-241. ICRAF, Nairobi, Kenya.

Elston, J. and Monteith, J.L. (1975). Micrometeorology and vegetation. *In* "Vegetation and the Atmosphere" (J.L. Monteith, ed.), Vol.1, pp.1-12. Academic Press, London, New York.

Fischer, R.A. (1981). Optimizing the use of water and nitrogen through breeding of crops. *Plant and Soil* 58, 249-278.

Forman, R.T.T. (1975). Canopy lichens with blue-green algae: a nitrogen source in a Colombian rainforest. *Ecol.* 56, 1176-1184.

Golley, F.B., McGinnis, J.T., Clements, R.G., Child, G.I. and Duever, M.J. (1975). "Mineral Cycling in a Tropical Moist Forest Ecosystem". Univ. Georgie Press, Athens, Georgia, USA.

Grossmann, W.D. and Schneider, T.W. (1980). Die angewandte Systemtheorie als Mittel zur Untersuchung von Funktion und Dynamik agroforstwirtschaftlich geprägter Lebensräume. [The applied systems theory as a means to study function and dynamics of agroforestry ecosystems.] *Mitt. Bundesforsch. anst. Forst-Holzwirtsch.* 132, 1-26.

Herrera, R.A. (1979). "Nutrient distribution and cycling in an Amazon caatinga forest on spodosols in southern Venezuela". Ph.D. Thesis, Univ. of Reading, Reading, UK.

Herrera, R.A. and Jordan, C.F. (1980). Nitrogen cycle in a tropical rainforest of Amazonia: the case of low mineral nutrient status in the Amazon caatinga. *In* "Nutrient Dynamics of a Tropical Rainforest Ecosystem and Changes to the Nutrient Cycle due to Cutting and Burning", pp.86-114. Inst. of Ecol., Athens, Georgia, USA.

Jordan, C. (1978). Stemflow and nutrient transfer in a tropical rainforest. *Oikos* 31, 257-263.

Jordan, C. and Centro de Ecologia, IUIC (1980). Nutrient cycling in an Amazonian rainforest. *In* "Nutrient Dynamics of a Tropical Rainforest Ecosystem and Changes to the Nutrient Cycle due to Cutting and Burning". Inst. of Ecol., Athens, Georgia, USA.

Jordan, C., Golley, F.B., Hall, Jerry and Hall, Jan (1980). Nutrient scavenging of rainfall by the canopy of an Amazonian rainforest. *Biotropica* 12, 61-66.

Kenworthy, J.B. (1971). Water and nutrient cycling in a tropical rainforest. *In* "Trans. First Aberdeen-Hull Symp. on Malaysian Ecology", pp.49-59. Univ. of Hull, Dept. Geography, Hull, UK.

Keulen, H. van (1981). Modelling the interaction of water and nitrogen. *Plant and Soil* 58, 205-229.

Lundgren, B. (1979). Research strategy for soils in agroforestry. *In* "Soils Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.523-538. ICRAF, Nairobi, Kenya.

Man and Biosphere German National Committee (1982). "MAB Mitteilungen" No.10 Transactions Third International MAB-IUFRO Workshop on Ecosystems Research (E.F. Brunig, ed.). German National MAB Committee, Bonn, W. Germany. 161 pp.

Manokaran, N. (1980). The nutrient contents of precipitation, throughfall and stemflow in a lowland tropical rainforest in peninsular Malaysia. *Malaysian For.* 43, 266-289.

Müllerstael, H. and Brunig, E.F. (1976). Wachstumsverhalten von Ramin in verschiedenen phasischen Waldgesellschaften. [Growth reaction of Ramin in different phasic forest communities.] *Ann. Rep. Bundesforschungsanst. Forst-Holzwirtsch., Hamburg-Reinbek.* 1976, pp.11-13.

Novoa, R. and Loomis, R.S. (1981). Nitrogen and plant production. *Plant and Soil* 58, 177-204.

Nye, P.H. and Greenland, D.J. (1960). The soil under shifting cultivation. *Commonwealth Bureau of Soils Techn. Comm.* No.51. Harpenden, UK.

Ojeniyi, S.O., Agbede, O.O. and Fagbenro, J.A. (1980). Increasing food production in Nigeria. 1. Effect of agrisilviculture on soil chemical properties. *Soil Science* 130, 76-82.

Schnitzer, M. and Khan, S.U. (1972). "Humic Substances in the Environment". Marcel Dekker, Inc., New York.

Stark, N. and Spratt, M. (1977). Root biomass and nutrient storage in rainforest oxisols near San Carlos de Rio Negro. *Trop. Ecol.* 18, 1-9.

Turvey, N.D. (1974). Water in the nutrient cycle of a Papuan rainforest. *Nature* 251, 414-415.

Vester, F. (1980). Zukunftsprognoses, Modelle, Strategien. [Forecasts, models and strategies.] *In* "Handbuch für Planung, Gestaltung und Schutz der Umwelt". [Handbook for planning, shaping and protection of the environment] (Buchwald and Engelhardt, eds), Vol.4, pp.32-73.

Went, F.W. (1970). Plants and the chemical environment. *In* "Chemical Ecology" (E. Sondheimer and J.B. Simeone, eds), pp.71-82. Academic Press, New York.

Whittaker, R.H. (1970). The biochemical ecology of higher plants. *In* "Chemical Ecology" (E. Sondheimer and J.B. Simeone, eds), pp.43-70. Academic Press, New York.

Wirakusumah, S. (1979). Diversified silvicultural and agrosilvicultural crops. *In* "Trans. Second International MAB-IUFRO Workshop on Tropical Rainforest Ecosystems Research" (S. Adisoemarto and E.F. Brunig, eds). Univ. of Hamburg, Dept. of Forestry, Hamburg-Reinbek, W. Germany.

DISCUSSION

LOOMIS - I question your assumption that diversity leads to stability. If this is true, mediaeval systems should have been much more stable than modern ones, but Stanhill has found that the standard error for English wheat yields has been constant for over a thousand years. The variability thus seems the same in intensive and non-intensive systems. Surely a good approach to getting stability is to look for the *safest* things to grow in any area. In each area there are crops which are reliable and ones which are not. In fact the most stable system in an area is often a low diversity one. On this issue I must agree with the Dutch workers on the need to maximize production on the best land with very few crops.

BRUNIG - Yes, a single crop is easier to manage and *can* be more stable than a diversity of crops. But this is only true if a single uniform crop is well adapted to the site, resilient and

not subject to the epidemic spread of pests and diseases. Also that it does not suffer from the build-up of adverse biotic or physical-chemical soil conditions. It is important, too, who is managing the crop. A narrowly optimized, less diverse crop is less adaptable to fluctuations and changes of the natural and economic environment and, often, high levels of technological inputs are needed to remedy the situation.

LOOMIS - If we take a really intensive crop like rice we find the year-to-year variability in experimental yields is less than that in actual production.

BRUNIG - Yes, but usually rice is grown on the best sites. In fact, diversity can be obtained by a mixture of monocultures. It is all a question of the scale on which we are considering mixtures.

HUXLEY - Surely some of these arguments are academic? All crops cannot be treated purely as commodities to be grown according to the optimum production models and then shipped around as required. People and their livelihood are in the places in which they find themselves and there [illegible] to be local production of food and fuelwood.

LOOMIS - There is a best crop for each place, and each place should grow the crop which it can produce best. Production should be concentrated in the areas where the crop can be produced efficiently.

HUXLEY - That is suitable for developed countries and some parts of the tropics but it is essential, in my view, for much of the tropics, for us to reach the best solution now for relatively unspecialized cases. In some of the societies for which we are working there just is not the notion of specialization. We do not have a 'product A' man who grows only that crop and sells it to the 'product B' man who does the same, in reverse.

JACKSON - Is it possible that multiple cropping is better suited to high irradiance zones where there is enough radiant energy for several cropping tiers?

LOOMIS - No, because nutrients become the limiting factor. Another thing we must remember is that farming twenty crops is much more difficult than farming one crop. The farmer never knows enough about each and he has more pests and diseases to worry about. The individual hazards may be less but the frequency of problems is greater.

CROP MODELS: COMPONENTS OF AND CONTRIBUTORS TO MODELS OF AGROFORESTRY PLANT ASSOCIATIONS

D.J. CONNOR
School of Agriculture, La Trobe University, Bundoora 3083, Australia.

ABSTRACT. Simulation models of crop systems are only a summary of selected findings arranged to display relationships in a meaningful way so as to help the researcher focus on well-specified objectives. In doing this they often expose the need for more experimental work. Models must be made appropriate to each set of research objectives, however, and then the processes of *definition of purpose - model building - experimentation* offer a valuable repetitive loop.

Simulation models almost invariably contain a mixture of fact and fantasy (hypothesis) because some physiological processes are better understood than others. Models do not work well if they are too unbalanced in this respect, and simple models based on limiting processes are often the most successful.

Research in agroforestry should be able to capitalize immediately on existing crop models constructed to investigate responses to management and environment. Particularly with regard to canopy design, and water and nutrient budgeting.

INTRODUCTION

Over the past twenty years there has been considerable progress and some consolidation amongst the variety of approaches that have been tested in the development of simulation models of crop growth and yield (for example, Loomis *et al.*, 1979). Agroforestry research is in a position to take advantage of these developments, not only because crop models can be incorporated into models of the more complex agroforestry plant associations, but also because generally applicable principles and techniques have emerged.

The general objective of agroforestry research is to uncover the relationships between the performance of tree/non-tree mixtures, particularly their productivity and sustainability, in

response to climate, weather, management and the characteristics of the component species. It shares this objective with research in crop agronomy but, in addition to the further complexity that is introduced by the anatomical and physiological diversity between the cohabiting species, there is the important additional concern of the longer time scale over which the performance of the individual associations must be considered.

SIMULATION MODELS IN RESEARCH

The question is not whether simulation modelling is an appropriate companion activity to experimental work directed towards unravelling causal relationships in biological systems, but rather at what level should the modelling be undertaken? Biologists are, in general, far less quantitative than their counterparts in the physical sciences. Not only is their training often deficient in numerical approaches, but it seems often to emphasize the undoubted complexity of biological systems rather than the need for, and value of, simplification as an aid to the development of understanding. For this reason I feel that biologists have great difficulty in accepting the simple abstractions of high level simulation models, preferring often to seek explanation of system behaviour by reductionist research, rather than by integration at an appropriate level.

Models of crop systems are only a summary of selected empirical f ndings of plant physiologists. The purpose of a model is to provide a framework within which the mathematical representations of the hypotheses concerning the behaviour of component processes can act and interact. This aspect of empiricism is important because it is not the purpose of a crop model to reproduce reality by, for example, taking explanation of the growth responses back to the fundamental laws of molecules. Models cannot be built to answer any question at any level of complexity. Their purpose is to abstract a system for what must be in each case a well-specified purpose.

Simulation models are an important adjunct to experimental research. A simulation model cannot be constructed unless the model builder has clear objectives and the model building furnishes the opportunity to focus what might otherwise remain as an obscure mental model. In research it is much better to discover an approximate answer to an exact problem than to discover an exact answer to an approximate problem (see Paltridge, 1973). Model building can play an important role in problem identification. For these reasons it is important that experimenters are modellers and vice versa. There is of course room for some specialization, but success is most readily achieved when there is close co-ordination between these two aspects of research.

DIAGRAMMATIC REPRESENTATION OF CROP SYSTEMS

The physiological processes of photosynthesis, transpiration, respiration, nutrition and phenological development are those to be related to the community level transfers of radiation, biomass, nutrients and water. Forrester (1968) developed a technique of representing the state and activity of systems and, although his is not the only diagrammatic technique that has

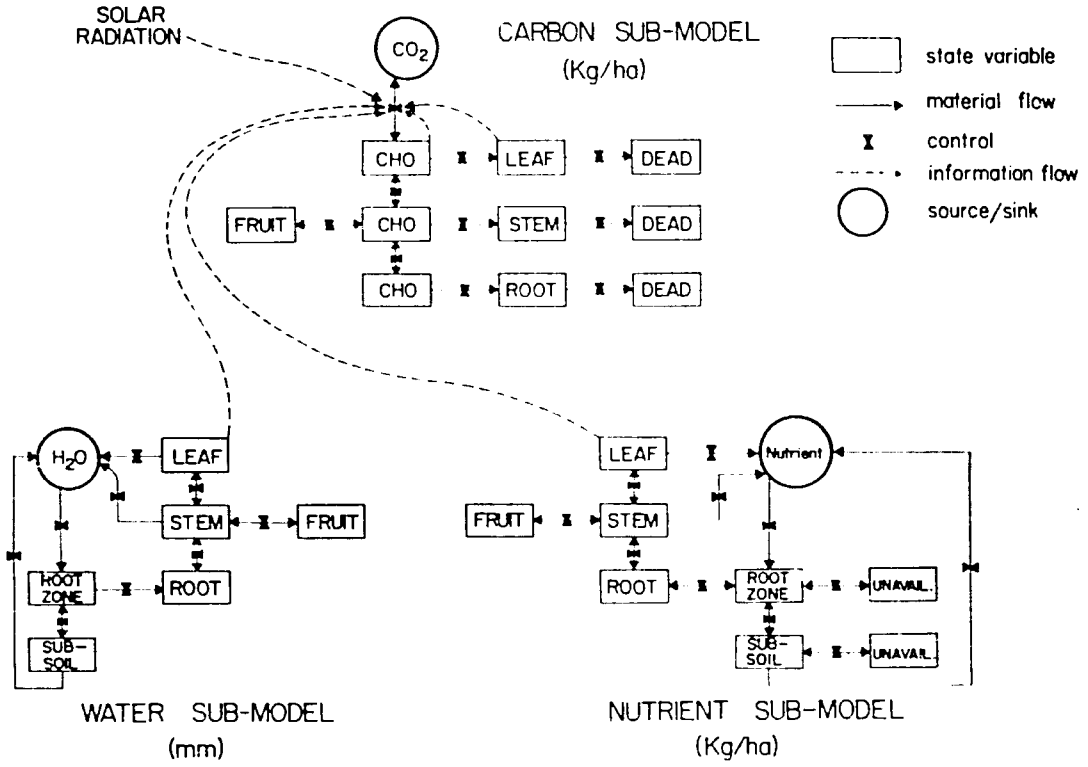


Fig. 1. A diagrammatic representation of a compartment model of the wheat crop. The model contains 24 state variables in the three submodels: carbon, water and one of a generalized nutrient. For simplicity only one example of the specification of information flow, namely to photosynthesis, is included.

been tried in agricultural and ecological modelling, it is the one that is currently considered to be the most valuable in building crop models.

To illustrate the technique a diagrammatic representation, suitable for the investigation of crop performance in relation to its environment, management and physiological properties, is depicted in Figure 1. This diagram is based upon a wheat crop simulator for which further explanation of structure and objectives can be found in Goutzamanis and Connor (1977). The important characteristics of the diagram are as follows.

- The system is comprised of subsystems each of which deals with a conservative quantity of the system. In this case water, carbon, and nutrients.
- Within each subsystem the modeller has chosen state variables which describe the distribution of the conservative quantities, and has defined the routes by which these materials can move around their respective subsystems.
- The flow of material between compartments is controlled by information which flows into the system from outside and which is generated within. Within the system there is no restriction on the flow of information. It may flow between as well as within subsystems and arise from the present or previous state of the system, that is, the values of the state variables or their rates of change in any combination.

The choice of state variables is the modeller's view of the system relative to his current objective. The abstraction of the system is enormous, in this case the biological intricacy of the wheat crop is replaced by 24 numbers, the values of the state variables (mm H_2O, kg ha^{-1} C, kg ha^{-1} N, and so on), which in this context completely define the system. The physiological and micro-environmental processes which determine the flows of material and information must themselves be treated at a level of detail determined by the choice of the state variables. There is, then, no one model of a wheat crop, or of an agroforestry association. There is a model appropriate to each set of objectives.

The diagrammatic presentation has been stressed because it is the first step in the development of a dynamic computer model. Also, it is often the only step that need be taken. If it is clear that insufficient empirical data is available to proceed with the construction of the model, then it has served the important initial purpose as an aid in the identification of the problem and of the level of abstraction of the system that is appropriate to its solution. Experimental work on system behaviour and process control within it has been defined, and its relationship to research objectives more clearly explained.

COMPUTER IMPLEMENTATION

There are four steps required to transfer a diagrammatic model of the type presented in Figure 1 into a dynamic model that can be used for experiment and prediction on a computer.

Identify equations for all flows of material and information. Select values for all parameters that are included in definition of process and response.

- Set initial values to all state variables.
- Solve the equations at appropriate time intervals to calculate the current values of the state variables.

The value of the Forrester representation is that it is expecially suited to translation into mathematical form. This is further aided by the special purpose simulation languages (CSMP, SIMCOMP, ASCL) that have been designed to allow the modeller to concentrate his attention on the specificities of his own model, by providing for him the general framework that is common to the class of compartment model.

PROCESS SPECIFICATION

In this section I wish only to comment briefly on how well the flows of material and information can be specified in current crop models. Another way to put this is to ask: What mix of fact and fantasy (hypothesis) do they contain? Clearly the models provide a valuable way to test hypotheses concerning the behaviour of some parts of the system against the proven behaviour of the rest. However, if the content of hypothesis is too high, then the chance of using the model effectively is limited (Passioura, 1973).

The general answer to how well do we understand physiological processes at a level appropriate to building crop models is that it is very uneven. I expect that the papers to be presented during this meeting on physiological processes within agroforestry associations will confirm this.

Some processes such as canopy photosynthesis, crop water use, soil water balance, respiration, nutrient uptake and phenological development are relatively well understood and can be specified well in mathematical form. Modelling at various levels is actually contributing significantly to the development of understanding. This is seen particularly in the advances that have been made in the study of respiration and carbon balance generally (Penning de Vries, 1975).

By contrast, other processes are poorly understood and significantly the question of assimilate allocation between various functional parts of plants, for example to leaves, stems and roots, which goes to the very core of the problem of the dynamic simulation of crop growth, belongs to this class. In a very early model of pasture growth, Paltridge (1970) proposed that at each time step the plant might allocate the assimilate available to roots or leaves so as to maximize its growth capacity relative to the above- and below-ground restrictions that it is currently facing. There have been few other ideas and many crop models rely upon phenologically based allocation ratios often not responsive to environment. A sound experimental basis is available for sugar beet (Fick *et al.*, 1973), but for few other plants. Most plant physiological work on assimilate relationships is directed towards understanding the mechanisms and responses of translocation within the plant. Whilst this may ultimately explain allocation patterns in plants, it is not appropriate to the current requirements of stand level crop models.

One of the consequences of this uneven appreciation of the various component physiological processes is that models can easily become unbalanced. For example, great detail on canopy

photosynthesis may overwhelm the limited treatments of the other components of a model. This has to be avoided and simplification should ensure that the internal operation of the model is appropriate to the objectives. Very simple models which focus on limiting processes are often the most successful. Thus excellent productivity models can be built from water use models by incorporating the notion of water use efficiency (WUE, dm $ha^{-1}mm^{-1}$ water), especially if a separation can be made between the transpiration and soil evaporation components of evapotranspiration. This is so because WUE is more closely related to the transpiration component (Fischer and Turner, 1978).

CONCLUSIONS

Agroforestry research can capitalize on the progress made in simulation modelling to unravel the complexity of processes that determine the response of crop systems to environment and management. Techniques are readily available and, quite likely, some components of available crop models could be incorporated directly.

Even for crop species there is a shortage of appropriate empirical response functions, surely a serious limitation for the more varied, less studied species of agroforestry associations? However, if the systems approach is adopted at the outset there is the opportunity to design the experiments to collect the appropriate responses quickly and efficiently.

Definition of purpose, model building and experimentation offer researchers a valuable repetitive loop. Components from crop models could even now be used to answer specific questions about the performance of agroforestry associations. For example, issues relating to tree canopy design and the illumination of understorey species. And for environments short of water or nutrients simple budgeting should give important clues as to the long-term stability of various alternative tree/non-tree combinations.

REFERENCES

Fick, G.W., Williams, W.A. and Loomis, R.S. (1973). Computer simulation of dry matter distribution during sugar beet growth. *Crop Science* 13, 413-417.

Fischer, R.A. and Turner, N.C. (1978). Plant productivity in the arid and semiarid zones. *Ann. Rev. Pl. Physiol.* 29, 277-317.

Forrester, J.W. (1968). "Industrial Dynamics". M.I.T. Press, Cambridge, Mass., USA.

Goutzamanis, J.J. and Connor, D.J. (1977). "A simulation model of the wheat crop". Bull. No.1, School of Agriculture, La Trobe Univ., Bundoora, Australia. 123 pp.

Loomis, R.S., Rabbinge, R. and Ng, E. (1979). Explanatory models in crop physiology. *Ann. Rev. Pl. Physiol.* 30, 339-367.

Paltridge, G.W. (1970). A model of a growing pasture. *Agric. Meteorol.* 7, 93-130.

Paltridge, G.W. (1973). On the shape of trees. *J. theor. Biol.* 38, 111-137.

Passioura, J.B. (1973). Sense and non-sense in crop simulation. *J. Aust. Inst. agric. Sci.* 39, 181-183.

Penning de Vries, F.W.T. (1975). The cost of maintenance processes in plant cells. *Ann. Bot.* 39, 77-92.

DISCUSSION

LEYTON - There seems to me to be a risk that in modelling we fail to see the wood for the trees. There are often too many peripheral factors brought in. Can we avoid some of these by identifying key physiological factors? For example, in considering plant and crop water relations the measurement of leaf water potential, leaf diffusion resistance, or, better still, crop diffusion resistance would enable us to replace a lot of other data. It is much more important to have a measurement of the water status of the crop than of the rate of water loss.

CONNOR - As I said in my paper, the type of modelling done must depend on the objectives of the modellers. In the example given our objective was to build a yield predictor based on site and weather without the need to take detailed plant records. The modelling approach is, however, very useful itself in determining which are the important plant parameters. For example, some recent very elegant work by Legg and others, which involved modelling, showed that stomatal activity was much less important than leaf area in the response of temperate cereals to water shortage.

JACKSON - This is the sort of question that modelling can answer very well. By using sensitivity analysis to see what happens if one factor varies, we can quickly determine the important ones.

KOZLOWSKI - Stomatal aperture is important, but something like the amount of water in the soil may have little effect on water stress in the plant. There can be water stress even with ample soil water, in fact waterlogged plants can wilt. The critical measurement is plant water status. For example, Thornthwaite did a series of experiments over a number of years, with apparently adequate irrigation, but found major differences in water stress because evaporative conditions varied from year to year.

CONNOR - I agree, but would point out that in some cases soil water can act as an adequate predictor and hence, in some circumstances, we can predict plant behaviour without the need for detailed plant records.

LOOMIS - I agree with Connor. Yield is formed when there is free transpiration and relative water content is high. Yield formation does not occur under stress.

KOZLOWSKI - Why use relative water content and not plant water potential?

LOOMIS - Because water potential shows hysteresis in relation to relative water content over the course of a day.

KOZLOWSKI - Even so water potential is a much better measurement of stress than is relative water content. The same relative water content in a young leaf and in an old leaf means very different things.

OWINO - What is the practical application of this work? Can models be used in crop - tree mixtures?

CONNOR - Much modelling is still at the research stage but there are examples of practical application, usually of simple models or of model components in, for example, determination of irrigation strategy, predicting wheat yield, designing orchard structures and in pest management models. There has been little work on mixed crop communities, but the applications are certainly there.

HUCK - Many models deal with only one layer; a two-dimensional model is much more complicated.

CONNOR - But there are many others that deal with layers both above and below ground.

TIESZEN - Some ecological models do deal with complex situations.

LOOMIS - There are also some good row-crop model available.

-251-

THE ROLE OF TREES IN AGROFORESTRY: SOME COMMENTS

P.A. HUXLEY
International Council for Research in Agroforestry, Nairobi, Kenya.

ABSTRACT. In agroforestry land use systems the woody perennial components ('trees') play a role in both productivity and sustainability. Some general characteristics of woody perennials are outlined and the need to consider the possible advantages or disadvantages of these in relation to specific agroforestry systems is emphasized. In deciding about introducing trees on farm land the challenge is to answer the questions: What trees? How many? How are they best arranged? Answers to the first of these will arise from the many existing and planned trials with multipurpose trees now being established worldwide. This paper addresses mainly the second question: How many trees?

Three-dimensional diagrams are used to illustrate the effects of a replacement series (tree-crop, crop-tree) on changes in total productivity and soil status with time. The types of response surfaces produced are discussed and various 'scenarios' shown to illustrate the value of this approach. Such diagrams are less a predictive tool than a means of comprehending the plant and environment changes involved.

The final section briefly discusses tree/shrub arrangement, which will depend on management considerations, soil/water conservation needs, and biological aspects of optimizing productivity.

INTRODUCTION

Agroforestry is the term given to sustainable land use systems which involve more or less intimate and interacting associations of agricultural/horticultural crops and woody perennials (trees, shrubs, palms, vines, bamboos), all on the same unit of land. This form of land use has two main objectives: productivity, involving a multiplicity of outputs; and sustainability, which implies the conservation, or even improvement, of the

environmental aspects of the system. In some cases, agroforestry systems may be used to bring about restitution or improvement of soils, so as to broaden future land use options. Some common tropical agricultural and horticultural crops are themselves ligneous and may, if appropriately managed, fulfil this role.

Agroforestry, as a science, is a new discipline, or rather a new synthesis of existing disciplines. But it cannot remain purely descriptive for long, if it is to serve an active development function. Immediate programmes of investigation and research are needed to improve existing agroforestry systems, and to offer agroforestry substitutes for agricultural or forestry land use systems that are failing to fulfil either production or conservation needs.

A fundamental issue in agroforestry is the role of the tree (using this term in its broadest sense to imply any woody perennial), and this paper addresses itself to some of the more general questions related to this theme.

Characteristics of trees

Certain characteristics of perennial woody plants are common considerations in *any* type of land use system. For example, and rather obviously, woody perennials have lengthy actual and economic life cycles; thereby influencing investment patterns and restricting cropping flexibility. They are often dominated plants in plant associations in their juvenile phase, in an intercropping sense; whilst becoming dominant when mature. Compared with many common agricultural crops, seed dormancies are more prevalent and, because many woody perennial species are outbreeding, germ plasm is often highly heterozygous.

Tree seedlings frequently require to be raised with care, and land preparation is usually more demanding as compared with many herbaceous agricultural crops. The long-term persistence of trees in a land use system will influence pest management needs. Their permanent woody structure, with dormant buds, affords a wide choice of management techniques — training, lopping, browsing, pruning — with which to modify their shape and growth patterns, and flowering and fruiting behaviour. Relatively large permanent organs (branches, trunks and large roots) facilitate the storage of carbohydrate and nutrient reserves, thereby modifying nutrient requirements, and assisting survival during adverse environmental periods.

Characteristics of trees which are generally considered to be environmentally beneficial are: a continuity of plant cover, implying amongst other things, with some species at least, an ability to utilize incoming solar radiation which might otherwise be lost by seasonally sown plants; the capacity to enrich the microsite by depositing litter in the topsoil, which can then be exploited by more shallowly rooted species; and a capacity to modify the microclimate, which can bring about favourable effects on the soil and associated plant species. Offsetting these are strong plant competitive attributes, such as the capacity to shade understorey plants, and a tendency to dominate the water economy at the microsite.

These, and other features, form a 'mixed bag' of attributes some perhaps helpful, and others not, for any particular land use system. Certainly they need to be known, categorized and

thought about in relation to agroforestry.

Experimental evidence about tree/crop mixtures

In practice the net effect of mixing trees with herbaceous crops (or grasses) will depend not only on the 'richness' of the environment, and the ways in which the various plant types can share environmental resources, but also on characteristics, partly modifiable by man, such as the geometry of the system and various temporal relationships with regard to the phenology of the separate plant components. Two examples give the extremes. First, a temporal advantage in a tree/crop mixture is clearly shown by *Acacia albida*, a soil-enriching, leguminous tree of African savanna regions, which loses its leaves in the wet season. Associated crops of sorghum, millets, groundnuts, and so on, can thus gain the advantages of the enriched site whilst avoiding the worst effects of competition from the tree for light and water (Felker, 1978). Second, the canopy architecture of a plot of well-spaced, mature coconut palms readily permits light penetration to lower storey crops. Hence this ligneous species is useful with a large number of other plant associations (Nair, this volume).

Except for a few clear-cut examples like those above, we have as yet very little experimental evidence on tree/crop combinations that tells us whether the species mixtures will interact with mutual inhibition, co-operatively, or through one form or another of compensation (Willey, 1979). This information is going to be difficult to come by, because estimates of actual land equivalent ratios for tree/crop mixtures will have to be evaluated over many years. In any case, some adjustment is needed in calculating these to allow for the different land occupancy periods for the various plant components being compared; trees representing a much more 'permanent' type of occupancy.

Even if a particular tree/crop association were to be mutually inhibitory the mixture might, in practice, be encouraged by planners because of the long-term beneficial environmental effects of the tree components. However, such an association would prove even more difficult to promulgate than many agroforestry systems because of a poor productivity cost/benefit ratio during the early years.

Choice of agricultural crops

The agricultural crop components in any existing agroforestry system, or in any newly postulated one, will be largely restricted to species which satisfy existing consumer and market preferences in any particular region. Introducing completely new food or cash crops is generally a lengthy business! An exception to this might be in relatively infertile, semiarid ecozones where agricultural cropping is not generally considered viable, yet possibilities of nutrient transfer and improved water economy exist if trees are planted and the litter and mulch materials from them are carried to adjacent strips to support agricultural crops. In these circumstances cropping is a new enterprise, anyway.

DECIDING ABOUT THE TREES

In most cases a considerable amount will already be known about the agricultural crop species in an agroforestry system, and about how to grow it. Much less is known about many of the tree species now being proposed for agroforestry systems (multipurpose trees), and on exactly how to define or evaluate their place in these systems.

Although agroforestry is concerned with the development of land use systems involving trees, it is not just 'scaled-down' forestry. This is more likely to be the case when developing community woodlots, or village fuelwood plantations, systems which might be termed 'microforestry'. The objectives, resources and socio-economic restraints underlying the adoption of tree-based farming systems will be more complex. Even the techniques of tree production and distribution could be optimized through quite different pathways in the two cases and, although the species used for fuelwood lots might well be the best adapted, adequately tested species selected for forestry purposes, many of these are decidedly *not* well suited to agroforestry systems on farmland. For example, *Eucalyptus* spp., which may be too competitive, poor at raising soil fertility, and inadequate in preventing soil erosion. Clearly, as a dominant partner, the role of the tree, and in many cases the individually spaced tree, is central to every agroforestry land use system. A challenge, then, is to answer the questions: What trees? How many? How are they best arranged? In the discussions that follow it is the position of trees in agroforestry systems suited to farm- or rangelands that is being considered.

What trees?

The current outburst of investigations on a whole new candidature of 'multipurpose' tree species is likely to provide a rich choice of different types for inclusion in agroforestry systems. Up to now many of these species have been noted as valuable only by ecologists. As their name implies they can be planted for a range of end uses and they can all be environmentally beneficial. Some genera currently being studied are: *Acacia*, *Albizia*, *Alnus*, *Azadirachta*, *Balanites*, *Brosimum*, *Cassia*, *Ceratonia*, *Cordeauxia*, *Gliricidia*, *Inga*, *Leucaena*, *Parkia*, *Prosopis*, *Sesbania*, and *Zizyphus* to name a few. Information about most of these has already been assembled (for example, National Academy of Sciences, 1980).

However, there is much still to learn about the characteristics of individual genera and species in relation to particular agroforestry situations. Important characteristics are: adaptability to soils and climate; rate of growth, particularly in the early stages; palatability as fodder; ability to withstand adverse conditions in the seedling/young plant stages; growth habit and spatial/temporal resource sharing characteristics, including rooting characteristics; shelter conferring and soil stabilization attributes; capacity to withstand lopping/pruning/browsing; vigour/productivity characteristics; nutrient cycling and/or nitrogen fixing capacity; and freedom from pests and diseases. A growing problem is to establish an adequate system, at both national and international levels, for collecting

and distributing properly authenticated germplasm of such multipurpose species.

Chosing multipurpose trees for a particular site is not just a question of finding the most adapted and vigorous species. The requirements for outputs may vary even within the same local area (for example, mainly fodder, or fuelwood, or woody mulch, and so on). Furthermore, the ideotype and phenological behaviour must be suited to the characteristics of the other species, woody or otherwise, in any particular plant associations. Some way of characterizing multipurpose tree species within any agro-ecozone, and according to some form of selection index procedure may, for output products or services, ultimately, be the most satisfactory method.

How many trees of the chosen kind?

An inherent feature of many agroforestry land use systems is the trade-off between requirements for productivity and the sustainability of the system. Trees can impart environmental benefits to a system but often, and certainly in their early years, this may be at the expense of productive outputs. If the intention is to replace some proportion of an existing agricultural cropping scheme with trees, then what sacrifice will have to be made in existing outputs? What new mixture of outputs can be expected later? What happens to the sustainability of the system during the course of time? And what exact proportion of species is needed to achieve any particular set of requirements?

A precise answer to these questions can only be evaluated site-specifically. But can any first approximations be made, however crude these may be? The sequence of the steps proposed below divides the process into two, both in relation to time: first, an estimate of the effects of tree cover on the overall soil environment status (sustainability), and second, the effects on productivity.

Unfortunately, studies of enrichment of the microsite by the individual tree are, as yet, relatively scarce compared with the many investigations of changes in soil fertility / soil conservation status under natural forests or tree plantations, or on agricultural lands (but see, for example, Charreau and Vidal, 1965; Kellman, 1980). Thus estimates will have to suffice, in most cases, especially for newly introduced tree species.

Some assumptions can reasonably be made. For example, the ultimate level of microsite improvement of any particular tree species can be assumed to reach an equilibrium with time and it may be possible to estimate what this might be. Again, the current status of soil fertility, and the average productivity under any particular agricultural cropping pattern will be known, and some estimate can probably be made of the trend in soil fertility / soil conservation status under existing management practices.

A common unit to measure both soil productivity and soil environmental status can be the net present value of a unit area of test crop (say, maize) which is produced, or could be expected to be produced, at the site. If this unit is used for both estimates of sustainability and productivity it makes the diagrams which follow both dimensional and comparable.

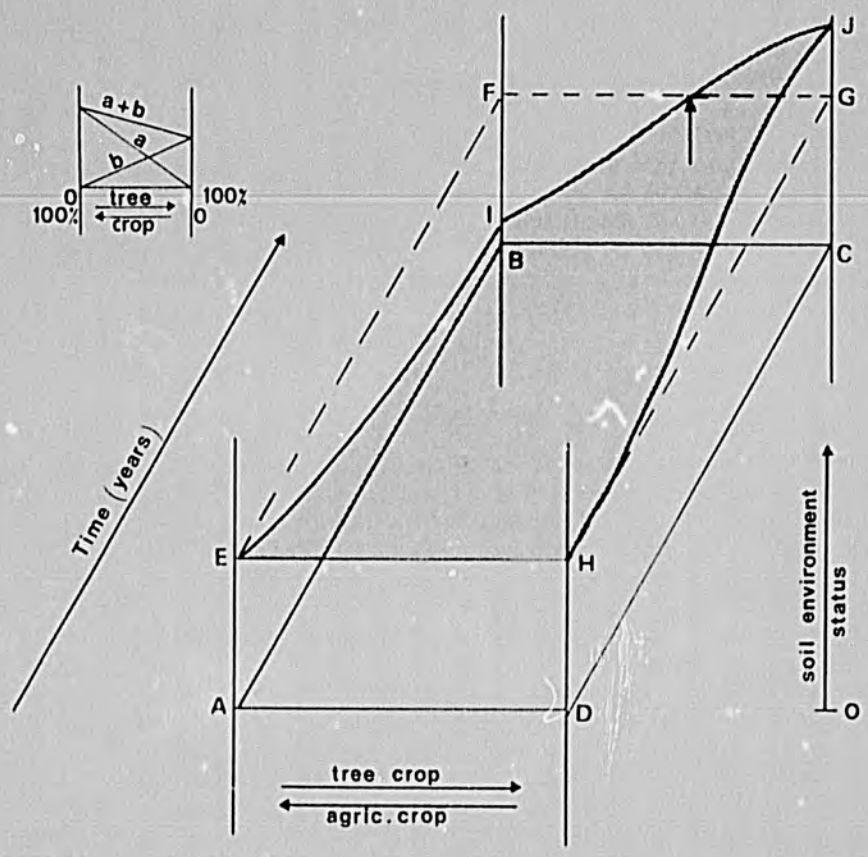


Fig. 1. Showing trends in the status of the soil environment with time. AD and DA represent a replacement series (see inset and Willey, 1979a, 1979b) which represents, at any one point on the x-axis, the sum of the effects that both species may have on the soil, depending on the percentage ground cover occupied by each. A-E (and D-H) indicate the current fertility/conservation status, and EIJH the response surface for all combinations of agricultural crop and trees (derived at any one time from a+b as in inset). See text for further details.

Soil environment status. Figure 1 indicates some postulated changes in the conditions of the soil (its fertility and state of conservation) for agricultural cropping, tree cropping, and all ratios of the two. ABCD represents a fertility level at which there is zero productivity, and the line E-H (also F-G) productivity at the current level of soil fertility. Projected soil fertility changes are then estimated for: continuous agricultural cropping (E-I), shown as declining; and the land under 100 per cent cover of trees of the chosen species (H-J), shown as improving with time.

EIJH then represents the response surface characterizing soil changes for all ratios of the agricultural and tree crops over time.

E-A should be known. And C-J might also be measurable if mature stands of the appropriate tree species are available on a similar, nearby site. Otherwise C-J will have to be estimated

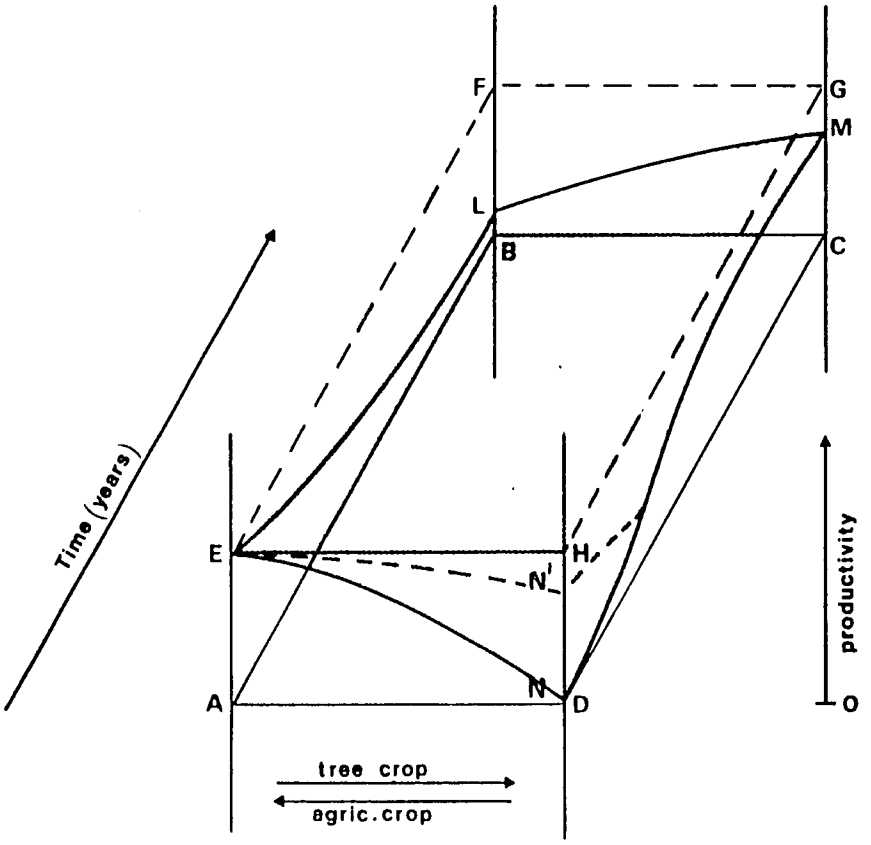


Fig. 2. Trends in total productivity with time, similar to Figure 1. At any one point on the x-axis (a replacement series) the response surface ELMD represents the combined productive output, of all kinds, for both species, (and see text).

from similar data in the literature The same applies to the rate of decline of soil fertility, and so on, under continuous agricultural cropping. The time taken to reach the maximum improvement in the condition of the soil after planting trees may be unduly long, because an equilibrium state will be reached only slowly in the last few years. Thus C-J in Figure 1 may be taken, more pragmatically, to represent an estimated 90 per cent or any stated percentage, of the ultimate value. The time scale of the diagram will clearly depend on when it is estimated that this level will be reached. C-J minus A-E represents the amount by which the level of soil status under current land use falls short of what it could be under a mature stand of trees.

Productivity. Figure 2 indicates the changes over the same time in total productivity. That is taking into account the respective values of the total agricultural and tree products. As before, ABCD represents zero productivity. E-L shows the estimated changes of value with time for continuous agricultural cropping, and N-M that for 100 per cent tree cover (N, the value of the tree crop in the first year, has been taken as zero in this

example). Response surface ELMN then represents the total production of all the different proportions of the agricultural and tree crops. As the common unit used is market value, E-I represents the soil status in Figure 1 and it is the same as E-L, representing productivity, in Figure 2.

The value of the tree products will need to be averaged out if annual harvests are not taken. In Figure 2 the annual value of the tree products at maturity with 100 per cent tree cover (C-M) could be either greater or lesser than the value at the present time from 100 per cent agricultural cropping (A-E). This will depend on current agricultural yields, reflecting the present fertility status of the soil, as well as the expected outputs of the agricultural and tree products with time.

The diagrams obviously lend themselves to more detailed economic analyses in terms of, say, estimates of variable and fixed costs, or of calculating returns to labour inputs, and so on. Furthermore, there might be changes of inputs with time which should be taken into account. The productivity response surface in Figure 2 can be adjusted accordingly.

Time trends. The curves plotted on the axes in Figures 1 and 2 have been drawn to represent changing conditions, as far as these can be estimated at present. Only sets of actual experimental data will show if these estimates truly simulate real conditions or not. For example, in Figure 1 the reduction in soil fertility under continuous agricultural cropping (E-I) will generally reflect a decline in soil organic matter which follows a negative exponential curve (Ahn, 1979). But to this must be added any effects of soil erosion which will be hard to estimate and erratic in occurrence.

Then again, soil fertility changes after planting young trees (H-J) have been represented by a sigmoid curve to indicate a maximum rate of change in the middle years. Planting relatively widely spaced trees on agricultural land will bring about a mosaic of improved fertility in the topsoil beneath the tree canopies. The effect may be enhanced if the trees fix nitrogen, and if nutrient catchment from windblown dust is involved. It has been assumed that, where there are relatively few trees per unit of land, both their growth and fertility conferring benefits might be diminished compared with a situation where tree cover is more complete. To account for this I-J in Figure 1 is also shown as a sigmoid curve.

In Figure 2, representing the productivity response surface, the value of the output of products from a pure stand of trees (N-M) will be very little in the first few years and it will reach a plateau at maturity. In the early stages after planting out young trees the agricultural crop can utilize more of the shared environmental resources because the size of the trees is so small. E-N will be convex therefore and, if some form of taungya is practised in the first year or two, so as to take maximum advantage of this situation, there need be little loss of productivity (see E-N'). As one is seeking plant associations which, in a replacement series, show either mutual co-operation, or, where one of the components shows a level of compensation which gives an overall increase in productivity (that is a land equivalent ratio greater than one), L-M will also be convex under

such favourable circumstances.

Further considerations. Figures 1 and 2 show the two basic shapes of the expected response surfaces for soil and productivity changes, respectively. These may be useful to help visualize the complex trends which will occur with time in converting from agriculture to a mixed cropping agroforestry system. They also indicate where more research data are needed. Figure 1 can help, also, to suggest what proportion of mature tree cover is required in order to achieve, ultimately, any particular level of soil fertility in the mixed cropping system. For the situation depicted, the present-day level of soil fertility will be maintained if approximately a 60 per cent tree cover is arranged (arrowed where I-J cuts L-G). Obviously fewer trees will be required should the soil fertility decline less rapidly under continuous agriculture, and/or a tree species is used which raises soil fertility to a greater extent. On this basis Figure 3 shows some land use situations in which options for agroforestry may or may not be promising.

The extent to which any improvement in topsoil fertility under or around the trees can be exploited by associated crops while the trees are still growing needs to be the subject of experimentation for particular combinations of species. Some transfer of litter and nutrients away from the tree's immediate surroundings is likely, and its extent will be influenced by management practices. Such effects will, perhaps, increase productivity (C-M), and serve to make the productivity response surface even more convex at its further end (L-M) (Figure 2).

By substituting relatively large trees for agricultural crop plants the total population of plants per unit of land will be diminished and the diagrams should be constructed to indicate percentage ground cover ratios. In addition, substituting trees for herbaceous crops will change the land occupancy ratio. Such factors affect the way we should interpret the yield curves and the validity with which we can make comparisons between them. In view of the need to adopt a 'first approximation' approach, however, these difficulties can just be borne in mind at this stage.

The actual number of trees per unit of land will obviously depend on the species under consideration. Many multipurpose trees are of small to medium stature. If the appropriate canopy area at maturity is known 'percentage cover' can be roughly translated into 'numbers of trees per unit area'.

To find the answer to our question 'How many trees?' may still not be easy, but some of the considerations underlying the processes involved in reaching a conclusion are, at least, outlined above, and some 'scenarios' are shown in Figure 3.

How are the trees to be arranged?

Once the kinds and the numbers of trees required have been decided upon, in relation both to the land user's objectives and resources, then the question of optimizing their spatial arrangement has to be considered.

There are three main factors: management considerations, soil and water conservation aspects, and theoretical aspects of optimizing biomass and/or particular plant products.

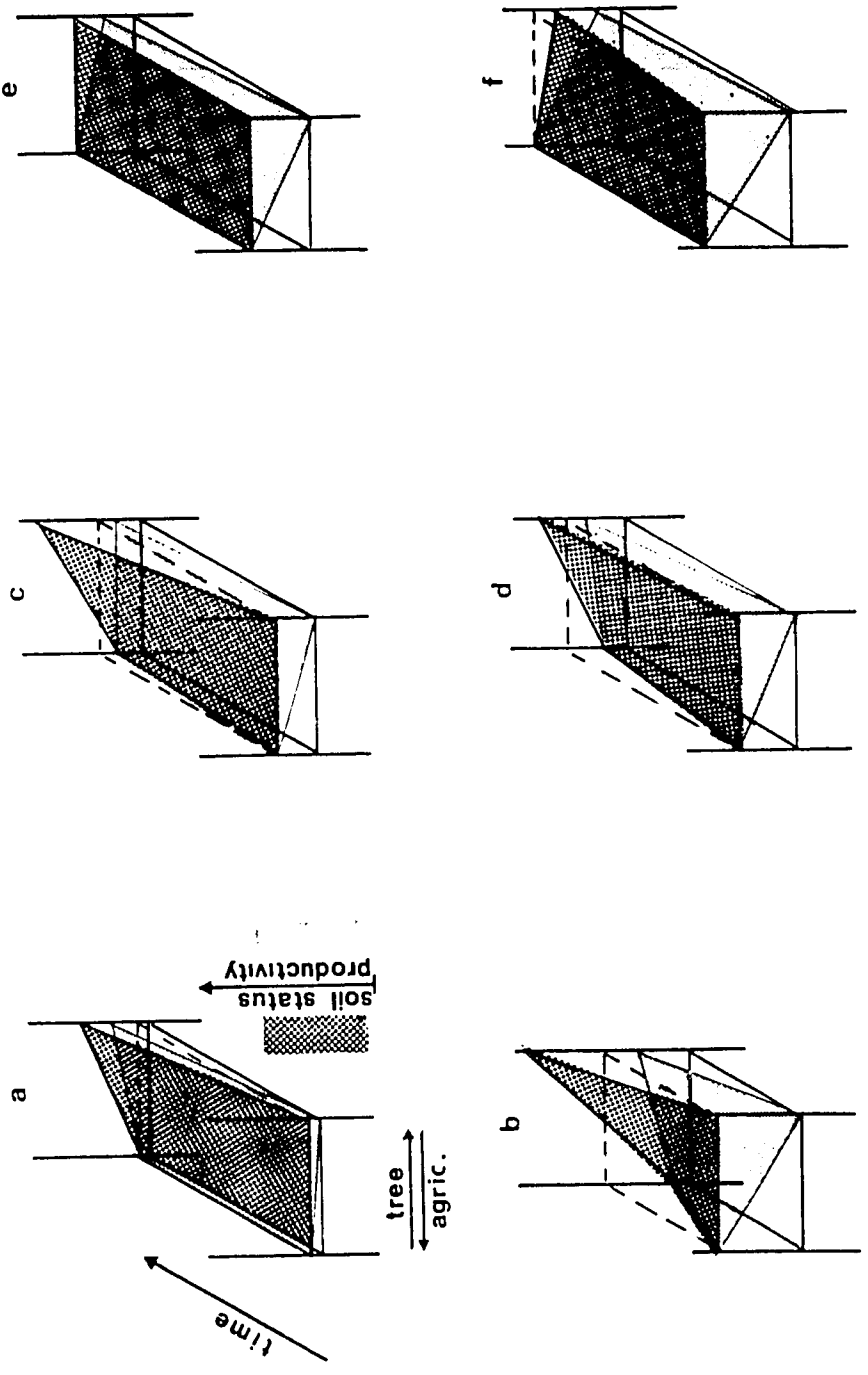


Figure 3.

Fig. 3 (*Opposite*) Some scenarios comparing different soil environment and productivity states for various agricultural crop/tree situations (linear trends drawn, for simplicity).
(*a*) Very low present fertility and productivity; for example, low rainfall rangeland undergoing desertification. Any attempt at agriculture fails to raise the soil environmental status or productivity except at great cost in terms of irrigation, fertilizers, and so on, but trees improve the soil and therefore, ultimately, enhance productivity. Agroforestry is definitely to be considered.
(*b*) Initially fertile land (for example, cleared forest) but agricultural cropping brings about a very rapid decrease in fertility and productivity. Note the shorter time scale. The tree species chosen, for example fast growing legumes, are supposedly very effective at enhancing even the initial high level of soil fertility. Agroforestry definitely to be considered as an alternative to high input agriculture.
(*c*) Rather low initial level of soil fertility with a slow decline under the present agricultural cropping system. The tree species has been chosen to raise soil fertility level, but tree products are of low value for this species. Agroforestry may be worth considering if environmental conservation is important, and as an alternative to increasing the level of agricultural inputs; especially as a system using a relatively small amount of tree cover might still be effective.
(*d*) Higher initial soil fertility is postulated which agricultural cropping decreases at a faster rate than in (*c*). The tree species chosen is deemed not to be especially effective at raising soil fertility, but its products are more valuable than in (*c*). So that, ultimately, 100 per cent tree cover will provide an output more valuable than that from the agricultural system. Agroforestry is to be evaluated against loss of income during the development years, and the level of environmental conservation (or enhancement) required.
(*e*) A moderately good initial fertility which high input agriculture maintains equally as well as the tree cover, for example, a maize farming system using minimum tillage with the litter left on the soil. Productivity under trees is less than in the agricultural system, so there is no case for agroforestry unless the tree products are specifically required.
(*f*) A high initial fertility, which is maintained (or even improved) by high input agriculture (for example, coffee farming using fertilizers and mulch) to a greater degree than a multipurpose tree cover would achieve. Productivity under trees is assumed to be rather low. There is no case for agroforestry.

Management decisions. The first is whether to adopt a mixed or a zonal agroforestry system (see Huxley, p.163, this volume). This basic choice is an important one which will depend on both technical and social considerations. Zonal agroforestry is likely to simplify management procedures because each tree or crop component can be dealt with largely as a sole cropping enterprise within the system. 'Alley cropping' (Kang *et al.*, 1981), a form of zonal agroforestry, is one convenient way to arrange the plants. In zonal agroforestry the extent of plant-to-plant interactions will depend on the species involved as well as the overall land unit size and the size, shape and arrangement of zones within it. Between-species interactions, as found in the more intimately associated mixed cropping systems, will occur only at the interfaces between zones.

The transfer of materials (litter or mulch) can easily become part of the management procedures in zonal systems. Where there is already some information about the potential for introducing a suitable agroforestry tree species, but little or nothing is known of the interactions with agricultural crops, then a zonal system may offer a less committed, and more flexible approach, than that of more intimately mixed alternatives.

Soil and water conservation considerations. Information about the use of trees for soil conservation is available from various sources, for example Tejwani (1979). Although more quantitative data are required, especially for many of the 'new' multipurpose species which are now attracting attention. Trees can actually encourage soil erosion in some circumstances. For example, if the wrong species are used and/or they are planted in the wrong places (Wenner, 1981). Thus an important aspect of agroforestry planning must be a consideration of the spatial arrangements of trees in relation to soil and water conservation.

Optimizing the product. Finally, it is possible to draw on a vast body of information from a range of different plant science studies concerning the theoretical aspects of optimizing productivity through proper spatial arrangement and management of the component plant species. In particular the work on plant canopies and light interception (see Jackson, this volume), on plant ideotypes and competitiveness (or commensalism), and the growing body of information from agricultural intercropping studies (see Cannell, this volume).

Because trees and shrubs lend themselves to easy modification of shape and size there will be many opportunities to manipulate the growth of trees in agroforestry systems by training, pruning and lopping. The extensive knowledge we already possess about these procedures for existing tree crop species, both temperate and tropical, can form a useful basis from which to start.

What is immediately required for all aspects of tree arrangement and management is a new synthesis of existing information.

CONCLUSIONS

Agroforestry may be biologically more complex than many ways of

using land through agriculture or forestry, consequently such systems often require greater management skills. Certainly the development of agroforestry needs to embrace a combined technical and socio-economic approach from the very start; with the rural land user being intimately concerned with the available choices at every stage. These choices relate to requirements for particular kinds and levels of productive outputs, and to the potential for sustainability. The characteristic of all agroforestry systems is that they can provide both.

Diagnosis and evaluation of any agroforestry system *must* encompass predictions about its performance in the future. This implies a joint deductive/inductive approach to evaluation and prognosis which utilizes methods of survey and sampling concerning what is already on the ground (Steppler and Raintree, this volume), and also attempts to evaluate potential future trends using such information as is presently available. In these processes decisions about how to chose and handle the trees stand out as a priority. We can usefully approach this through the steps of: What trees? How many? How do we best arrange them?

The diagrammatic method outlined in this paper which can help to answer the second question is not intended as a predictive tool; far too much conjecture is implicit in the construction of such diagrams. Where they may be helpful is to illustrate the processes which have to be considered, and what type of experimental data we require before such an approach can be undertaken with confidence. Only when we have such data will it be possible to assess the productivity and sustainability roles of trees in any particular agroforestry system with any precision.

REFERENCES

Ahn, P. (1979). The optimum length of planned fallows. *In* "Soils Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.15-40. ICRAF, Nairobi, Kenya.

Charreau, C. and Vidal, P. (1965). Influence de l'*Acacia albida* Del. sur le sol, nutrition minérale et rendements des mils *Pennisetum* au Sénégal. [The influence of *Acacia albida* Del. on soil, mineral nutrition and millet production of *Pennisetum* in Senegal.] *L'Agron. Trop.* 6, 600-626.

Felker, P. (1978). State of the art: *Acacia albida* as a complementary permanent intercrop with annual crops. *Report AID Contract AID/afr-C-1361*. USAID, Washington, USA. 133 pp.

Kang, B.T., Wilson, G.F. and Sipkens, L. (1981). Alley cropping maize (*Zea mays* L.) and leucaena (*Leucaena leucocephala* Lam.) in southern Nigeria. *Plant and Soil* 63, 165-197.

Kellman, M. (1980). Soil environment by neotropical savanna trees. *J. Ecol.* 67, 565-577.

National Academy of Sciences (1980). "Firewood Crops". National Academy of Sciences, Washington D.C., USA.

Tejwani, K.G. (1979). Soil fertility status, maintenance and conservation for agroforestry systems on wasted lands in India. *In* "Soils Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.141-174. ICRAF, Nairobi, Kenya.

Wenner, C.G. (1981). Trees in erosion and soil conservation. *In* "Proc. Kenya National Seminar on Agroforestry" (L. Buck, ed.),

pp.199-234. ICRAF, Nairobi, Kenya. (Mimeograph)
Willey, R.W. (1979a). Intercropping - its importance and research needs. I. Competition and yield advantages. *Field Crop Abstracts* 32, 1-10.
Willey, R.W. (1979b). Intercropping - its importance and research needs. II. Agronomy and research approaches. *Field Crop Abstracts* 32, 73-85.

DISCUSSION

CONNOR - The processes shown in the diagrams need a good deal of experimentation in order to establish actual curves. Such diagrams will be the output of actual models.

BRUNIG - These diagrams are useful in assessing the direction in which the systems are likely to move. However, they indicate only the trends; accurate and precise predictions are not possible.

BIOECONOMIC CONSIDERATIONS IN THE DESIGN OF AGROFORESTRY CROPPING SYSTEMS

J.B. RAINTREE
International Council for Research in Agroforestry,
Nairobi, Kenya.

ABSTRACT. The productivity of multipurpose agroforestry systems cannot be assessed on the basis of conventional measures of productivity in monocultural fields. Indices such as the land equivalent ratio, developed for arable intercropping systems, will prove useful in the development of improved agroforestry based land use systems, but the ultimate unit of evaluation in agroforestry is the enterprise, not the field. Even the most sophisticated index of yield per unit of land will be the most relevant index of productivity only where land is the limiting production factor. The relationship between trees and their understorey intercrops can be competitive, complementary, supplementary or some composite of these relationships; which of these predominates in a given intercropping system depends not only on the genotype, number and espacement of components, but also on which growth factors are limiting for the respective components under realistic field conditions. An analysis of interactional effects indicates that certain highly promising agroforestry complementarities are significant only under low input production conditions. This suggests that a number of synergistic intercropping potentials in agroforestry will remain seriously underdeveloped if agroforestry research retains the traditional experiment station orientation to production conditions characteristic of 'high access' farmers, rather than concentrating on the low input conditions typical of the majority of farmers and potential agroforestry technology adopters in developing countries. Following a discussion of bioeconomic considerations involved in deciding when it is advantageous to add trees to arable crop fields, the main bioeconomic principles for a decision on the optimum number of trees are presented. Budgeting techniques are discussed and an illustration is given of the use of linear programming as a practical bioeconomic design tool in agroforestry.

INTRODUCTION

Bioeconomics, that branch of economic science that deals most directly with biological processes, has an important role to play in the design of research on agroforestry cropping systems. In order to understand the nature of this role it is important to distinguish between bioeconomic and socioeconomic aims and methods. For the purposes of this paper they may be differentiated most simply on epistemological grounds: if socioeconomic dimensions of agroforestry cropping systems are not taken into account, researchers will have no way of knowing whether the technologies they develop will have any relevance to the resource endowments, production constraints, and end use requirements of potential users. On the other hand, if bioeconomic considerations are ignored, agroforestry researchers will have no way of assessing the economic significance of interesting plant combinations, interactions, and cultural manipulations. Concerned with the middle ground between determinants of technical feasibility and determinants of socioeconomic adoptability, bioeconomic considerations impinge directly on the conduct of plant research in agroforestry.

The elementary bioeconomic thought is that the figure of merit, when evaluating the productivity of agroforestry systems, is not the per hectare biological yield *per se*, but *some transform* of that figure which takes account of its net value to the producer. A full and adequate discussion of all of the considerations involved in defining the precise nature of that value accounting function for even a simple real world production situation is beyond the scope of this brief contribution.

This paper will only scratch the surface of bioeconomic concerns in agroforestry, but it will attempt to make some headway toward a bioeconomic perspective on the evaluation of competitive, complementary, and supplementary relationships among potential agroforestry crops, particularly as they affect assessment of optimum productivity under realistic field conditions. Although we will not progress very far toward the goal in this paper, the ultimate aim is to develop practical bioeconomic measures and procedures which will eventually contribute to our ability to give reasonably optimal answers to the basic agroforestry design questions: 'What trees?', 'How many?' and 'What arrangements?' (see Huxley, pp.267-270, this volume).

RETURNS TO LAND

In agroforestry, production and conservation are two sides of the same coin. The concept of sustainable land use is basic to a definition of agroforestry. Consequently, the development of objective indicators of 'sustainability' is high on the agenda of research needed to develop adequate evaluation and design methods for agroforestry systems. Bioeconomic methods will play an important role in operationalizing this concept, but at the moment there is little to report. One bioeconomically significant factor, however, is that conservation benefits in themselves are seldom viewed as sufficient incentives for adoption of a new technology. Farmers the world over respond favourably to innovations in conservation technology only if they entail additional short-run economic incentives. In advanced economies

this often takes the form of government subsidies on designated land use practices. In agroforestry systems for developing countries, adoption incentives will probably take the form of economic 'byproducts' (Raintree, 1980a). If this is so, then it becomes imperative for agroforestry researchers to identify and develop suitable multiproduct components and intercropping systems.

One immediate consequence of the multiproduct nature of agroforestry production systems is that their productivity cannot be assessed by conventional measures of the per hectare yields of the separate crops taken individually. This is true for the simple reason that, although the yields of the individual intercrops may be depressed relative to their yields in monocultures, the total production of the field may be higher than that obtainable when the individual crops are grown side by side as sole crops on the same amount of land.

Land equivalent ratio

The concept of land equivalent ratio (LER) has been developed to deal with this aspect of nonagroforestry intercropping (International Rice Research Institute, 1974, 1975; Trenbath, 1976; Willey, 1979), and it is equally applicable to agroforestry systems. Assuming equivalent levels of management, LER may be defined as the relative land area under sole crops that is required to produce the yields achieved by intercropping (Willey, 1979). When LER is experimentally assessed on the basis of uniform planting density of both intercrop and sole crops, the resulting LER figure is equivalent to the relative yield total (RYT) of de Wit and van den Bergh (1965). When intercropping gives a yield advantage, however, the total optimum intercrop density may be higher than that of either sole crop optimum (Willey, 1979). It has been suggested, therefore, that calculations of LER and other indices of yield advantage should be made on the basis of optimum, rather than constant density in order not to distort the true practical potential of intercropping (Huxley and Maingu, 1978). In any case, the practice of intercropping is assumed to be beneficial when LER > 1, of neutral value when LER = 1, and detrimental to yields when LER < 1. LERs of as much as 1.6 have been reported for traditional farmers' fields (Norman, 1973) and up to 2.0 for experimental plots (Andrews and Kassam, 1976). The ratio should prove useful in agroforestry applications, providing some additional means is used to assess differences in duration of the production period.

WHEN IS IT BENEFICIAL TO ADD TREES TO ARABLE CROP FIELDS?

It is often tacitly assumed, even by proponents of agroforestry, that the addition of a tree component to a field crop situation will almost always decrease the yield of the field crop, although the additional tree crop production may offset this decrease to give an overall LER > 1. The assumption that understorey arable crop components in mixed agroforestry systems will suffer from association with trees is usually based on the notion that the trees, being the dominant partner in the association, will compete with understorey crops, particularly for light, and that as a result of this competition the arable crop yields will be

depressed. There is little doubt that evolution has conferred a competitive advantage on trees in the form of their greater stature, but whether, in the contexts of particular agroforestry systems, they are always competitive with understorey crops and whether, being competitive, they always reduce net yields, are questions which require closer analysis.

This type of problem has been given a general treatment in economics by means of production possibility curves. Under the assumption of fixed resources (the isoresource condition), production possibility curves show what happens to the quantity of each of two products when resources are transferred from one to the other. In this case the resource in question is land. Conventional economic analysis is usually content to deal with land as a unitary quantity on a par with the other main production factors, labour and capital. For purposes of bioeconomic analysis, however, it is necessary to disaggregate this production factor and recognize that 'land' implies access to variable amounts of a whole set of associated plant growth factors, including light, CO_2, nutrients and water.

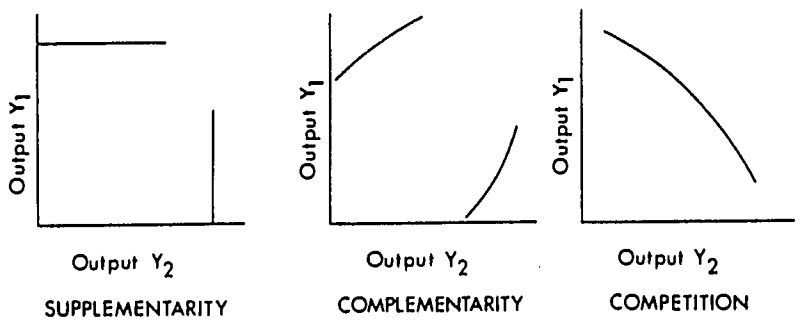


Fig. 1. Production possibility curves under isoresource conditions.

As shown in Figure 1, there are three general relationships possible between two products under iso-resource conditions: *supplementarity*, *complementarity* and *competition*. Which of the three relationships obtain between products or components in an agroforestry association depends upon a number of complex interactional factors discussed in greater depth in other papers in this volume. I would like to suggest, however, that among the most important factors are: the genotypes involved; the proportion and arrangement of trees in the mixture; and which plant growth factors are limiting for the respective components under field conditions. Actual production possibility curves for specific combinations will often be some composite of the three general relationships (Figure 2).

Supplementarity

Two products are supplementary if the production of one can be increased with neither an increase or decrease in the other, that is the outputs are essentially independent within the range of supplementarity. An example in agroforestry is multistorey

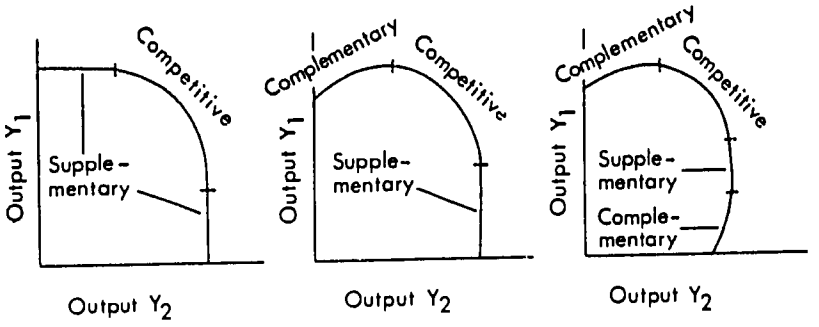


Fig. 2. Some examples of composite production possibility curves.

intercropping with coconuts (Nair, 1979). Providing that light is not normally the limiting factor for the understorey crops when grown as sole crops on farmers' fields, the presence of tall, well-spaced, mature coconuts will have little effect on crop yield. Nutrients or water will normally be more limiting than light under smallholder conditions outside the continuously humid tropics, and coconut palms offer only localized competition for these growth factors.

Another possible example of supplementarity in agroforestry is that of sorghum under *Parkia clappertoniana* in farmed parkland of the Guinea savanna in Nigeria (Pullan, 1974). Farmers in this zone say that the sorghum yield under naturally occurring locust bean trees is no different from that of the surrounding fields. They report that the plants grow taller in the shaded, more fertile environment under the tree, but no change in grain yield is observed. If the observation is valid, perhaps the reported supplementarity is the net result of mixed competitive and complementary interactions which cancel each other out on balance. But even though the light intensity of the savanna environment is high, it is reasonable to suppose that at some density of *Parkia* trees light would become limiting and sorghum yields would be noticeably depressed. Considering the economic value of the locust beans themselves, which local farmers collect and sell for more than three times the price of soya beans, it would be interesting to have some exact data on these interactions.

Complementarity

Two products are complementary if increasing the production of one results in a corresponding increase in the other. The by now nearly classic example of complementarity in agroforestry is that of *Acacia albida* with millet, sorghum, or groundnuts. Due to the particular deciduous foliage habit of this tree legume, the shading effects are conveniently withdrawn during the rainy season when the grain crops are in the field, leaving only the beneficial effects of improved soil fertility and water regime. Consequently, the tree stands in a net complementary relationship to the understorey arable crop.

The benefits of *A. albida* are fairly well documented (Felker, 1978) and more research is under way, but how

representative is this unique tree of the potential for complementary agroforestry associations? I suggest that our awareness of complementarity in agroforestry is just beginning, although we already have quite a few examples from among the tree legumes. It has been fairly well established that what *A. albida* does automatically for the fertility status of associated soils can also be achieved, with appropriate inputs of labour and management, by other tree legumes such as *Leucaena leucocephala*, *Cajanus cajan*, *Gliricidia sepium* and *Tephrosia candida* (Centro Internacional de Agricultura Tropical, 1977, 1978; Benge, 1979; International Institute of Tropical Agriculture, 1979, 1980; Wilson and Kang, 1980; Rachie, this volume; Wilson and Raintree, 1981). Several other tree legumes have been suggested for trial (Raintree, 1980b; Rachie, this volume) in 'mixed' or 'zonal' agroforestry systems (see Huxley, p.163, this volume).

Complementarity in mixed agroforestry systems need not be achieved only through the effects of deciduousness as in *A. albida*. An example from Western Rajasthan of increased yields of arable crops and range grasses under *Prosopis cineraria* (Mann and Shankarnarayan, 1980) is a case in point. Nor are yield improving fertility increases achieved only by leguminous or other nitrogen fixing trees such as *Alnus*, as the practice of farmers in high population areas of Eastern Nigeria of planting and managing *Acioa barteri* for its value as a 'nutrient pump' amidst shallowly rooted crops on leached soils may indicate (Okigbo and Lal, 1979).

A search for examples of complementary relationships among agroforestry intercrops quickly leads one to the conclusion that interactional effects are important in determining which growth factors are limiting and, therefore, which plants are complementary in a given environment. Of particular bioeconomic significance are the interactions between soil fertility and other growth factors. Two examples serve to illustrate the nature of the bioeconomic concerns.

Felker *et al.*, (1980) have recently reviewed the literature on the effects of soil fertility status on water use efficiency and drawn some interesting conclusions on agroforestry potentials in semiarid ecosystems. The basic effect was established by Hanks and Tanner (1952) in their experiments on water use efficiency of field crops on fertilized and unfertilized Wisconsin soils. These experiments showed that, while water might be limiting crop yields, the biomass increase per unit of water used is lower at lower fertility levels. In their two-year field trial, water use efficiencies for maize and oats on fertilized plots averaged 143 and 175 per cent more, respectively, than unfertilized control plots. In a later range fertilization study in Montana Wight and Black (1979) discovered a yield plateau of 1250 kg ha^{-1} for the unfertilized plots which was present in both the wettest and driest years, suggesting that water was not limiting plant productivity above this level. The fertilized plots showed an average 10-year increase of 120 per cent over unfertilized rangeland. Felker *et al.* (1980) estimated natural nitrogen inputs to semiarid ecosystems and compared them with data on water use efficiency. Their analysis indicates that plant productivity in the semiarid zone may be 10 times more limited by nitrogen than by available water.

The second example relates to the effects of shade in mixed intercropping systems at different levels of fertility. All of the examples of complementarity between trees and their understorey intercrops considered so far refer to situations in which the tree canopies are either light, seasonal, or heavily pruned. These examples do little to question the common assumption that shading *per se* is always in some measure detrimental to understorey crops. The tendency in recent years to remove the traditional shade trees from coffee, cacao, and tea plantations has lent credence to the general impression that shade is never, in itself, beneficial. In a more critical light, however, it becomes obvious that the issue is dependent on a number of factors that can be quite complex in their interaction (Willey, 1975). From their investigations on the effects of artificial shade on cacao yields in Trinidad, Murray and Nichols (1966) reported that in plantations fertilized with adequate amounts of NPK the highest yields were obtained in full sunlight, but that unfertilized plantations of low nutrient status gave their highest yields under shade. Comparable experiments with tea in northeast India showed a similar interaction between light and nitrogen level (Wight, 1958). In the case of coffee, workers have concluded that where soil fertility is low and adequate fertilizer cannot be added, shading may be desirable in order to prevent periodic overbearing and dieback (Hardy, 1962; Fernie, 1970; Huxley, 1970). The function of shading in this case is to regulate yield to a level which is sustainable on the basis of inherent soil fertility (Willey, 1975).

These two examples are bioeconomically significant because they relate to two of the most limiting and ubiquitous constraints on smallholder production in the tropics, low soil fertility and inadequate supplies of mineral fertilizer. In both examples the conventional wisdom, that is that water is the most limiting factor in dry regions, and that shade is always detrimental to understorey crops, is overturned in situations where soil fertility is low and adequate amounts of mineral fertilizer cannot be added. *But these are precisely the conditions which characterise smallholder production in most developing countries.* The assumption that water is most limiting or that shade always reduces yields of understorey crops could only be made in the context of the production conditions enjoyed by research stations and a select group of 'high access' farmers (Roling, 1980) wherein all otherwise more limiting production factors are routinely topped up to optimal levels by inputs from outside the system. The assumption is that the 'best' farmers will do the same.

In fact, in the world outside the agricultural laboratory, the inputs are not always available, or at least not in sufficient quantity to reach the majority of farmers. In many cases the economics of fertilizer use are questionable (Raintree and Turay, 1980), but even where government subsidies have reduced farmgate fertilizer costs to economic levels, the infrastructure to deliver them in adequate supply is often simply not there. The supply situation in Nigeria, a country which has an exceptionally good foreign exchange balance and which maintains fertilizer subsidies of more than 80 per cent (Knipscheer, 1979; Menz, 1980), is perhaps more typical than we like to admit. An analysis (Raintree, 1980b) of data from the British Overseas

Development Ministry's Central Nigeria Project Farming Systems Survey (Gosden, 1978) shows 100 per cent of the survey villages reporting *lack of inputs generally* and 95 per cent reporting *lack of fertilizer specifically* as major production constraints.

The general conclusion to be drawn from these examples is that, while the potential for complementarity between components of well-designed agroforestry systems would appear to be quite promising, unless agroforestry research is designed with realistic field conditions in mind, this potential is likely to remain seriously underdeveloped.

Competition

Two products are competitive if increasing the production of one results in a decrease in the production of the other, given a fixed level of resources. The products of trees and associate arable crops which are limited by the same factors, which draw these factors from the same environmental resource pools, and which have no compensating interactions, will stand in a relationship of net competition. Does this mean that intercropping would be uneconomic? Not necessarily, since the total productivity of the association might still be higher in terms of LER or gross margin per hectare than the monocultural alternative. The only competitive situation which can be ruled out immediately on biological grounds is one in which the components are *mutually inhibiting*, or amensalistic. As long as one component is benefited by the association, there is the economic possibility that a higher LER may be achieved by intercropping.

It is an economic truism that the rational, profit maximizing producer will always operate in the region of diminishing returns. In the present context this means in the region of competition on the production possibilities curve. As explained in the next section, the level of competition which is appropriate and desirable depends upon the relative prices of the products and the rate at which they substitute for each other in the production process. Examples of competitive relationships among agroforestry components are too numerous to mention. Even complementary products become competitive at high production densities (Figure 2).

WHAT IS THE OPTIMUM NUMBER OF TREES?

I do not, of course, propose to give a numerical answer to this question, nor even to assay a general computation algorithm. Instead, the rather modest aim of this section is to review some of the elementary bioeconomic principles by which an answer to the question might eventually be approached in specific applications.

Supplementary product relationships should be taken advantage of by increasing production at least to the point where the products become competitive. In the case of complementary products, resources should be transferred from one product to the other as long as doing so increases the production of both. Increasing the transfer of fixed resources (land) beyond the range of complementarity into the range of competition will decrease the production of one of the products. How far into the competitive range it is profitable to go will depend on the relative

prices of the products In general, maximum profit is obtained at the point at which the rate of transfer of resources from one product to the other ($\Delta Y_2/\Delta Y_1$) is equal to the rate at which the products exchange in the market, that is the price ratio (P_1/P_2) (Bishop and Toussaint, 1958; Flinn, 1979).

All of this follows from the fact that the rational producer will continue to transfer resources (land in this case) from one product (Y_1) to another product (Y_2) as long as the value of increased production of the one ($\Delta Y_2.P_2$) is greater than the cost in decreased production of the other ($\Delta Y_1.P_1$), that is $\Delta Y_2.P_2 > \Delta Y_1.P_1$. If the value added to the one is less than the cost of decreased production in the other ($\Delta Y_2.P_2 < \Delta Y_1.P_1$), the resources should be transferred in the opposite direction. The optimum resource allocation is reached when the value of the last increment of the one product is equal to its cost in terms of the other, that is when $\Delta Y_2.P_2 = \Delta Y_1.P_1$, or equivalently, when $\Delta Y_2/\Delta Y_1 = P_1/P_2$. This is the *principle of equimarginality*. If the production possibilities curve is graphed in terms of net revenue, the optimum combination of products for maximum returns to land can be identified by the tangent to the curve at the point where its slope is equal to the price ratio (Figure 3).

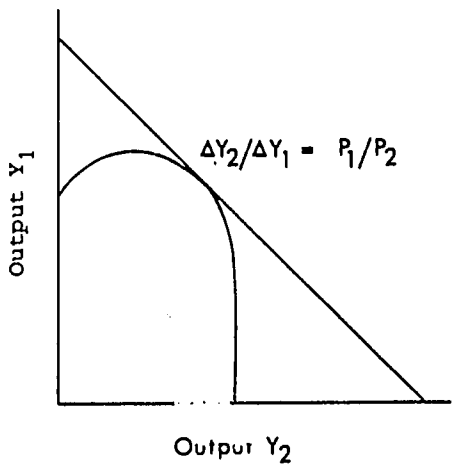


Fig. 3. The maximum profit combination of products.

In more concrete terms, the principle states that it pays to go on adding trees to an arable crop field until the point at which the value of an additional tree is equal to the opportunity cost to the intercrop of the land allocated to the tree. Given the relative prices of the two products and data on their physical rate of substitution, the principle of equimarginality can be applied to ascertain the optimum intercropping combination. In the absence of replacement series data or the like on the effects of intercropping, some method of estimation (see Huxley, p.257, this volume) can be used to arrive at a first approximation or 'best bet' design for maximum returns to land. This is only a partial formulation of the relevant decision criterion, since the only cost it takes account of is land, and an extension of the method into more detailed economic analysis is required, as Huxley points out.

RETURNS TO THE MOST LIMITING PRODUCTION FACTOR

In the foregoing discussion we have tacitly assumed, for the sake of simplicity, that profit can be maximized by maximizing returns to land. In as much as agroforestry is an approach to improved land use systems it is useful and necessary to develop techniques to evaluate the productivity of land under alternative agroforestry systems, but it would be misleading to imply that returns to land are always the best indication of productivity. *The unit of success or failure in agroforestry is the enterprise, not the field.* As with other forms of agricultural production, the appropriate general criterion for evaluation of agroforestry systems is *maximum returns to the most limiting production factor.* Yield per hectare, or more sophisticated measures of returns to land, such as LER, will be the best index of productivity only in cases where land is the most limiting factor.

In point of fact, any one of a large number of production inputs could be limiting. If agroforestry systems are to be designed for adoptability under realistic production conditions, researchers must be prepared to collect sufficient field data to evaluate a range of important output/input ratios and diagnose which production factors are typically limiting in a given land use system. The results of the diagnostic investigation would then provide a set of specifications for design of more 'field hardy' agroforestry systems (see Steppler and Raintree, this volume).

The analytical procedures for going beyond purely physical measures of productivity to compare diverse output/input ratios in a common analytical framework and come to an overall assessment of net return are collectively known as 'budgeting' techniques. The literature contains several excellent discussions of budgeting techniques as applied to intercropping research (Hildebrand, 1976; Norman and Palmer-Jones, 1977; Flinn, 1979) which are also applicable to agroforestry. As the name implies, the common thread is money. The reason for choosing money as the common unit of the analysis is that it affords a means to take account of the entire range of inputs and outputs involved in a production process and arrive at a figure for the net return or gross margin (GM) of the enterprise as a whole. It has been argued against critics of a purely monetary analysis that market value is the only available measure of output which meets all of the necessary criteria for evaluation of intercropping systems; namely, it is common to all products, relatively easy to measure, capable of reflecting differences in product quality, and able to serve as a means for comparing different cropping systems (Hildebrand, 1976).

The conversion of all inputs and outputs into monetary equivalents may prove difficult in many subsistence economies, but there are ways of arriving at reasonable estimates. The effort to overcome these problems would seem well justified in view of the value of budgeting techniques in providing a basis for comparison of existing practice against some theoretically 'optimal production system'. The value of such a construction is not in its 'truth value' or accuracy, but in its utility as a baseline for comparison with actual production strategies in order to identify deviations from the theoretical optima or 'compromises'

(Collinson, pers. comm.) which are presumably necessitated by more complex strategic factors in the local situation. In such cases the use of budgeting techniques is one of several discovery procedures for investigating complex nonmonetized economies.

Table 1. Commonly used measures of returns to major factors of production. (After Flinn, 1979, and Norman and Palmer-Jones, 1977.)

Factor	Specific return	Method of calculation
Land	$ ha^{-1}	Gross margin (GM)
	$ $ $land^{-1}$	(GM)/land rent
Labour	$ $man\text{-}day^{-1}$	(GM + total labour cost)/ total man-day
	$ family labour $man\text{-}day^{-1}$	(GM + family labour cost)/ family labour
	$ man-day of $peak^{-1}$	(GM + labour cost in non-peak period)/total man-days in period
Cash	$ $ $cost^{-1}$	(GM + variable costs)/ variable costs
	$ $ money $cost^{-1}$	(GM + money costs)/money costs
	$ $ cost $constraint^{-1}$	(GM/total cost) cost in period

A checklist of various output/input ratios often found useful in evaluating returns to the major factors of production is presented in Table 1. Of course, any specific input requirement could become limiting in a given production situation, in which case the returns to that input would have to come under careful scrutiny. Hildebrand (1976) cites the example of farmers in Columbia who are more concerned with yield per unit of seed than per unit of land because seed, which can be eaten, sold, or spoiled before planting time, is a much scarcer production factor than land. In any case, the checklist can be expanded as needed for bioeconomic purposes in a manner analogous to the preceding treatment of 'land' as a composite category implying access to a whole set of plant growth factors (light, CO_2, nutrients, water) which can be disaggregated at will.

The decision criterion in budgeting is not essentially different from what we have already discussed as the principle of equimarginality. Generalizing to the multiproduct, multifactor situation, we may restate the principle as follows: *the maximally profitable combination of products is achieved when the value productivity of the final increment of the most limiting factor is equal for all products.* In practice the identification of this combination is usually accomplished with the aid of linear programming.

LINEAR PROGRAMMING AS A PRACTICAL BIOECONOMIC DESIGN TOOL

If the budgeting technique is computerized and used to analyze

Table 2. Linear programming matrix for model of leucaena - rice alley cropping system (based on data from Sierra Leone).

	Row	Column	PRODUCTION ACTIVITIES 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	CONSTRAINTS 16	17
			R 0	RF 20	RF 40	RF 60	RF 80	RF 100	FB	L	RL 20	RL 40	RL 60	RL 80	RL 100	LH	RS	EQ	RES
	1	GM	0	0	0	0	0	0	var[a]	0	0	0	0	0	0	var[b]	var[c]	0	0
Resources	2	Land	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	-1	2
Resources	3	Family labour	220	225	225	225	225	225	0	24	220	220	220	220	220	-1	0	-1	170 var
Resources	4	Hired labour	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	-1	120 var
Transfer rows	5	Fert. N	0	20	40	60	80	100	-1	0	0	0	0	0	0	0	0	0	0
Transfer rows	6	Leuc. N EQ	0	0	0	0	0	0	0	-347	20	40	60	80	100	0	0	0	0
Transfer rows	7	Rice	-866	-1159	-1421	-1653	-1855	-2026	0	0	-1159	-1421	-1653	-1855	-2026	0	1	0	0

R 0: rice production with zero nitrogen input ha^{-1}.
RF 20 to RF 100: rice production with 20 to 100 kg ha^{-1} elemental nitrogen from mineral fertilizer sources.
FB : fertilizer buying activity (kg N). L: leucaena growing activity (kg N-equivalent).
RL 20 to RL 100: rice production with 20 to 100 kg ha^{-1} elemental nitrogen equivalent from leucaena hedgerows.
LH : labour hiring activity (man-days). RS: rice selling activity (kg). EQ: equality. RES: resource.
a) Fertilizer prices (Leones kg^{-1}N): ammonium sulphate 1.22(1972), 3.96(1980), 7.38(1990); urea 0.36(1972), 1.18(1980), 2.20(1990). *b*) Prices of hired farm labour (Leones $man\text{-}day^{-1}$): 0.33(1972), 1.50(1980), 2.96(1990).
c) Farmgate prices of rice (Leones kg^{-1}paddy): 0.094(1972), 0.239(1980), 0.420(1990).

a whole farm enterprise to identify the optimum combination of crops to maximize profit under the given resource constraints of the enterprise, a typical example of a *farm management application* of linear programming (LP) is obtained. If in the modelling effort sufficient attention is given to the biological details of cropping systems, and especially if a particular cropping system is disaggregated to the *component level* and each component is represented by a distinct production function, and furthermore if use is then made of transfer rows and equality constraints to model interactions *between* components, then a *bioeconomic application* of linear programming will be arrived at.

A bioeconomic *design* application of linear programming is one in which the detail and structure of the model is such that the LP optimizing procedure can be used to solve a critical design problem such as the optimum number or proportion of trees and understorey arable crops in an agroforestry association. An example of such an application in agroforestry is the LP model of an experimental leucaena - rice alley cropping system. Since this work is described in some detail elsewhere (Raintree and Turay, 1980; Turay, 1981), the results of the investigation will be summarized briefly before focusing on the design features of the model.

Using production data representative of upland family rice farms in Sierra Leone (Spencer, 1974) and representative nitrogen response data from the Rokupr Rice Research Station (Anon., 1980) a model was developed to investigate the relative profitability of various rice growing alternatives using 0 to 100 kg elemental nitrogen ha^{-1} (in 20 kg increments) from three different sources: urea, ammonium sulphate, and *in situ* leucaena hedgerows. Linear regressions on farmgate price data were used to explore the behaviour of the model through time. The LP matrix, and the main results, are shown in Tables 2 and 3, and Figure 4.

Table 3. Linear programming solution for the maximum profit farm plan for the years 1972, 1980 and 1990 based on data from Sierra Leone. (For key see Table 2.)

Activity	Unit	1972	1980	1990
L	ha	0.37	0.37	0.37
RL 100	ha	1.28	1.28	1.28
LH	man-days	120	120	120
RS	kg	2589	2589	2589
Resources consumed				
Land	ha	1.65	1.65	1.65
Labour				
- family	man-days	170	170	170
- hired	man-days	120	120	120
Cash	Leones	51.63	210.59	409.16
Net profit	Leones	191.76	408.24	678.16

The results indicate that under the conditions of small-

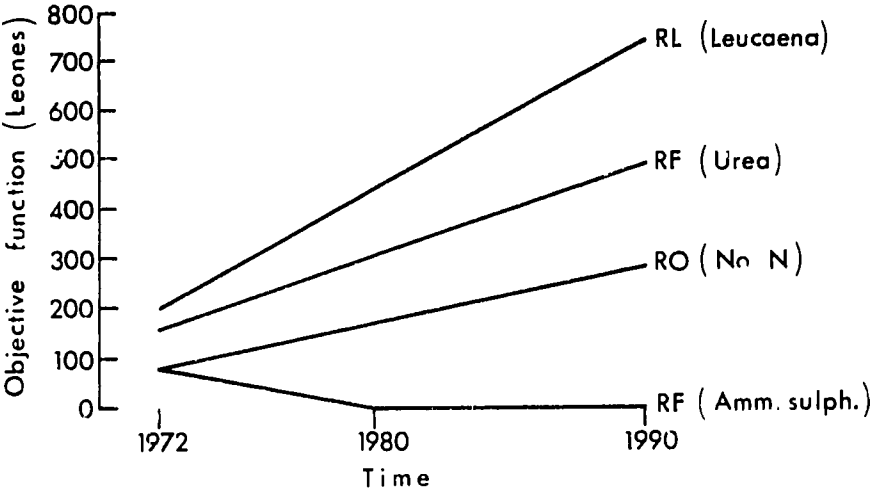


Fig. 4. Profitability as a function of time (based on data from Sierra Leone).

holder production represented by the model, it is consistently more profitable to grow rice with nitrogen from leucaena hedgerows than from either of the two mineral nitrogen sources. In the absence of substantial subsidies, the use of ammonium sulphate is particularly uneconomic. If price trends continue, lower priced urea will remain an economic alternative to rice growing without nitrogen inputs for the foreseeable future, but it is uneconomic relative to the alley cropping alternative. Part of the rise in GM with time (Figure 4) is an artefact of inflation, but differences between the slopes of the curves indicate that the relative profitability of the alley cropping alternative increases, rather than decreases, with time. An additional set of runs to evaluate the effects of fertilizer subsidies indicated that subsidy levels of 97 and 99 per cent, respectively, would be required to make urea and ammonium sulphate competitive with leucaena as a source of nitrogen for smallholder rice production.

The main design feature of this LP model is the construction of distinct production functions treating N-sources and N-sinks as separate activities linked by transfer rows. This device required the LP optimization algorithm not only to select the profit maximizing combinations of production activities but also, in so doing, to solve for the optimum proportion of land allocated to leucaena and rice, respectively, in the maximum profit plan. Once this is known, and given the hedgerow design shown in Figure 5 it is a relatively simple matter to work out the field espacement pattern.

The most striking feature of the optimum farm plan (Table 3) is its stability over time. The two components of the experimental leucaena-rice alley cropping system always combine in the same economically optimal proportions of 0.37 ha (3,700 linear metres) of leucaena hedgerow to 1.28 ha of upland rice, grown in the alleys between the hedgerows, for an optimum field

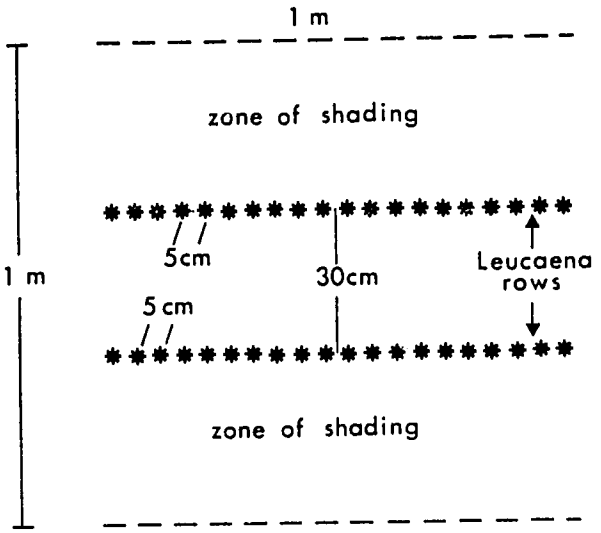


Fig. 5. Leucaena hedgerow design

size of 1.65 ha. Figure 6 shows a sample section of the optimum field pattern for a field measuring 100 × 165 m (field width = hedgerow length). A series of additional runs with altered coefficients for all of the major variables indicated the remarkable stability of the basic intercropping ratio. But note, however, that the optimum proportion of the two components could be expected to change at nitrogen levels higher than 100 kg ha^{-1}. This was not modelled for the simple reason that the available data on rice response to nitrogen on representative Sierra Leone soils did not go beyond the 100 kg ha^{-1} level, and it was considered hazardous to extrapolate beyond the data base.

The second most striking feature of the optimum cropping system is that, even though the land resource was constrained to

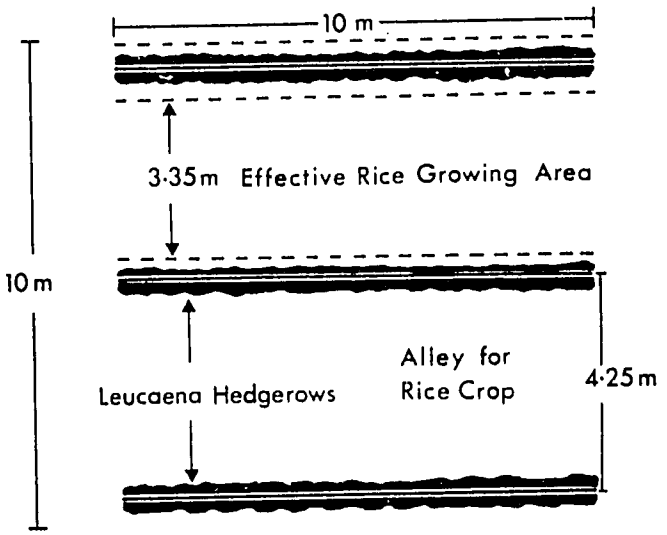


Fig. 6. Section of sample field pattern.

a maximum of only 2 hectares in the model, not all of the available land is used in the optimum farm plan. This is because labour, rather than land, is the limiting constraint in the typical family farm enterprise in Sierra Leone, as is the case in most parts of Africa. This makes the overall result all the more interesting, since the pivotal trade-off between the two production systems is the cost of buying fertilizer in a bag versus the cost in land and labour of growing your own. Land must be taken out of rice production to grow the leucaena green manure, but labour is the most limiting input. Even so, it still pays to grow your own.

This is the kind of critical design information which is not available without doing bioeconomic homework. Neither biological nor economic methods are in themselves sufficient to the task of developing appropriate agroforestry cropping systems. When they are combined, however, in the form of a genuinely interdisciplinary *bioeconomic* approach, research and development is then endowed with the necessary element of feedback to successfully track that most rare and elusive of goals, the *genuinely adoptable technology*.

ACKNOWLEDGEMENT

The author wishes to express his appreciation to The Rockefeller Foundation Social Science and Agriculture Fellowship Program for support of work at the International Institute of Tropical Agricultuve and the International Council for Research in Agroforestry leading to this paper, and also to the Social Science Research Council for support of a postdoctoral study in tree crop horticulture and forestry at Oregon State University.

REFERENCES

Andrews, D.J. and Kassam, A.H. (1976). The importance of multiple cropping in increasing world food supplies. "Multiple Cropping", pp.1-10. American Society of Agronomy, Madison, Wisconsin, USA.

Anon. (1980). Final draft report, UNDP/FAO/IITA Sierra Leone Rice Project. International Institute of Tropical Agriculture, Ibadan, Nigeria. (Mimeograph)

Benge, M.D. (1979). Use of leuceana for soil erosion control and fertilization. *US Agency for International Development*, Washington.

Bishop, C.C. and Toussaint, W.D. (1958). "Introduction to Agricultural Economic Analysis". John Wiley & Sons, New York.

Centro Internacional de Agricultura Tropical (1977). Annual Report for 1976, pp.G35-39. CIAT, Cali, Columbia.

Centro Internacional de Agricultura Tropical (1978). Annual Report for 1977, pp.F5-12. CIAT, Cali, Columbia.

Felker, P. (1978). State of the art: *Acacia albida* as a complementary permanent intercrop with annual crops. *US Agency for International Development*, Washington. 133 pp.

Felker, P., Clark, P.R., Osborn, J. and Cannell, G.H. (1980). Nitrogen cycling - water use efficiency interactions in semiarid ecosystems in relation to management of tree legumes (*Prosopis*). *In* "Browse in Africa" (H.N. le Hourerou, ed.),

pp.215-222. International Livestock Centre for Africa, Addis Ababa, Ethiopia.

Fernie, L.M. (1970). The improvement of arabica coffee in East Africa. *In* "Crop Improvement in East Africa" (C.L.A. Leakey, ed.). Commonwealth Agricultural Bureau, Farnham Royal, UK.

Flinn, J.C. (1979). Agro-economic considerations in cassava intercropping research. *In* "Intercropping with Cassava" (E. Weber, B. Nestel and M. Campbell, eds), pp.87-101. International Development Research Centre, Ottawa, Canada.

Gosden, P.N. (1978). Land resources of Central Nigeria. *In* "Present Farming Systems" Vols 1 to 3. Land Resource Report No.17, Ministry of Overseas Development, Surbiton, UK.

Hanks, B.J. and Tanner, C.B. (1952). Water consumption by plants as influenced by soil fertility. *Agron. J.* 44, 98-100.

Hardy, F. (1962). Cacao soils. III. The problem of shade for cacao. *Gordian* 62, 685-690. (*In* Willey, 1975.)

Hildebrand, P.E. (1976). Multiple cropping systems are dollars and 'sense' agronomy. *In* "Multiple Cropping" (R.I. Papendick *et al.*, eds.), pp.347-371. ASA Special Publication No.27. Madison, Wisconsin, USA.

Huxley, P.A. (1970). Some aspects of the physiology of arabica coffee: the central problems and the need for a synthesis. *In* "Physiology of Tree Crops" (L.C. Luckwill and C.V. Cutting, eds), pp.255-268. Academic Press, London.

Huxley, P.A. and Maingu, Z. (1978). Use of a systematic spacing design as an aid to the study of intercropping: some general considerations. *Expl Agric.* 14, 49-56.

International Institute for Tropical Agriculture (1979). Annual Report for 1978, pp.72, 92-93. IITA, Ibadan, Nigeria.

International Institute for Tropical Agriculture (1980). Research Highlights for 1979. IITA, Ibadan, Nigeria.

International Rice Research Institute (1974). Annual Report for 1973. IRRI, Los Baños, Philippines.

International Rice Research Institute (1975). Annual Report for 1974. IRRI, Los Baños, Philippines.

Knipscheer, H.C. (1979). Prices (1972-79) of fertilizers in Nigeria and other African countries. *Agric. Econ. Inf. Bull.* No.5. IITA, Ibadan, Nigeria. (Mimeograph)

Mann, H.S. and Shankaranarayan, K.A. (1980). The role of *Prosopis cineraria* in an agropastoral system in Western Rajasthan. *In* "Browse in Africa" (H.N. le Hourerou, ed.), pp.437-442. International Livestock Centre for Africa, Addis Ababa, Ethiopia.

Menz, K.M. (1980). Fertilizer prices on an elemental basis. *Agric. Econ. Inf. Bull.* No.7/80. IITA, Ibadan, Nigeria. (Mimeograph)

Murray, D.B. and Nichols, R. (1966). Light, shade and growth in some tropical plants. *In* "Light as an Ecological Factor" (Bainbridge *et al.*, eds). Blackwell, Oxford, UK.

Nair, P.K.R. (1979). "Intensive Multiple Cropping with Coconuts in India". Verlag Paul Parey, Berlin.

Norman, D.W. (1973). Economic analysis of agricultural production and labour utilization among the Hausa in the north of Nigeria. *African Rural Employment Paper* No.4. Dept of Agric. Economics, Michigan State Univ., East Lansing, MI, USA.

Norman, D.W. and Palmer-Jones, R.W. (1977). Economic methodology

for assessing cropping systems. *In* "Proc. Symp. Cropping Systems Research and Development for the Asian Rice Farmer", pp.241-259. IRRI. Los Baños, Philippines.

Okigbo, B.N. and Lal, R. (1979). Soil fertility maintenance and conservation for improved agroforestry systems in the lowland humid tropics. *In* "Soils Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.41-77. ICRAF, Nairobi, Kenya.

Pullan, R.A. (1974). Farmed parkland in West Africa. *Savanna* 3, 119-151.

Raintree, J.B. (1980a). Production constraints as reported by savanna farmers in Nigeria. *Agric. Econ. Inf. Bull.* No.11/80. IITA, Ibadan, Nigeria. (Mimeograph)

Raintree, J.B. (1980b). Conservation farming with soil improving tree legumes: a farming systems approach to tropical agroforestry. *Agric. Econ. Discussion Paper* 9/80. IITA, Ibadan, Nigeria. (Mimeograph)

Raintree, J.B. and Turay, F. (1980). Linear programming model of an experimental leucaena - rice alley cropping system. *IITA Res. Briefs* 1, 5-7.

Roling, N. (1980). Alternative approaches in extension. *In* "Progress in Rural Extension and Community Development" (G.E. Jones and M. Rolls, eds). John Wiley & Sons Ltd, Chichester, UK.

Spencer, D.S.C. (1974). The economics of traditional and semi-traditional systems of rice production in Sierra Leone. *In* "Proc. WARDA Seminar on Socio-economic Aspects of Rice Cultivation in West Africa". West African Rice Development Ass., Monrovia, Liberia.

Trenbath, B.R. (1976). Plant interactions in mixed crop communities. *In* "Multiple Cropping" (R.I. Papendick *et al.*, eds), pp.129-169. ASA Special Publication No.27, Madison, WI, USA.

Turay, F. (1981). "An optimization model of leucaena - rice alley cropping system for upland rice region of Sierra Leone". BSc Thesis, Njala Univ. Coll., Njala, Sierra Leone.

Wight, J.R. and Black, A.L. (1979). Range fertilization: plant response and water use. *J. Range Mgmt* 32, 345-349.

Wight, W. (1958). The shade tree tradition in the tea gardens of northern India. *In* Annual Report, Tocklai Exp. Stn, Indian Tea Ass.

Willey, R.W. (1975). The use of shade in coffee, cocoa and tea. *Hort. Abstr.* 45, 791-798.

Willey, R.W. (1979). Intercropping - its importance and research needs. I. Competition and yield advantages. *Field Crop Abstr.* 32, 1-10.

Wilson, G.F. and Kang, B.T. (1980). Developing stable and productive biological cropping systems for the humid tropics. *In* "Biological Husbandry: A Scientific Approach to Organic Farming" (B. Stonehouse, ed.), pp.193-203. Butterworth, London.

Wilson, G.F. and Raintree, J.B. (1981). The leucaena - maize - yam alley cropping system. IITA, Ibadan, Nigeria. (Mimeograph)

Wit, C.T. de and Bergh, J.P. van den (1965). Competition between herbage plants. *Neth. J. agric. Science* 13, 212-221.

DISCUSSION

LEYTON - You have given us some examples of nitrogen problems. Have you had any experience of phosphorus deficiency?

RAINTREE - No, but if this was the case we could look to see if a greater volume of the phosphate pool is tapped by the deep roots of trees.

LOOMIS - It seems from your figures that even 20 to 30 kg of product does not pay for one kg of fertilizer nitrogen. This is an artificial situation with far too low a price paid to the farmers. The limited wealth available is divided unevenly between the farmer and the urban centre. We must not expand systems which are essentially low in inputs and perpetuate poverty; to do so would be socially irresponsible.

RAINTREE - Yes, social problems are the hardest to solve. In the years since the 'green revolution' per capita food supply has gone up but so have the indices of hunger. There is a distribution problem, not so much of the product but of the *means* of production. A peasant farmer not involved in production does not become involved in consumption! The challenge is to develop technologies that are useful to the majority of small farmers.

BUDOWSKI - A main consideration in having timber trees on smallholdings is to possess what amounts to a bank with ready cash that can be called upon when needed. Another reason is to provide a permanent and clear demarcation of boundaries. *Eucalyptus* spp. in Peru are used to show farm boundaries and this offers real security to the farmer in defining his property.

von MAYDEL - For smallholders the first priority is not to maximize the total yield of single crops. In general, the smaller the holding the more diversified it is. Since increasing pressure on land is the general trend, we should follow the lead of the smallholders and concentrate on developing diversified, multipurpose agroforestry systems. On the input side, we should try to develop ways to replace fertilizers. In the Sahel the priority for farmers and herdsmen is to *reduce risk*. Misuse of land increases risk. The development of agroforestry land use systems can contribute to risk reduction.

RAINTREE - The sustainability of tree production is also a key point, though I did not elaborate this. We are at an elementary stage in the development of bioeconomics for agroforestry. We now look at the current situations; later we will be able to consider the problems over time.

THE GLOBAL ENVIRONMENT MONITORING SYSTEM: ITS VALUE FOR ANALYSIS AND DEVELOPMENT OF AGROFORESTRY LAND USE SYSTEMS

H. CROZL and M.D. GWYNNE
Global Environment Monitoring System, Programme Activity Centre, United Nations Environment Programme, Nairobi, Kenya.

SCOPE AND ACTIVITIES

The Global Environment Monitoring System (GEMS) is a worldwide collection of co-operative environment monitoring networks, dedicated to the harmonization of data collection and analysis methodologies. The main function of data generated by the network is to provide managers and planners with timely and comprehensive assessments of environmental state and trends, in order to incorporate such information into decision making.

GEMS works through the United Nations' specialized agencies to carry out monitoring activities in order to make use of the existing expertise and infrastructure of such agencies as the Food and Agriculture Organization (FAC), the World Meteorological Organization (WMO), the World Health Organization (WHO), the United Nations Educational, Scientific and Cultural Organization (UNESCO), and so on. Thus, the relatively modest GEMS Programme Activity Centre (PAC) within the United Nations Environment Programme (UNEP) can co-ordinate some two dozen projects in the general fields of pollution (health-related monitoring, and the monitoring of transboundary transport of airborne pollutants), ocean monitoring (now operationally within the UNEP Regional Seas PAC), climate-related monitoring and, of special interest to agroforesters, the monitoring of renewable natural resources.

The renewable natural resource monitoring programme is currently concerned with: development (with FAO and UNESCO) of a soils degradation assessment methodology; promulgation, with FAO and others, of ecological monitoring units throughout the world's arid and semiarid rangelands; monitoring, with the International Union for the Conservation of Nature and Natural Resources (IUCN) of the status of threatened plant and animal species and their habitats; monitoring, with FAO, of tropical forest cover; and assessment, again with FAO, of the world's forest resources.

The pilot project on the monitoring of tropical forest cover was carried out in three West African countries: Benin,

Cameroon and Togo. Using the GEMS 'three-tiered' approach, data were gathered from the ground, from light aircraft and from LANDSAT imagery. For each of the three countries, a composite forest cover map was produced which delineated forest cover whilst incorporating species composition, vegetation physiognomy, and ecological 'background' factors such as rainfall, altitude, and topography. The project also carried out a series of retrospective analyses to estimate the current rates of change in forest cover, using both conventional aerial photography and LANDSAT imagery.

FOREST AND RANGELAND ASSESSMENT RELEVANT TO AGROFORESTRY

The recently completed global assessment of tropical forest resources has produced for the first time a comprehensive picture of the state (Fig. 1) and trends (Figs 2a, 2b, 2c) in tropical forests in 76 countries grouped by region: Africa, Latin America, and Asia. The data in the assessment will be used as a baseline from which to monitor trends and to produce updated assessment statements at regular intervals, initially every five years. The results suggest that although the global rate of deforestation (approx. 0.6 per cent per year) is less than previously thought, there are a number of countries which will be in serious trouble by the end of this century.

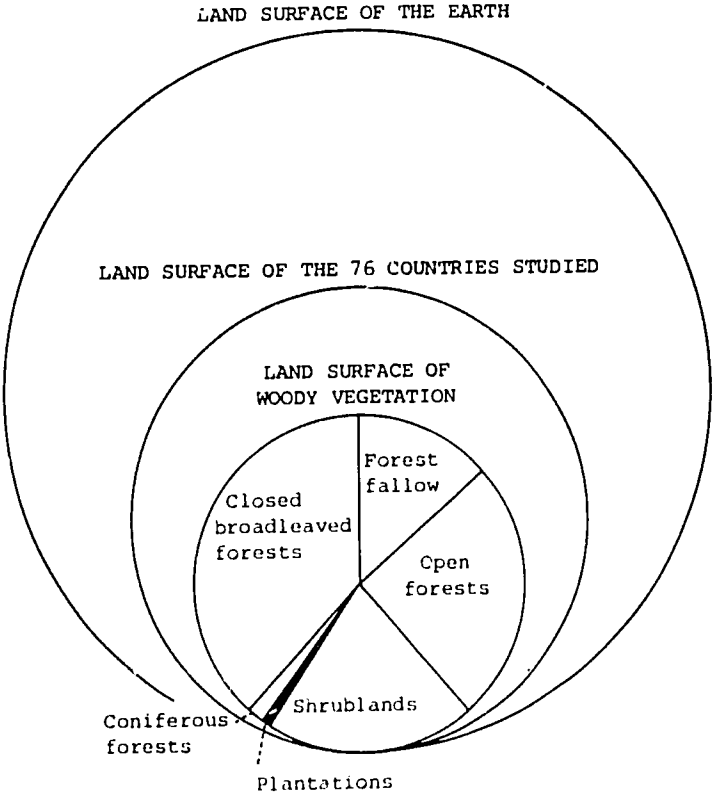
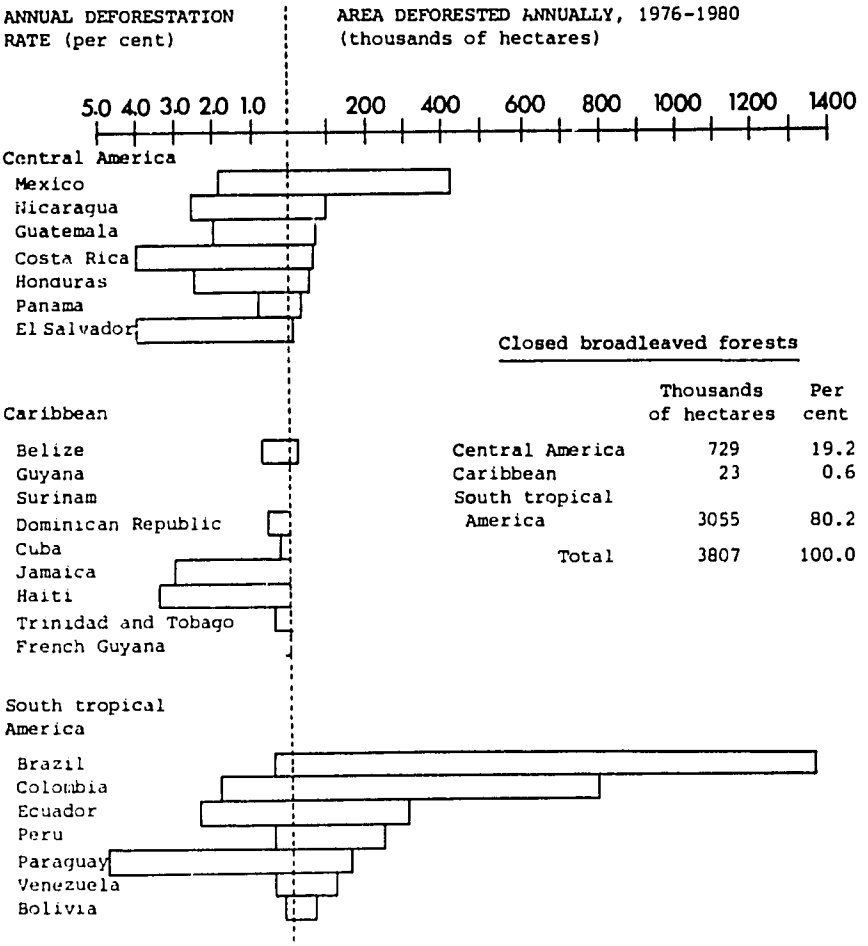


Fig. 1. Global areas of tropical woody vegetation (from UNEP, 1982a).



Closed broadleaved forests

	Thousands of hectares	Per cent
Central America	729	19.2
Caribbean	23	0.6
South tropical America	3055	80.2
Total	3807	100.0

Fig. 2a. Deforestation of closed broadleaved forests by countries in tropical America (from UNEP, 1982b).

Forest monitoring and assessment will be continued within the GEMS activities along four specific lines.

- Extension of tropical forest cover monitoring to other regions; Southeast Asia initially.
- Development of a standard global system of classification of woody vegetation.
- Continuation of forest assessment to update and improve the information collected during the first global assessment, and to include oceanic islands and, eventually, temperate as well as tropical forests.
- Development of a computerized global resource information database which will incorporate forest data.

It should be emphasized that forest monitoring and assessment activities are closely related both in philosophy and operations to rangeland monitoring. Data are gathered from the same three tiers, but typically, in the monitoring of arid and semi-

arid lands, greater emphasis is put upon the aerial reconnaissance component. Ecological monitoring of rangelands is of relevance to agroforestry from at least two points of view: on the one hand it produces data on current land use and its ecological constraints; on the other, it provides primary data on state and trends of woody vegetation.

PROPOSED RELEVANT ENVIRONMENTAL ASSESSMENTS

In the next biennium it is planned to initiate two specific environmental assessments, both of which are also relevant to agroforestry. One is the assessment of the global loss of croplands, and the other is the assessment of the causes and effects of shifting cultivation.

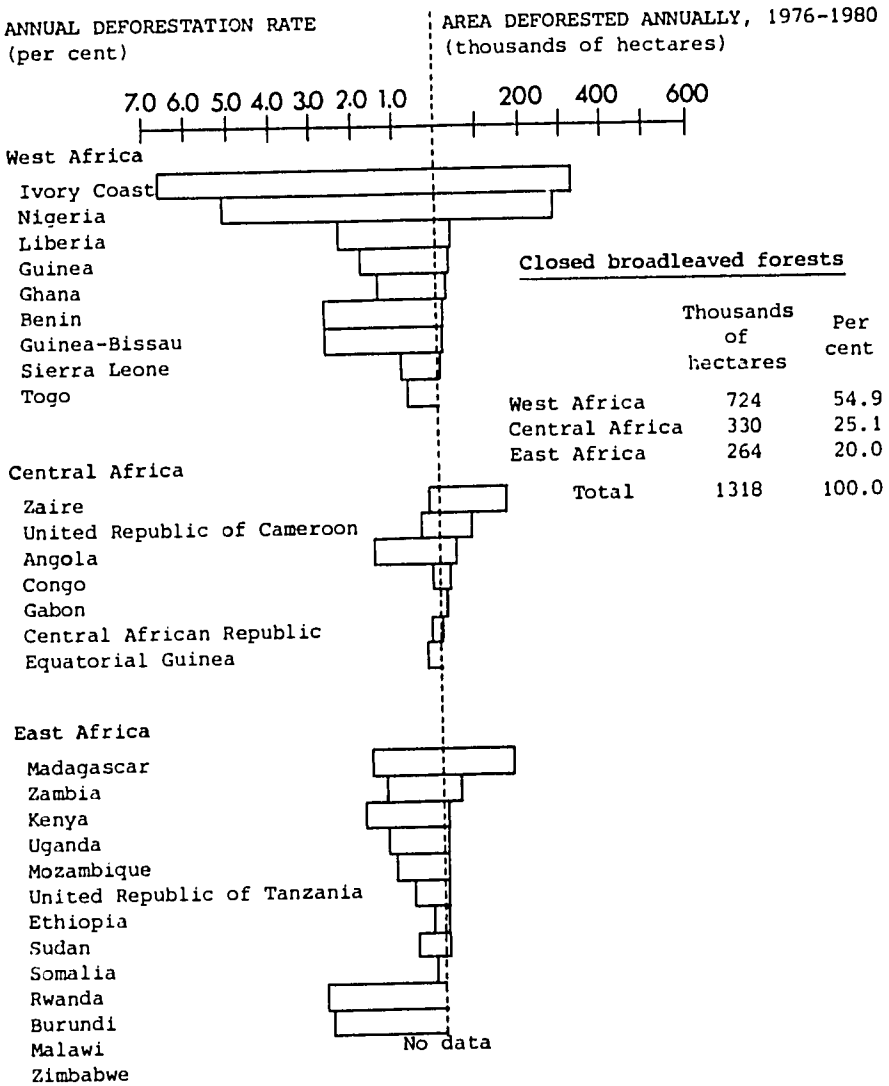
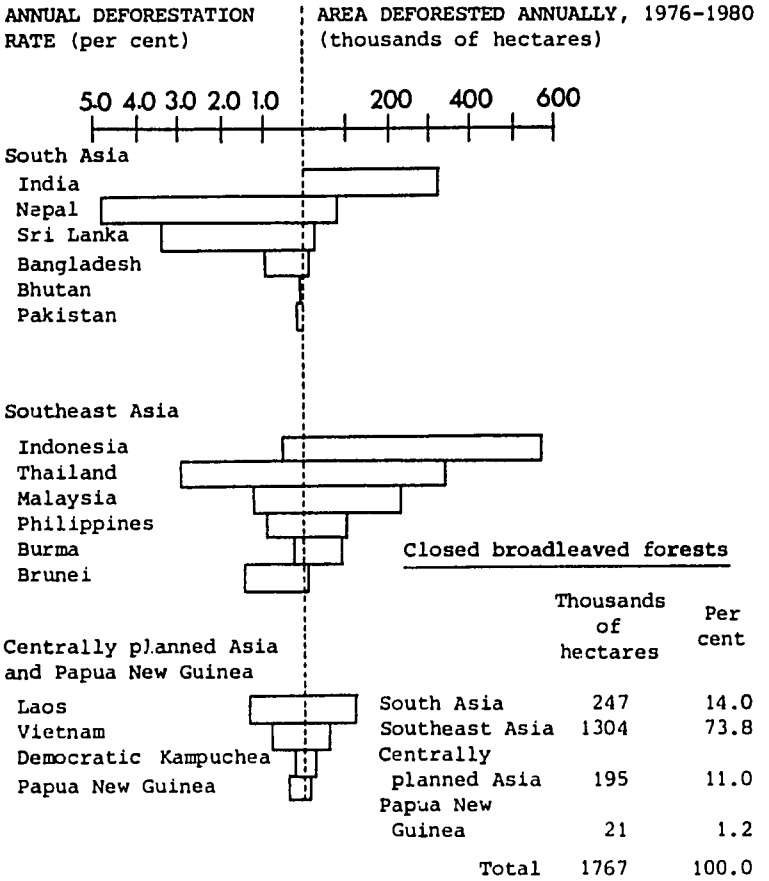


Fig. 2b. Deforestation of closed broadleaved forests by countries in tropical Africa (from UNEP, 1982b).



Closed broadleaved forests

	Thousands of hectares	Per cent
South Asia	247	14.0
Southeast Asia	1304	73.8
Centrally planned Asia	195	11.0
Papua New Guinea	21	1.2
Total	1767	100.0

Fig. 2c. Deforestation of closed broadleaved forests by countries in tropical Asia (from UNEP, 1982b).

There appears to be a need for more inventory and monitoring activities in agroforestry in order to augment the existing research effort. Agroforesters should consider quite carefully the context of their operations and the scales at which effects will be felt (see also Huxley, p.257). Research, by and large, must be conducted on a somewhat restricted scale for logistical reasons. Land use planning decisions, however, inevitably cover large areas of land. There is a need for a modality by which information is extended from points or small areas at which, for example, research takes place, to large areas about which decisions are made. The GEMS renewable resource monitoring approach provides such a mechanism.

REFERENCES

UNEP (1982a). GEMS PAC Information Series No.3. UNEP, Nairobi, Kenya.

UNEP (1982b). Tropical Forest Resource Assessment, Annex II. UNEP, Nairobi, Kenya. 15 pp.

THE ICRAF RESEARCH STRATEGY IN RELATION TO PLANT SCIENCE RESEARCH IN AGROFORESTRY*

H.A. STEPPLER and J.B. RAINTREE
International Council for Research in Agroforestry,
Nairobi, Kenya.

ABSTRACT. ICRAF has developed an institutional strategy to filfil its international co-ordinating role *vis-à-vis* agroforestry and is now evolving, through research in Kenya, a set of tactical principles and a methodology to implement that strategy. In order to guide agroforestry research and development along lines that are relevant to the needs of potential practitioners there is need for a diagnostic methodology to identify significant local problems and agroforestry potentials. While agroforestry systems are often location specific, the methodology for developing appropriate agroforestry systems is likely to be fairly general. This paper sets forth the main outlines of ICRAF's evolving multidisciplinary methodology and explores its relationship to international plant science research.

INTRODUCTION

The International Council for Research in Agroforestry (ICRAF) has been charged in its charter with the responsibility 'to encourage and support research and training relevant to agroforestry; to facilitate the collection and dissemination of information relevant to such systems and to assist in the international co-ordination of agroforestry development.' The goal is to promote improved agroforestry land use systems to enhance the social, economic and nutritional wellbeing of the people of the developing countries.

The need for a clear strategy

The Council's mandate is broad in scope and explicit in respect

---

* Those interested in the developments and outputs relating to the subject of this paper since it was written (April, 1981) should write to ICRAF for further information. (Ed.)

to its responsibilities, but it does not specify the strategy by which the Council is to pursue its objectives. In developing its institutional strategy ICRAF has had to deal with unique problems not normally encountered by institutions oriented to more traditional aspects of agricultural research. The methodologies of crop breeding, animal nutrition research, or plant propagation studies, for example, are well developed and documented. There is also a vast body of data against which to compare one's results. Such is not the case with agroforestry.

In agroforestry research one is faced with a multitude of questions for which there are no ready answers. Thus, one finds that:

- although many agroforestry practices are not new, existing agroforestry systems are not adequately and scientifically - if at all - described;
- a research methodology for the study of agroforestry systems and potentials has not been developed, particularly one with a diagnostic capability based on recognition of the interdisciplinary nature of the problem;
- likewise, there is as yet no satisfactory research and development methodology to generate and test new agroforestry technologies.

The problems associated with these gaps in our knowledge are complex and interrelated. As a result, there is some difficulty in establishing research priorities in agroforestry.

The paradigm

The situation may be summarized by saying that agroforestry is still essentially *preparadigmatic*. History tells us that no science can develop in the absence of a paradigm: that explicitly or implicitly shared set of taken-for-granted assumptions which shapes scientific thinking, and which governs the course of scientific development by defining, not only the nature and scope of the subject and the methodologies considered legitimate for its investigation, but also the nature of the *questions asked*.

Paradigms may be powerful but they are never permanent. Science progresses by a series of 'paradigm revolutions' followed by periods of relative calm when research is directed to 'paradigm elaboration'. It is a normal consequence of such research, however, that factual and theoretical anomalies are inevitably generated which eventually signal the downfall of the old paradigm and the rise of a new one.

This historical pattern (Kuhn, 1962) is clearly visible in the emergence of agroforestry. World food, energy and environmental problems are such that it is no longer scientifically prudent to ignore the conservation benefits and sustained yield potentials of age-old agroforestry practices. The old paradigm, which enforced a strict and rigid separation of agricultural and forestry research, has broken down under the weight of accumulated anomaly. And agroforestry — the fledgling interdisciplinary science which has arisen recently to fill the gap created by the time-honoured but artificial separation of agriculture and forestry — is now in its *early or preparadigm development stage*. The difficulties of working at this stage are great, but so also

are the opportunities.

THE ICRAF RESEARCH STRATEGY

Developing methodology

In view of the historical context of ICRAF's mandate, the international scope of its responsibilities, and the location specific nature of most agroforestry technologies, the Council has determined that it can best fulfil its mandate by concentrating its efforts, not on the development of technology *per se*, but on the development of *methodologies* for the generation of appropriate agroforestry technologies. The Council is seeking to implement this strategy by developing a research programme of its own, initially focused on sites in Kenya but eventually moving out to other countries to test and further develop its methodological approach. As it accumulates experience in agroforestry diagnosis and research design, ICRAF envisions that its mode of operation will shift increasingly toward that of a consultative role in the design and monitoring of national agroforestry research and development programmes.

Since it is impossible to develop a methodology for doing something without actually doing it, ICRAF's methodology development efforts will inevitably result in the generation of a number of location specific agroforestry technologies, but this should not obscure the Council's methodological research focus. The strategy for this research follows from an analysis of the nature of agroforestry.

Agroforestry is both a system of land use which lends environmental stability to an area, and a system for the production of food and tree products essential to the wellbeing of the people of developing countries. Agroforestry combines elements of agriculture, be they crops or animals, with elements of forestry in sustainable production systems. Agroforestry is the new name given to the old practice, followed by many farmers for generations, of mixing or retaining trees in their crop/animal production fields.

The systems approach

The key word in all this is *systems*. In agroforestry we are not dealing with clear-cut commodities or components, but with interacting combinations of these. In a sense, the 'commodity' in agroforestry is a complete land use system and, as such, will vary from area to area, from culture to culture, from national goal to national goal and, even within a seemingly homogeneous farming system, will show variation from farm to farm. A single system will be composed of subsystems which may be defined, depending on the purposes of the analysis, in terms of output classes, the farmer's objectives, or even single commodity components; but permeating the logic of all such analysis is the concept of systems. Hence, the ineluctable need for ICRAF to adopt, as the basis of its research strategy, the 'systems approach'.

The diagnosis

The systems approach implies, first, that one does not engage in

piecemeal consideration of problems and, second, that there is an analytical rather than merely intuitive approach to land use systems. ICRAF's strategy is to develop that analytical approach — the diagnostic methodology — which enables one to analyze the state of the system, to identify the critical subsystems, and to determine the problems or operative constraints as well as the potentials for improvement of system performance. From the diagnosis will then flow the capability to identify existing agroforestry technologies which are appropriate to system needs, and also the capability to define the research and development problems which must be solved in order to generate new agroforestry technologies which possess the specific capacities required in order to improve system performance. In this way ICRAF aims to target agroforestry research and development to real world problems and conditions.

The basic logic of ICRAF's research programme is dictated by the cycle of development depicted in Figure 1. Each phase in the cycle embraces a series of research activities. Each situation to which the cycle is applied will require a different mix of the particular activities in order to complete the cycle. The cycle takes its starting point from the inescapable conclusion that the process of developing a solution to a problem begins

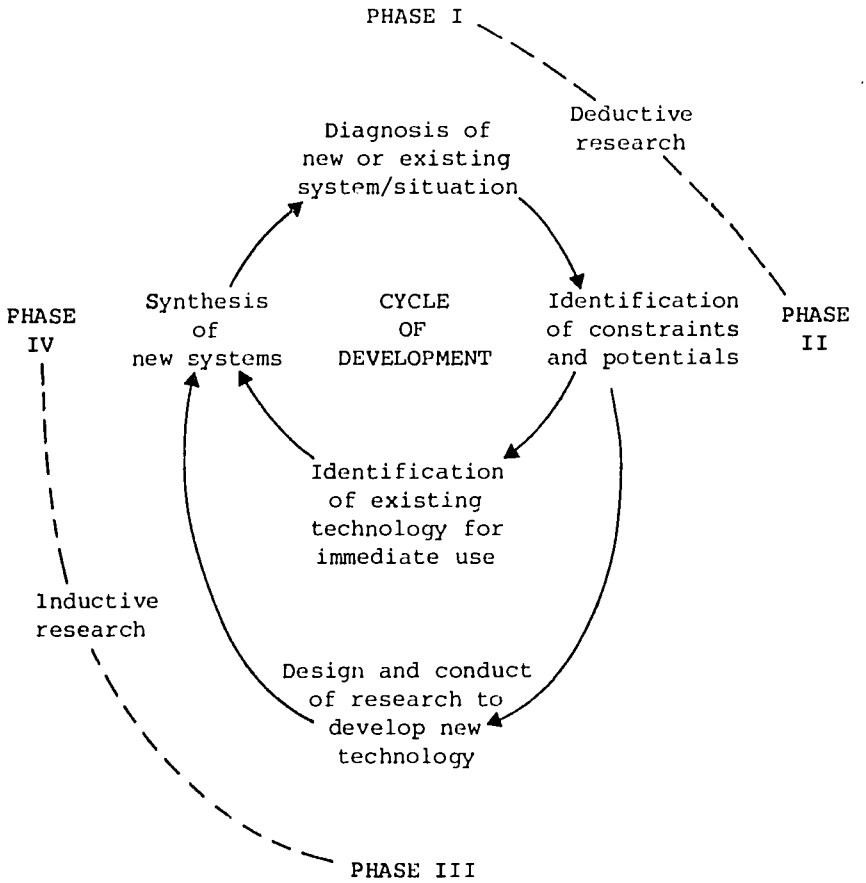


Fig. 1. The cycle of technology development.

with the capacity to analyze the problem situation, in this case the land use system in which agroforestry technology is deemed to have a role. The diagnosis of existing land use systems is aimed at discovering the agroforestry-related constraints and potentials. This is the deductive, analytical, or diagnostic part of the technology development cycle.

One of the main conclusions to come out of the agricultural development research of the past decade or so is that the conditions under which the majority of farmers operate often bear little resemblance to those on agricultural research stations. With the consequence that, unless a special effort is made to take account of these conditions, the resulting technology is often inappropriate for the majority of farmers. In order to identify the full set of operant constraints and potentials which govern decision making with regard to land use practices in a given area, ICRAF has determined that the multidisciplinary expertise of a team of biological and social scientists will be required to diagnose factors ranging from climatic constraints to cultural values.

One important outcome of the first phase of the land use system diagnosis will be the identification of land use subsystems. In this effort, ICRAF is developing a 'basic needs' approach to the identification of production subsystems in terms of output categories which answer the universal human need for food, energy, shelter, cash and community integration. It insures that *what* is analyzed will be highly relevant to people's needs.

How it is analyzed in the second phase of the diagnostic research is also a subject of intense methodological interest at ICRAF. Agroforestry, by definition, is equally concerned with both production *and* conservation. In this respect it differs from most other branches of plant science, in which conservation aspects of production systems are frequently of secondary, if any, concern. This difference in purpose requires a difference in methodology. ICRAF is now exploring analytical techniques to diagnose the performance of basic output subsystems in terms of both their *productivity* and their *sustainability*, thus encompassing both aspects of its diagnostic objective.

Design

The final output of the diagnostic part of the cycle will be a set of general design specifications for agroforestry technologies in terms of functional or end use requirements. These then become the primary input for the inductive, synthetic or research and development (R & D) part of the cycle of agroforestry development.

Two courses of action are possible in the first part of the R & D cycle (Phase III). One is to identify existing agroforestry technologies that are generally appropriate to local needs and that can be used directly to bring about an improvement in the immediate situation. The other course is to develop an R & D programme to generate new technology which is specially designed to meet the diagnostic specifications. These two courses of action are not mutually exclusive. In fact, the most likely situation will be that in which a temporary improvement is gained by using existing technology while new technology is being developed. The cycle of development is a continuous,

iterative process. One seeks the best technology but settles for a better one, hoping to continuously improve it.

Phase IV in the cycle of development encompasses the research necessary to synthesize a new land use system which incorporates the new agroforestry technology into the existing pattern of land use in a manner consistent with local and regional production purposes and constraints. Finally, the process comes full circle with a new round of diagnostic research in order to identify the set of constraints and potentials now operating, and which must be addressed by a new round of R & D activities if the system is to be further optimized. The four phases of the cycle of technology development define the scope of ICRAF'S research programme. Each phase embraces a series of research activities. Each situation in which the cycle is applied will require a different mix of the particular activities to complete the cycle. An interdisciplinary approach is essential throughout.

IMPLEMENTING THE STRATEGY

The two-fold methodological objective of the ICRAF research strategy will be approached through two distinct but complementary research activities.

- The development of the diagnostic capability for the identification of agroforestry needs and potentials. This will be done through field investigations of existing smallholder land use systems; initially restricted to Kenya but later extended to sites in other countries.
- The development of R & D methodologies; such research activities will be carried out at the ICRAF Machakos field station in Kenya, and elsewhere.

Generally speaking, the results of the diagnostic research will identify the priority problems for field station research. Experimental research on the station, in turn, will help develop biological indicators and measurement techniques to sharpen the diagnostic capability.

Methodology versus technology generation

It should be emphasized again that, although a number of technological spin-offs will inevitably result from ICRAF's research, the primary objective is to develop methodology. This does not mean that ICRAF is not interested in agroforestry technology *per se*, but rather that the Council feels that it can best serve the international development of agroforestry by concentrating its resources on methodology development. ICRAF will, certainly, endeavour to ensure that appropriate national or international institutions pursue the generation of technology by using effective methodologies. And that through such institutions technology will be tested on farmers' fields.

This points to another important feature of ICRAF's role, namely its complementary relationship to national and international institutions. It might be useful to briefly explore other aspects of this relationship.

ICRAF's approach to a diagnostic situation makes the

assumption that the national agencies responsible for that sector have the capability to do everything that is required of them to support the diagnostic activity and implement its recommendations. The diagnosis would not only analyze the situation but would also test this assumption. Those areas in need of strengthening would become known and external sources of assistance identified. One obvious agency for general research assistance would be the International Service for National Agricultural Research (ISNAR), while training in some specialized areas for commodity development might be found at other International Agricultural Research Centres, or at ICRAF.

Interacting with other research organizations

The diagnostic project would further serve to highlight two additional needs. One of these would be the need for specialized research methodology. For example, the diagnosis of several zones may indicate that one component requirement is a maize cultivar that will perform well under reduced light. This could require modifications in breeding methodology, selection criteria, and so on. Such a methodology could be developed better by an International Agricultural Research Centre such as the Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) or the International Institute of Tropical Agriculture (IITA) than by ICRAF. ICRAF would bring such a need to the attention of the appropriate centre and work together with its scientists in developing the methodology. The second need would be that of the required germplasm itself. Again, ICRAF would be in a position to draw this need to the attention of the appropriate Research Centre and urge its breeders to begin screening their germ plasm in anticipation of the demand from national agencies.

PRIORITY ASPECTS OF PLANT SCIENCE RESEARCH

It would be tedious to attempt an enumeration of all the many aspects of plant science research that are relevant to ICRAF's research strategy and the needs of agroforestry. It might be useful, however, to highlight a few research areas which are considered of outstanding importance.

For purposes of diagnosing land use problems and potentials ICRAF is concerned with identifying *indicators* of present states and long-term trends in land use systems. To apply the medical metaphor implicit in the idea of diagnostic research, what is needed is to identify the 'critical diagnostic variables' and associated measurement techniques which enable one to ascertain the 'health' status of the land use system. That is, the ecosystemic analogues of temperature, pulse rate, blood pressure, and so on. This implies a knowledge of land use 'symptomatology' which can only be developed with the aid of extensive biological and bioeconomic *modelling techniques*, another area of crucial research interest at ICRAF.

Needless to say, not all land use problems are amenable to an agroforestry solution. In recognition of this, ICRAF will endeavour to play the role of the 'honest broker' and to identify which of the three — agriculture, forestry or agroforestry — represents the best general land use system for an area. Nevertheless, ICRAF will tend to concentrate primarily on

developing reliable rapid assessment indicators for agroforestry type land use problems.

On the R & D side, and particularly in the generation of new technology, the understanding of plant - tree - animal interactions is critical if one is hopeful of optimizing the production and conservation benefits under the prevailing ecological and enterprise constraints in the target area. The challenge is not only to bring all available talents and disciplines to bear on elaborating the nature of these interactions but, equally important, to devise research methodologies appropriate to their further study.

One final area of priority research lies neither wholly on the diagnostic nor the R & D side of ICRAF's research interests but, in fact, forms a kind of bridge between them. This is the area of research leading to the identification of ideotypes and screening techniques for agroforestry plant materials. Plant materials selected for inclusion in viable agroforestry intercropping systems must somehow satisfy two distinct sets of requirements.

- The interactional requirements of the managed biological systems which comprise their immediate environment.
- The functional end use requirements and suitability criteria of the larger socioeconomic and geographical systems in which they are embedded.

There is no such thing as a 'halfway appropriate' agroforestry component. The effort to define the particular set of biological features which makes a particular agroforestry component or combination appropriate in the context of its total management environment typifies, perhaps better than any other single research activity, ICRAF's approach to agroforestry land use systems.

REFERENCE

Kuhn, T.S. (1962). "The Structure of Scientific Revolutions." University of Chicago Press, Chicago, USA.

DISCUSSION

CROZE - The development of indicators which you mention in your paper requires a large investment. There are two ways to develop indicators: a) from a knowledge of system causality, and b) from correlations established between variables on the basis of a large data base. The first is the most demanding, but both require a large investment of resources.

STEPPLER - That is one of the reasons we have chosen the Machakos area to develop our diagnostic methodology. The existing data base on this area is excellent. We hope to use it to identify what data are critical for diagnosis of agroforestry constraints and potentials. We will then have to develop methods for collecting these data in areas where they are not available.

CANNELL - It is one thing to diagnose problems, but how do you identify agroforestry potentials in a healthy system? The

complexities of this kind of activity will require a multidisciplinary approach.

STEPPLER - The medical metaphor does not really apply to the case of healthy systems. It would not be easy, and it will take time, to develop the methodology to diagnose healthy systems. We agree that a multidisciplinary approach is necessary.

BRUNIG - I was involved in the meetings which took place at Reading University before ICRAF was established and I am pleased to see ICRAF developing this systems approach. The emphasis on analysing the context of the problem is similar to that of the Man and Biosphere Programme. There is a possibility here for future collaboration. ICRAF's diagnostic objectives can be achieved by means of instruments now being developed by other groups, for example by Jeffers in the UK. There are many types of systems applications which can help you solve problems quickly. In agroforestry you can use a systems approach and simulation modelling to analyse the problem and preselect possible solutions for testing.

STEPPLER - ICRAF will be using modelling techniques, but how far do we go into modelling? To become preoccupied with developing models will be to the detriment of our overall programme.

BRUNIG - ICRAF's role should be to identify collaborators specialized in modelling to work with.

OLDEMAN - I agree with Dr Brunig's comment in favour of the approach ICRAF is taking. I disagree with the statement you sometimes hear about agroforestry that 'We know the basics, it is just a matter of filling in the details'. Just because we know how to build a canoe does not mean we know how to build a transoceanic liner. A similar kind of diagnostic approach in Tunesia by Wageningen students has predicted a crisis in ten years, but what can be done now? The indigenous people do not see that there is anything wrong with their land use. How do you communicate with them about these things? It is important to place sufficient emphasis in your diagnosis procedures on the socio-economic questions.

STEPPLER - That is why ICRAF views a multidisciplinary team as absolutely necessary. The social side of agroforestry is very important.

OLDEMAN - I am concerned about predicting the specific kind of crisis that can be expected to occur in any particular system. What is ICRAF's role in this connection? Will you try to diagnose specific future problems?

STEPPLER - The majority of ICRAF's research is now 'focused' and attempting to address present problems. I cannot say how good our ability to diagnose future problems will be, but we recognize the need to try and develop a predictive capability.

301

Applications of Plant Science to Agroforestry

ASPECTS OF EVOLUTION IN HERBACEOUS AND TREE CROPS RELEVANT TO AGROFORESTRY

B. PICKERSGILL
Department of Agricultural Botany, University of Reading, Reading, UK.

ABSTRACT. Agroforestry involves the cultivation on the same unit of land of herbaceous and tree (or sometimes shrub and tree) species. One component of the system is usually fully domesticated, while the other (often grown for forage, shade, fuelwood or pulpwood) is frequently little changed from the wild state. Guidelines for improvement of the latter component may be sought from the changes which have taken place in the fully domesticated crops (including forest trees). Attributes of successful crops include a ready supply of propagules, easy germination and establishment, reliable yields in as short a period as possible, and easy handling and processing. The different adaptive strategies of herbaceous and woody wild species, particularly as regards the components of their genetic systems, are reflected in the success with which they adapt to, and can be improved under, cultivation. Breeding systems also influence strategies for collecting wild material for future improvement of crop species for agroforestry. Large-scale agroforestry is too new a development for significant studies to have been made on the co-adaptation of the various components, but potential areas for investigation include effects on soil composition, pollination biology, and pests and diseases.

INTRODUCTION

The term agroforestry currently covers a wide range of associations of herbaceous and woody (or even woody and woody) plants grown together under man-managed conditions. Some of these attempt to simulate the natural environment of one component: for example coffee and cacao, both of which occur naturally as understorey trees in tropical rainforest, are often cultivated under shade trees. Other agroforestry systems combine crops from very dissimilar environments. Trials of 'Desiree' potatoes under coconut palms in eastern Peru bring together a North European

cultivar of a highland South American crop and a palm from the strand zone of the Pacific islands, in an environment where the natural vegetation is lowland rainforest. Sometimes the perennial crop is the economically important one, as in rubber plantations undersown with leguminous fodder or cover crops. In other instances, the herbaceous component is valued more, as in most combinations of annual food crops with tree legumes such as *Leucaena* or *Acacia* for fodder or fuel. The different components may yield simultaneously, as in cacao plantations shaded by coconuts, or successively, as in the taungya system whereby forestry plantations are intercropped with annual or short-duration food crops while the trees are becoming established. Agroforestry may also refer to the system of agriculture practised rather than to the actual crops grown. In this context, it has been used to cover the spectrum from primitive shifting cultivation to mixed cropping in plantation agriculture.

Since such diverse associations of plants, and such different types of systems are included under the one term, it is not easy to formulate valid generalizations about evolutionary aspects of agroforestry systems. However, agroforestry, like both agriculture and forestry, involves a reduction in genetic diversity. Rigorous selection of the parents that contribute progeny to the next generation, establishment of crop populations from small samples of wild plants, and an inevitable element of inbreeding all erode variability and produce a genetic structure in the man-managed populations different from that in conspecific wild populations. These genetic changes are in fact the first stages in domestication, and a further characteristic of many agroforestry systems is that a fully domesticated crop (usually the herbaceous component) is combined with a crop which is only at the stage of incipient domestication (usually the tree component, although many tropical forage and ground cover crops are not fully domesticated either). Agroforestry also, and increasingly, involves cultivation of crops for purposes which were previously met by exploitation of natural vegetation. Various species are under trial as fuel-, timber, pulpwood or cover crops, and these are still only a generation or so removed from the wild.

Some basic concerns of agroforestry are therefore, first, to predict which species will prove amenable to cultivation; second, to identify and incorporate in the cultivated populations the most desirable of the variants present in the wild; third, to improve by breeding and selection the comparatively undomesticated components in the system. Evolutionary changes which have occurred in the fully domesticated crops may offer useful guidelines on changes which should be sought, or induced, in the newer and less domesticated crops. The effects of mixed cropping on reproductive biology and on the build-up of pests and diseases in the crops concerned, together with other aspects of co-adaptation, also deserve consideration.

ATTRIBUTES OF SUCCESSFUL CROP PLANTS

The ideal crop plant is one which establishes readily; produces economic returns as soon as possible; yields reliably despite year-to-year fluctuations in climate; yields at levels that are

both profitable in themselves and competitive with other species; is reasonably uniform both in the field and in terms of its product; is easily handled and/or processed; and can be grown in different regions.

Supply of propagules

The first essential in the establishment of a crop is a readily available supply of high quality propagules. Many herbaceous crops are derived from wild annuals which are colonizing species and produce abundant seed every year. Examples include wheat, barley, sunflower, lentil and many cucurbits. Since many of these crops are also cultivated for their seeds or fruits, seed for propagation is always available.

Perennial species in stable, closed communities are not dependent on regular annual seed crops to maintain population size and may produce heavy seed crops at regular or irregular intervals with little or no seed production in the intervening years (mast fruiting, biennial bearing, monocarpy, and related phenomena). Shortages of seed have periodically limited the cultivation of *Eucalyptus citriodora* (National Academy of Sciences, 1980); and the perennial groundnut (*Arachis glabrata*), under trial as a fodder and cover crop in various parts of the tropics (National Academy of Sciences, 1979), often does not produce seed so it must be propagated vegetatively.

Populations established from seed are usually more variable than populations of vegetatively cloned plants. Outbreeding species are more heterozygous and their populations contain more diverse and different genotypes than inbreeders, but even in inbreeders, seed-established populations are likely to be derived from more than one parent and contain significant heterogeneity. Seed-propagated crops thus have a capacity to respond to natural or human selection which is lacking in vegetatively propagated crops. Progress in breeding sexually sterile crops, such as yams, therefore involves first restoring seed fertility followed by conventional programmes of crossing and selection (Sadik and Okereke, 1975).

Outcrossing plants will not breed true from seed, so superior genotypes are lost by recombination unless they can be multiplied clonally. This is often worthwhile in perennial crops, where heterogeneous stands established from seed may have significantly lower yields than clonal stands in which every individual has the same high-yielding genotype. Yields of rubber in Malaysia approximately doubled when plantations were established from budwood of selected trees rather than from unselected seedlings (Purseglove, 1968). Replication by cloning may also facilitate distinction between genetic and environmental effects in yield trials of woody species (Longman, 1976), and the product is more uniform than when seed propagation is used. This uniformity has proved very advantageous in tea and certain other perennial crops.

An ideal crop plant thus has the capacity for both sexual and asexual reproduction. Improved techniques of tissue culture, manipulation of breeding systems, use of hormones to root cuttings and other technical advances are conferring this facility on species which in the wild never possessed such versatility.

Germination

Difficulty in germinating seed is a barrier to successful cultivation of some species, particularly tropical timber trees. Sometimes this is due to ignorance of germination requirements, for example species of open habitats such as *Eucalyptus microtheca* may require light for germination (National Academy of Sciences, 1980). Wild species often have dormant seeds, which do not germinate until conditions are favourable and then germinate irregularly, which prevents the entire crop of seedlings being destroyed by a single catastrophe. Man, on the other hand, requires crop seeds to germinate rapidly and uniformly, to produce a dense stand which will keep down weeds and in which the plants are all the same age and so can be harvested together. Many crop plants have, therefore, lost the seed dormancy characteristics of their wild progenitors; for example, cereals (Harlan *et al.*, 1973) and grain legumes (Smartt, 1978). Many trees suitable for agroforestry still have dormant seeds, and this dormancy has to be broken by mechanical scarification, chilling or treatment with boiling water or concentrated acid (see National Academy of Sciences, 1980, for examples).

Complete absence of dormany may be disadvantageous if crop seeds sprout before harvest, thereby reducing seed yield and seed quality. Lack of dormancy may also be associated with a short period of seed viability. *Inga* spp. are often used as shade crops for coffee and cacao and are established from seed. However, the seed lacks a testa and it soon loses viability, especially if dried. Cacao seed is notorious for its short viability, which may be lost in the few days necessary for transport, customs clearance and delivery (Goldbach, 1980), seriously hampering dissemination of this crop. Although selection by man may eliminate dormancy in domesticates, it has not so far been possible to select for dormancy in species where seed dormancy is absent.

Establishment

Most crops are sown on cleared ground, so their seedlings compete with one another rather than with previously established vegetation. Large seeds often produce more vigorous seedlings, which can emerge from deeper planting, than smaller seeds (Harlan *et al.*, 1973). Large seeds have been favoured during domestication of many crops grown for their seeds, although the effects on crop establishment have been unconscious by-products of selection for increased yield.

Some crops depend on associations with micro-organisms for successful establishment and early growth. Certain cultivated legumes, for example *Arachis*, *Glycine* and *Vigna*, nodulate reasonably effectively with a wide range of strains of *Rhizobium*. Others, for example *Leucaena*, nodulate with a very restricted range of strains, so that inoculation of the seed may be necessary to ensure effective nodulation, especially when the crop is introduced to new areas (Date and Halliday, 1980). *Alnus acuminata*, a non-leguminous nitrogen fixer grown for fuelwood, timber and soil improvement, requires inoculation of soil with the appropriate *Actinomycetes* species if *Alnus* has not been grown previously (National Academy of Sciences, 1980).

The role of vesicular-arbuscular (VA) mycorrhizas in the mineral nutrition of plants has only recently become clear (Mosse, 1973). According to Janos (1980), pioneer species (which include many recently advocated for cultivation for fuelwood, pulp and paper) are often non-mycorrhizal, their ability to start growth without infection giving them a competitive advantage in their short-lived ecological niche. Species of disturbed or nutrient-poor habitats, such as *Pinus* and various Caesalpinioideae, are often ectomycorrhizal, while lowland tropical trees are mostly obligate mycotrophs. Since the fungi involved in VA associations produce few spores, of short viability, Janos (1980) suggests that ectomycorrhizal species could divert succession by decreasing spore populations of the VA mycorrhizal fungi so much that characteristic forest species might be unable to re-establish. Continued cultivation of non-VA plants might likewise preclude later cultivation of VA species on that same piece of land.

Time to harvest

Selection under domestication has converted some perennial seed and fruit crops to annuals. Returns are produced in the first year, the crop passes the unfavourable season of low temperature or low rainfall as seed, and the carry-over of pests and diseases is reduced. Annual cottons, evolved in response to the shorter growing seasons of high latitudes, have therefore displaced perennial cottons, even in low latitudes. Selection for improved harvest index may also reduce the amount of vegetative material produced, and hence the time to onset of the reproductive phase. New cultivars of temperate fruits such as apple and cherry are being developed which have a dwarf habit, crop heavily at an early age (and thus have a short productive life) and can tolerate planting at high plant populations.

Where vegetative parts are harvested selection under domestication may delay the onset of flowering. Wild beet becomes reproductive in its first season; domesticated beet behaves as a biennial, producing a large harvestable root in the first favourable season and flowering, after vernalisation during winter, in the second. Improved cultivars of cassava branch less freely than primitive types. Since cassava branches when inflorescences are initiated this is, in effect, selection against flowering (Jennings, 1976), although the effects on root yield and quality are not reported.

Amongst woody crops rapid growth rates are desirable in species grown for shade, soil conservation, or coppicing for fuel. A corollary of rapid growth is often lack of strength and/or density in the wood produced, and especially fast growing trees, such as *Macaranga* and *Cecropia*, which occupy a weedy niche as wild plants in forest clearings and the like, may be suitable only for chipboard, pulping or fuel. Ashton (1976) therefore suggests that the most attractive candidates for commerical cultivation for timber are neither the pioneers nor the slow growing, light-intolerant climax species but those of intermediate successional stages which will tolerate bright light and which grow relatively rapidly but produce reasonably hard, dense wood.

Ease of handling or processing

Foliage and seeds of many plants are vulnerable to attack by herbivorous predators, particularly insects. Thus, wild plants have evolved various forms of mechanical or chemical protection, but this process is often reversed under domestication when man selects crops for improved palatability to himself or to his domestic animals, or for easier handling. Wild lettuces are prickly, whereas the domesticates have smooth leaves. On the other hand, spininess is retained in safflower grown for seed under traditional cultivation in Turkey and India because the spines deter birds from taking the seeds (Knowles, 1969). *Leucaena* is a valuable forage for cattle in the dry tropics, but the foliage contains mimosine, which makes the hair of horses and pigs fall out and is toxic even to ruminants if fed alone for too long. Low-mimosine strains have, however, now been selected (National Academy of Sciences, 1979). Gossypol-free cotton was developed so that flour from the seeds could be used as a protein supplement for man and other non-ruminant animals, but glandless cottons suffer far more insect damage in the field than normal, glanded types. By selecting for increased palatability in his crops man has, therefore, often inadvertently selected for increased vulnerability to pests and, consequently, a greater need for crop protection activities.

Janzen (1969) distinguishes two strategies which plants can adapt to evade seed predation: production of numerous small seeds, some of which escape predation; or production of a few large seeds in which the metabolic cost of chemical protection is justified because each seed represents a significant amount of the total effort invested in reproduction. Large-seeded species are more likely to have been selected for cultivation by man in the early stages of the development of agriculture, and to have persisted in cultivation thereafter. Many cultivated pulses have large seeds and are notorious for containing toxins and antimetabolites (cyanogenic glycosides, trypsin inhibitors, non-protein amino acids, phytohaemagglutinins, and so on). Most of these are removed by prolonged cooking, but this may become increasingly less desirable as fuelwood becomes limiting in many parts of the tropics. Although these pulses have been domesticated for thousands of years, there is obviously still scope for further improvement in processing, palatability and nutritional qualities.

Some crops have recently been losing ground because they require elaborate processing. *Chenopodium quinoa* contains saponins in its seeds, which have to be leached out by repeated washings. For this and other reasons the crop is being increasingly supplanted by barley in the Andes. The Andean lupin, *Lupinus mutabilis*, needs similar, elaborate processing to remove alkaloids from the seeds, and is giving way to the introduced *Vicia faba*.

Breeding system

The genetic systems of plant species represent a balance between ecological 'flexibility' and 'fitness'. That is, between factors favouring recombination, which generates variability, and factors restricting recombination, which conserves particular

genotypes (Stebbins, 1950; Grant, 1958). In short-lived colonizing species, the brief generation time and large numbers of progeny favour recombination, but these are often offset by self-pollination, which increases homozygosity and restricts opportunities for recombination. Chromosome numbers are often low in herbaceous plants, so that many genes are linked, but chiasma frequencies in inbreeders tend to be high, so that maximal variability is released in the generations immediately following an occasional outcross. Long-lived species in stable communities, on the other hand, produce comparatively few progeny which survive to reproductive maturity, and recombination is further restricted by the long generation time. However, these plants are often outbreeders, thus heterozygous at many genetic loci. Outbreeding woody species generally have higher chromosome numbers but smaller frequencies of chiasmata than inbreeding herbaceous plants, so variability is released in a steady trickle rather than a sudden burst, and by reassortment rather than crossing-over.

Herbaceous crops grown for their seeds or fruits are often habitually self-pollinated and derived from self-pollinated ancestors, for example many cereals and pulses. In others, selection under domestication has favoured a shift from out- to inbreeding. Wild relatives of *Lycopersicon esculentum* have exserted stigmas and are insect-pollinated; domesticated tomatoes have the stigma included within the anther cone and pollen is shed directly on to it (Rick, 1976). Self-pollination is advantageous in crops grown for seed or fruit because reliable yields are obtained even when conditions at flowering are not favourable for animal pollinators, and because spread of the crop is not restricted by absence of pollen vectors in certain regions. The latter advantage is also shared by wind-pollinated plants. Thus self-pollinated groundnut and chili pepper, and wind-pollinated maize, spread rapidly throughout the tropics whereas, among the insect-pollinated crops, Smyrna figs failed in California until the fig wasp was introduced, sunflowers have failed in some parts of Africa because of insufficient bees for pollination, and the New World *Vanilla* has to be hand-pollinated in the Indian Ocean islands which now produce the spice commercially. Self-pollinated crops have further advantages over outbreeders in that they are more likely to breed true from seed, a process which would have facilitated rapid improvement by selection in the early stages of their domestication. In addition, they contain less plant-to-plant variation in the population, a desirable trait under modern mechanized agriculture.

Tree crops, even those grown for seed or fruit, are mostly derived from outbreeding ancestors and have remained outbreeding in cultivation. Mechanisms include genetic self-incompatibility, found for example in apples, cherries, cacao, tea and teak; dichogamy, as in avocado and black pepper; and monoecy or dioecy as in nutmeg, pawpaw, rubber, oil palm and mahogany. Problems of plant-to-plant variation in outbreeding crops may be overcome by clonal reproduction, or by the use of F_1 hybrids produced by crossing artificially inbred (hence largely homozygous) lines so that every plant in the F_1 population has virtually the same heterozygous genotype. Clonal propagation is used for crops such as tea and rubber. F_1 hybrids are used when the crop lacks the

capacity for vegetative propagation, as in maize and coconuts, or where hybrid vigour may be exploited, as in oil palm. However, in many tree species it is impractically time consuming to produce inbred parents in order to obtain a uniform F_1. F_1 hybrid varieties produced by crosses between heterozygous parents may be as heterogeneous as the original population.

Domestication itself may entail a degree of inbreeding, since crop populations are often established from comparatively few selected parents. Species which are naturally self-pollinated even if only facultatively so, will tolerate this increasing homozygosity in successive sexual generations better than obligate outbreeders. The type of breeding system is therefore relevant to success in cultivation even of crops which are not grown for fruit or seed. Furthermore, the type of breeding system markedly affects the strategy to be adopted in sampling from the wild, especially where it is necessary to enhance the diversity present in future populations of crops.

Adaptability and adaptation

Many successful crops are those that are grown on a large enough scale to sustain basic research on agronomy and improvement. Successful crops must therefore be adaptable to changes in management, in its modest sense. Wild species vary very considerably in this trait. Whitmore (1976) contrasts *Casuarina equisetifolia*, a morphologically invariable species confined to a single habitat, with *Campnosperma brevipetiolatum*, which is restricted to dry land in the southern Solomon Islands and to freshwater swamps in New Guinea. Since introductions into cultivation are usually made on the basis of a small quantity of seed from a limited area, the subsequent fate of the crop may be influenced by sampling accidents at the start. Serendipity resulted in seed of the widely planted tropical pines *Pinus caribaea* and *P. kesiya* being obtained from populations (in Belize and the Philippines, respectively) which were subsequently shown to be productive in a wide range of environments. Seed of *P. oocarpa*, on the other hand, came from populations poorly adapted to growth in other areas (Burley, 1976). It was just chance that Wickham's collections of rubber seeds, on which the Southeast Asian plantations were founded, were all *Hevea brasiliensis*, the best yielding species in the genus, and that Wickham happened to collect them in the central Amazon, where the trees produce better quality latex than those down river. However, had Wickham collected even further up the Amazon he could have secured seed from trees which combine large yield, good quality and disease resistance, and the Far Eastern rubber industry might not be as vulnerable to the spread of leaf blight as it is today (Imle, 1977).

Factors which affect the distribution and rate of spread of genetic variation, and thus the strategies for collecting seed from the wild to establish or improve species in cultivation, are population size, population density, dispersal of pollen and dispersal of seeds. Colonizing annuals and temperate trees such as conifers commonly occur in large populations and nearly pure stands. Tropical forests, on the other hand, are conventionally thought to contain many species per unit area but few individuals of any one species. However, several tropical tree species do

occur in clumps (Hubbell, 1979). Genetic differentiation is likely to occur more rapidly in small, semi-isolated populations than in large interbreeding populations (Ehrlich and Raven, 1969) but Levin and Kerster (1969) have shown that, in some animal-pollinated plants, genes migrate more slowly in dense populations so that density may, paradoxically, lead to genetic subdivision of a population. This occurs because movement of pollen is usually strictly limited, reaching an extreme in the case of self-pollinated plants. Even anemophilous outbreeders, such as many temperate trees, are likely to be pollinated by their near neighbours to which, in the absence of effective seed dispersal, they may be genetically related. Opinions differ on the relative importance of outbreeding (Bawa, 1974) versus apomixis (Kaur *et al.*, 1978) in tropical forests. Outbreeding species have various flowering strategies (Gentry, 1974). These range from the 'big bang' in which a massive crop of flowers is produced for a few days only, so that most pollen movement is likely to be from flower to flower in the same crown (geitonogamy), to 'steady state' in which a few flowers are produced each day over long periods, so cross-pollination between different individuals is more likely. Superimposed on this are differences in the foraging behaviour of pollinators. Honey bees work systematically on individual plants or patches of flowers before moving on, hence they disperse pollen over limited distances. Euglossine bees, on the other hand, are often trapliners (Janzen, 1971), and follow the same foraging route each day, visiting plants separated by considerable distances so that they can effect cross-pollination between apparently isolated individuals. Data on seed dispersal are even more limited than data on pollen dispersal, but in general seeds do not move as freely as pollen, and restricted seed dispersal may be primarily responsible for the clumped distributions of some tropical forest species (Hubbell, 1979).

Consideration of these factors led Bawa (1976) to suggest that between-population variation in tropical hardwoods may be greater than in temperate trees. So that breeders would be better advised to sample a small number of individuals from a large number of populations rather than a large number of individuals from a small number of populations, as in temperate forestry.

Species thus show inherent differences in adaptation and adaptability based on differences in their reproductive biology. However, occasionally, breeding programmes have conferred on particular cultivars immediate adaptation to a wide range of environments. The 'green revolution' wheats were bred in Mexico by raising two generations a year, one in high latitudes in summer, and one in low latitudes in winter. The resultant cultivars could initiate inflorescences under either lengthening or shortening days and were thus pre-adapted to cultivation in various latitudes and at various seasons of the year.

CO-ADAPTATION IN AGROFORESTRY SYSTEMS

Herbaceous and tree species growing together may interact in various ways. Their root systems may be distributed differently in the soil profile, giving the tree species access to nutrients and water unavailable to the herbaceous crop. The plant nutrients may then be returned to the surface layers in the leaf litter and

become available to the herbaceous crop. *Acacia albida* comes into leaf in the dry season and sheds its leaves at the start of the rainy season. The leaves decay rapidly, releasing nutrients for crops planted under the trees in the wet season, when the *Acacia* does not shade them. Groundnuts and millet have yielded significantly more when grown directly under *A. albida* rather than further away. In the dry season, livestock are pastured and feed in the shade of the trees, and their droppings further improve the soil (National Academy of Sciences, 1979).

Leaf litter of certain other species has deleterious effects. *Tamarix* spp. have been recommended for shelter belts, soil stabilization, shade and fuelwood. Their extensive root systems extract from the soil large quantities of soluble salts which are accumulated in, and excreted from, the leaves and thus returned to the topsoil. Tamarisks can therefore cause salinization of the topsoil even on non-saline soils. Crop yields may be reduced up to 50 m from a tamarisk shelter belt (National Academy of Sciences, 1980).

Agroforestry may require different habits and canopy structures in the crop compared to those favoured under monoculture. Bunting (1980) gives an instructive example from cowpeas, where selection for short-season, small-statured, non-climbing types proved misdirected in a context where growers wanted cowpeas that could withstand shading in the lower layers of mixed crops and reach the light by climbing up other components of the stand. More work is required on morphological and physiological plant attributes which are desirable for agroforestry, as compared with either agriculture or forestry.

Competition for pollinators may reduce yields where two components of a mixed crop flower simultaneously and are both insect-visited. Dandelions, growing as weeds in grassed orchards notoriously attract pollinating bees away from the fruit trees. Many shade and timber trees are valuable sources of high quality honey, for example *Eucalyptus*, *Acacia*, *Inga* and *Prosopis*, and they could conceivably lessen yields of lower storey crops which require bee pollination.

One often cited advantage of mixed cropping, or agroforestry, over monoculture is that pests and diseases may be less severe; presumably because they cannot build up to such devastating levels as in stands of uniformly susceptible individuals. However, Bunting (1980) has cautioned that cross-infestations may occur in some circumstances. For example, the stem borer of sorghum is the same pest as the bollworm of cotton. Again, bruchid beetles are serious pests of many legume seeds, including pulses such as *Phaseolus* and *Cajanus* as well as trees such as *Acacia* and *Prosopis*. Many tree legumes are prolific producers of seed which is not harvested by man and so falls to the ground as a potential source of infestation for other crops. Bruchids vary in their host specificity, some being confined to a single legume species and others being more catholic, but host ranges are not yet well enough known to permit the dangers of intercropping legumes with legumes to be assessed precisely.

When pests or diseases do become established in mixed crops control may be more difficult than in monoculture, at least in high-input systems. This is because of such factors as the different sensitivities of plant species to chemical sprays, and

the difficulty of getting spray machinery through mixed crops and achieving adequate penetration of the canopy by the spray.

SUMMARY AND CONCLUSIONS

Although man has probably been interplanting herbaceous and tree crops, at least on a garden or orchard scale, since the beginning of agriculture, agroforestry in the modern sense is a comparatively new development. Suggestions about the directions that evolution might take in such systems are necessarily speculative. In the immediate future, the tree or herbaceous forage components of the system may need improvement, since in yield, morphology and adaptation to cultivation they are often still close to the wild populations from which they have been derived only recently. Sometimes improvement may require expanding the genetic base of the populations in cultivation, and studies of the biosystematics of the wild populations may enable new introductions to be made from provenances likely to contain desirable traits. Eventually, however, the species will have to be considered as components of an integrated system, rather than in isolation, and this will require work on morphology, physiology and crop protection, and will include attention to reproductive as well as vegetative features.

REFERENCES

Ashton, P.S. (1976). Factors affecting the development and conservation of tree genetic resources in Southeast Asia. *In* "Tropical Trees: Variation, Breeding and Conservation" (J. Burley and B.T. Styles, eds), pp.189-198. Academic Press, London.

Bawa, K.S. (1974). Breeding systems of tree species of a lowland tropical community. *Evolution* 28, 85-92.

Bawa, K.S. (1976). Breeding of tropical hardwoods: an evaluation of underlying bases, current status and future prospects. *In* "Tropical Trees: Variation, Breeding and Conservation" (J. Burley and B.T. Styles, eds), pp.43-59. Academic Press, London.

Bunting, A.H. (1980). The future of research on mixed cropping in tropical agriculture. *In* "Opportunities for Increasing Crop Yield" (R.G. Hurd, P.V. Biscoe and C. Dennis, eds), pp.247-252. Pitman, London.

Burley, J. (1976). Genetic systems and genetic conservation of tropical pines. *In* "Tropical Trees: Variation, Breeding and Conservation" (J. Burley and B.T. Styles, eds), pp.85-100. Academic Press, London.

Date, R.A. and Halliday, J. (1980). Relationships between *Rhizobium* and tropical forage legumes. *In* "Advances in Legume Science" (R.J. Summerfield and A.H. Bunting, eds), pp.597-601. Royal Botanic Gardens, Kew, London, UK.

Ehrlich, P.R. and Raven, P.H. (1969). Differentiation of populations. *Science* 165, 1228-1232.

Gentry, A.H. (1974). Flowering phenology and diversity in tropical Bignoniaceae. *Biotropica* 6, 64-68.

Goldbach, H. (1980). Imbibed storage of cacao seeds in osmotic solutions. *Plant Genetic Resources Newsletter* 43.

Grant, V. (1958). The regulation of recombination in plants. *Cold Spring Harbor Symp. Quant. Biol.* 23, 337-363.

Harlan, J.R., Wet, J.M.J. de and Price, E.G. (1973). Comparative evolution of cereals. *Evolution* 27, 311-325.

Hubbell, S.P. (1979). Tree dispersion, abundance and diversity in a tropical dry forest. *Science* 203, 1299-1309.

Imle, E.P. (1977). *Hevea* rubber: past and future. *In* "Crop Resources" (D.S. Siegler, ed.), pp.119-136. Academic Press, New York.

Janos, D.P. (1980). Mycorrhizae influence tropical succession. *In* "Tropical Succession" (J. Ewel, ed.), pp.56-64. *Biotropica* 12 Supplement.

Janzen, D.H. (1969). Seed eaters versus seed size, number, toxicity and dispersal. *Evolution* 23, 1-27.

Janzen. D.H. (1971). Euglossine bees as long-distance pollinators of tropical plants. *Science* 171, 203-205.

Jennings, D.L. (1976). Cassava - *Manihot esculenta* (Euphorbiaceae). *In* "Evolution of Crop Plants" (N.W. Simmonds, ed.), pp.81-84. Longman, London.

Kaur, A., Ha, C.O., Jong, K., Sands, V.E., Chan, H.T., Soepadmo, E. and Ashton, P.S. (1978). Apomixis may be widespread among trees of the climax rainforest. *Nature* 271, 440-442.

Knowles, P.F. (1969). Centres of plant diversity and conservation of crop germplasm: safflower. *Econ. Bot.* 23, 324-329.

Levin, D.A. and Kerster, H. (1969). Density-dependent gene dispersal in *Liatris*. *Amer. Nat.* 103, 61-74.

Longman, K.A. (1976). Conservation and utilization of gene resources by vegetative multiplication of forest trees. *In* "Tropical Trees: Variation, Breeding and Conservation" (J. Burley and B.T. Styles, eds), pp.19-24. Academic Press, London.

Mosse, B. (1973). Advances in the study of vesicular-arbuscular mycorrhizae. *Ann. Rev. Phytopathol.* 11, 171-196.

National Academy of Sciences (1979). "Tropical Legumes: Resources for the Future". National Academy of Sciences, Washington D.C., USA.

National Academy of Sciences (1980). "Firewood Crops: Shrubs and Tree Species for Energy Production". National Academy of Sciences, Washington D.C., USA.

Purseglove, J.W. (1968). "Tropical Crops: Dicotyledons". Longman, London.

Rick, C.M. (1976). Tomato - *Lycopersicon esculentum*. *In* "Evolution of Crop Plants" (N.W. Simmonds, ed.), pp.268-273. Longman, London.

Sadik, S. and Okereke, O.U. (1975). A new approach to improvement of yam, *Dioscorea rotundata*. *Nature* 254, 134-135.

Smartt, J. (1978). The evolution of pulse crops. *Econ. Bot.* 32, 185-198.

Stebbins, G.L. Jr (1950). "Variation and Evolution in Plants". Columbia University Press, New York.

Whitmore, T.C. (1976). Natural variation and its taxonomic treatment within tropical tree species as seen in the Far East. *In* "Tropical Trees: Variation, Breeding and Conservation" (J. Burley and B.T. Styles, eds), pp.25-34. Academic Press, London.

DISCUSSION

STEPPLER - Domestication of plants has involved moving them from associations, in their natural forms, to planting them in monoculture. For monocultural systems plant breeding objectives can be clearly established. Do you envisage difficulties in developing breeding objectives for agroforestry, where you will be dealing with the outcome of numerous interactions between plant species?

PICKERSGILL - We will need to wait for information from other disciplines, such as plant morphology and physiology, in order to plan breeding programmes designed to select plants specifically for agroforestry land use systems. For example, cowpea breeders have tended to concentrate on developing determinate cultivars which are suitable for monoculture; whereas in intercropping situations, the semi-climbing ones are preferred.

LEDIG - In systematic forest breeding programmes we select plants from a broad area in order to conserve a wide genetic diversity.

PICKERSGILL - In outbreeding crops, such as many tree species, you get considerable segregation in early generations following subcrossing or inbreeding. And I think this segregation accounts for some of the diversity observed by tree breeders. Also, tree breeding work is comparatively recent and we are now aware of the need to maintain genetic diversity. This was not true of early work on the improvement of herbaceous crops.

LEDIG - You have tended to generalize too much when discussing seed dormancy, and there are a number of exceptions from the broad generalization.

PICKERSGILL - Where seed dormancy is present, and viability is quickly lost, you tend to have potential variation which can form the basis for selection for or against dormancy. Some species do not have seed dormancy at all and breeding for dormancy as far as I know has not been possible in those species.

STEPPLER - There are cases where seed dormancy has been transferred between species. For example, in wild to cultivated oats.

RACHIE - Relatively undomesticated plants may be subject to many unexpected hazards when brought under more intensive cultivation. By intercropping, however, it may be possible to buffer the pest and disease problems until more information and expertise are available to deal with these environmental and biological hazards.

PICKERSGILL - That is entirely correct. But, the crop protection industry will invest efforts only for crops grown on a large enough scale to afford an economic outlet for their products. This is why it is important that any new crops be adapted to cultivation on a reasonably large scale. Furthermore, diversification of genotypes may provide an additional measure of protection.

PHOTOSYNTHETIC SYSTEMS: IMPLICATIONS FOR AGROFORESTRY

L.L. TIESZEN
Department of Biology, Augustana College, Sioux Falls, South Dakota, USA.

ABSTRACT. Three principal mechanisms of CO_2 reduction occur in terrestrial plants. The C_3 system is certainly the most common and generally characterizes all woody plants and most evolutionarily old families. The C_4 system has evolved relatively recently and is most common in the Poaceae (Gramineae) and Cyperaceae and less common in families of the Centrospermeae. CAM plants (not considered here) are generally restricted to the most arid environments and are not highly productive but they may be very important as sources of certain secondary compounds.

C_3 and C_4 systems are characterized by suites of interrelated anatomical, biochemical, and physiological characteristics. These are fundamental in determining maximum rates of photosynthesis, and productivity, as well as in determining the responses to a variety of environmental factors. Thus, these characteristics are also important in establishing the distributions of native species and in determining what species or photosynthetic types should perform best in various agroforestry systems.

C_4 plants generally require less water and less N to support a given rate of photosynthesis than do C_3 plants. Their light saturated rates are also usually greater, although they can be matched by C_3 plants with a tremendous investment of N in carboxylase protein. Thus, C_4 characteristics should be important in selecting species for systems of low nutrient status, limiting water, and an open canopy. In closed canopies, however, the apparently greater quantum efficiency of C_3 systems becomes important; and closed canopies are composed, in general, of C_3 species. Thus, for intercropped species an ideal canopy should consist of a C_4 overstorey and a C_3 understorey. Unfortunately, very few of our potential overstorey species are C_4 with the exception of some larger grass crops, for example maize and sugar cane. Many potential understorey species are C_3, although some native vegetables are C_4.

INTRODUCTION

The conversion of light energy to chemical potential in the photosynthetic reduction of CO_2 is accomplished in a remarkably similar manner in all plants. This similarity may reflect an early origin (2.5 to 3.3 billion years BP) under atmospheric and environmental conditions largely different from those existing today. An oxygenic atmosphere, for example did not develop until 1.8 to 2.3 billion years BP. Our understanding of CO_2 fluctuations and absolute temperature and moisture conditions during these early periods is less clear. However, relatively recently (60 M BP) climatic conditions became more seasonal, and certainly in some geographical areas, more arid.

Two variants of our typical C_3 photosynthetic system apparently evolved during the early period of angiosperm development and became common in families present around 60 M BP. These two systems (C_4 and CAM) are not new systems but are best considered variants of the basic C_3 mechanism. Each photosynthetic system is associated with a suite of anatomical, physiological, and biochemical characteristics which results in different rates of photosynthesis, different responses to environmental factors, and different ecological distributions. An understanding of these characteristics is important for traditional agriculture systems as well as for the development of agroforestry systems.

A REVIEW OF THE PHOTOSYNTHETIC SYSTEMS

Taxonomic distributions

C_4 systems are relatively recent innovations on the evolutionary scene and occur in a small percentage (<1%) of extant species (Kennedy *et al.*, 1980). This syndrome is highly polyphyletic and occurs in at least 18 families (Table 1). Among the dicot families, the syndrome is most common within the Centrospermae (Figure 1), a group which is related to arid and more open habitats.

In most dicot families, the C_4 syndrome is restricted to herbaceous annual or perennial species. However, in the Euphorbiaceae, some C_4 tree forms do occur (Pearcy and Troughton, 1975). It may be significant that a recent and rather exhaustive

Table 1. Comprehensive list of monocot and dicot families known to possess some species with C_4 photosynthesis.

Monocotyledonae	Dicotyledonae	
Cyperaceae	Acanthaceae	Euphorbiaceae
	Aizoaceae	Molluginaceae
Liliaceae ?[1]	Amaranthaceae	Nyctaginaceae
	Asteraceae	Polygonaceae
Poaceae	Boraginaceae	Portulacaceae
	Capparaceae	Scrophulariaceae
	Caryophyllaceae	Zygophyllaceae
	Chenopodiaceae	

[1]See Ziegler *et al.* (1981)

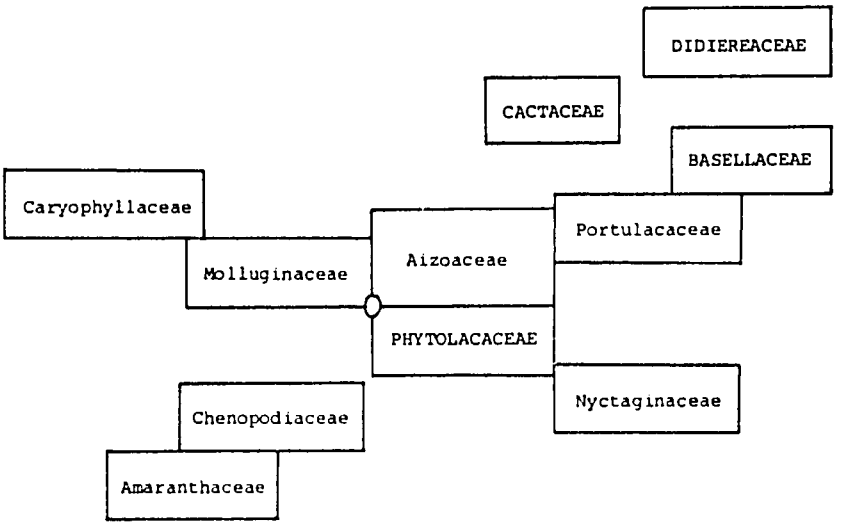


Fig. 1. Postulated phylogenetic affinities within the Centrospermae. Families in lower case letters possess known species with the C_4 pathway. (From Kennedy *et al.*, 1980).

Table 1. The number of Kenyan grass genera and species in each tribe arranged by photosynthetic type. Determination was based on leaf anatomy and $\delta^{13}C$. (From Tieszen *et al.*, 1979a.)

C_3 Tribe	Genera	Species	C_4 Tribe	Genera	Species
Agrostideae	4	14	Andropogoneae	30	73
Arundineae	1	3	Aristideae	2	17
Aveneae	6	13	Arundinelleae	2	6
Bambuseae	1	2	Chlorideae	12	33
Brachypodieae	1	1	(Danthonieae)	(1)	(1)
Bromeae	1	4	Eragrostideae	19	95
Centotheceae	1	1	Leptureae	1	2
Danthonieae	1	3	Paniceae	20	149
Ehrharteae	1	1	Pappophoreae	2	4
Isachneae	2	3	Sporoboleae	1	39
Meliceae	1	1	Zoysieae	5	9
Olyreae	2	6			
Oryzeae	2	6			
(Paniceae)	(10)	(20)			
Phalarideae	1	2			
Phareae	1	1			
Poeae	7	20			
Stipeae	1	1			
18	44	102	11	95	428

study in the Middle East and the USSR (Winter, 1981) has shown that a very high percentage of the flora is C_4, especially in the Chenopodiaceae and Polygonaceae. And, furthermore, a number

of these species are tree or tall shrub forms of high biomass and of economic importance. Winter (1981) indicates that many of these are fast growing and are useful as sand binders, for fuel, as forage, and as a source of alkaloids. Clearly, we need more information on the occurrence of C_4 species, especially from arid and semi-arid regions outside North America.

C_4 species are most common in the Poaceae (Brown, 1977) and Cyperaceae where perhaps half the species may be C_4. In Kenya, for example, most grass species are C_4 due largely to the abundance of Paniceae, Andropogoneae, and Eragrosteae in the East African lowlands. C_4 photosynthesis has been reported (Brown, 1975) in three of the seven tribes of the Cyperaceae: Cypereae, Fimbristylideae, and Rhynchosporeae (Takeda *et al.*, 1980). However, we know little about the relationships within the sedges or about the quantitative occurrence.

Ecological distribution

It has been clear for some time that the broad distribution patterns for C_3 plants differ from those of C_4 plants. This comparison, however, is perhaps best made within related taxonomic groups, since C_3 plants are much more numerous than C_4 plants. C_4 plants within all groups and throughout all parts of the world tend to be more abundant in warmer, more arid, and more open habitats. In addition, they are common in localized areas of high salt accumulation.

We know more about comparative ecological requirements in the Poaceae than in any other group. In temperate zones there is a clear and marked decrease in C_4 occurrence with increasing latitude (Teeri and Stowe, 1976). This latitudinal gradient is paralleled by an altitudinal gradient in tropical areas (Rundel, 1980; Tieszen *et al.*, 1979a) as shown for Kenya (Figure 2). These gradients are obviously complexes of environmental factors which include decreasing temperatures and increasing water availability. Few C_4 grasses occur with minimum temperatures less than 8°C during the growing season. The overriding importance of temperature, rather than moisture, is suggested by the temporal displacements of activity shown by Ode *et al.* (1980) and Tieszen *et al.* (1980) in North American prairie and even more conclusively by Ellis *et al.* (1980) who show C_4 grasses in South Africa mainly where temperatures are low. The exceptions in high temperature areas are hydrophytes or sciophytes. Interestingly, those C_4 grasses which do extend into colder environments often occupy regions of salt accumulation, e.g. *Spartina* (Long *et al.* 1975; Ode *et al.*, 1980) and *Muhlenbergia*.

We have less information on the distributions of other groups. The general patterns, however, are similar as shown in the comparison of C_4 grasses and C_4 dicots in Kenya (Figure 3). However, these superficial similarities may change as we learn more about the dicots, especially in areas where they seem very common, for example, the deserts of the Middle East and the USSR (Winter, 1981). A number of analyses of the 'World's worst weeds' show C_4 species to be much more numerous than C_3 species (May, 1981).

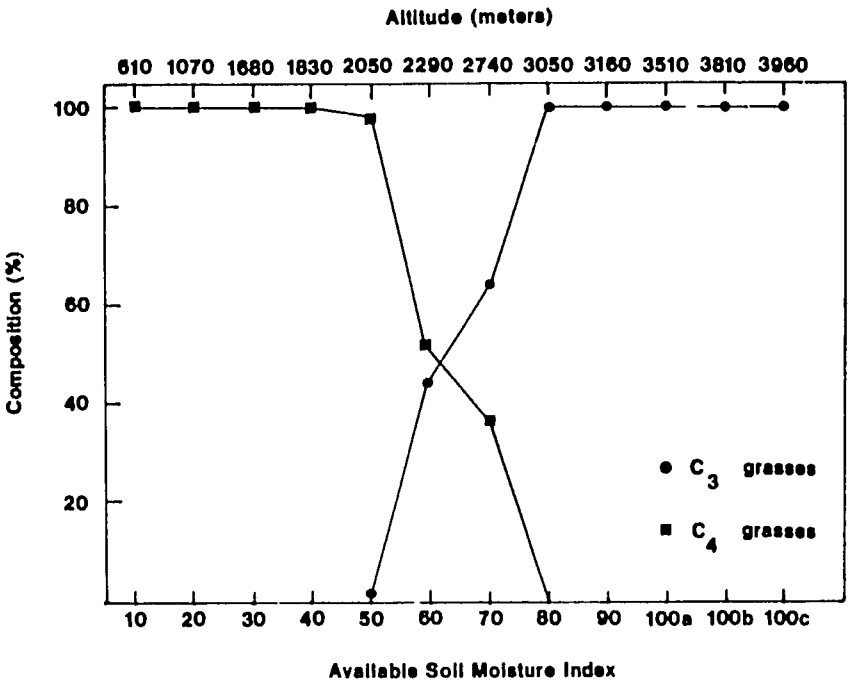


Fig. 2. Occurrence of C_3 and C_4 grasses from open habitats along an altitudinal gradient in Kenya. Closed canopy systems at low altitudes will have C_3 grasses. (From Tieszen *et al.*, 1979a.)

IDENTIFYING FEATURES

Essential characteristics of the syndrome

Because of polyphyletic origins of C_4 systems we might expect a high degree of divergence. However, as Table 3 suggests, most C_4 species share a suite of characteristics, some of which are quite diagnostic. The clearest description of what is meant by a C_4 pattern of CO_2 uptake must include the initial carboxylation of PEP carboxylase and a subsequent transfer of that CO_2 to RuBP carboxylase for reduction by normal Calvin Cycle processes. It is not sufficient to simply possess high PEP carboxylase activity as some C_3 plants and numerous aquatic organisms do. Only the coupled transfer via a peculiar anatomical compartmentalization of carboxylase enzymes allows the plant to photosynthesize at high rates and without apparent photorespiration. It is, in fact, the ability of C_4 plants to maintain high rates of CO_2 uptake at low intercellular concentrations of CO_2 that is the important distinguishing feature.

Anatomical criteria

The anatomical compartmentalization which supports C_4 photosynthesis is perhaps best illustrated by the typical 'Kranz' anatomy of some grasses. Here the enzymes of the Calvin Cycle are localized in the well-developed, thick-walled parenchymatous bundle sheath (PBS) layer which surrounds the vascular bundles. These

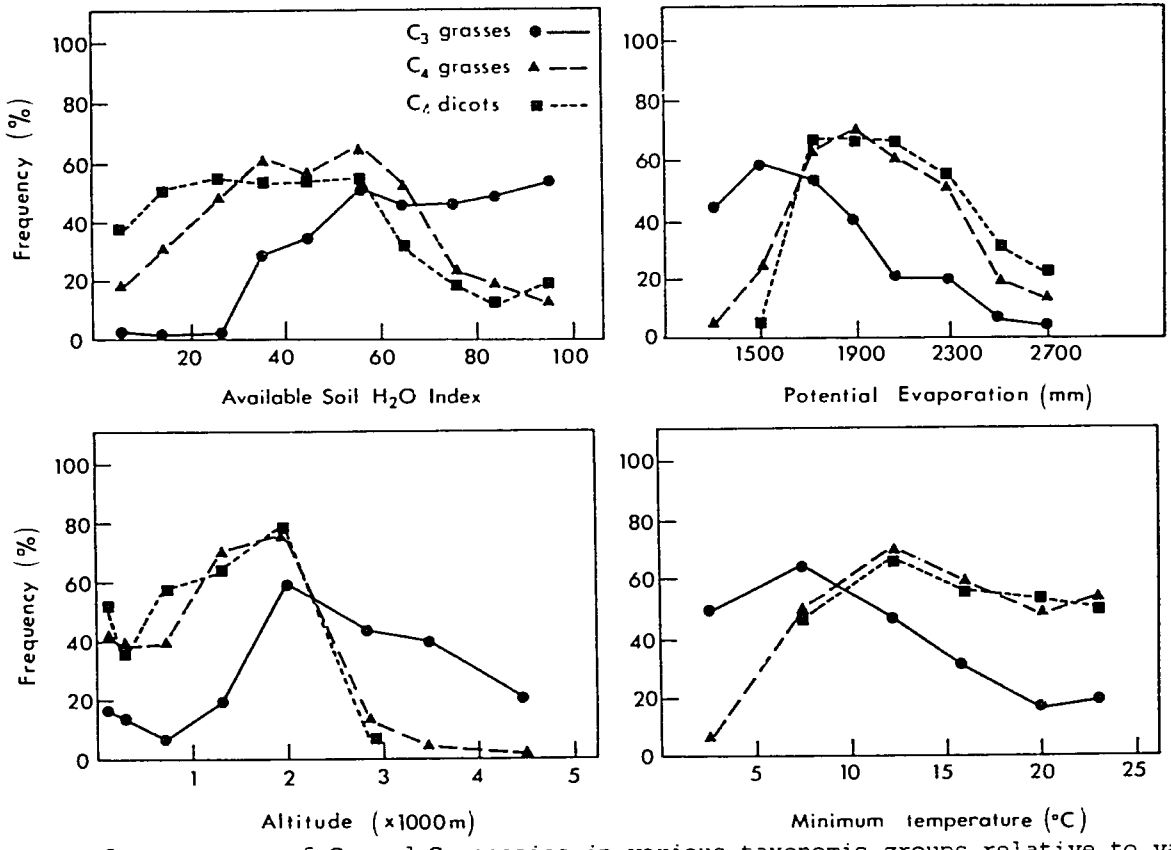


Fig. 3. Frequency of occurrence of C_3 and C_4 species in various taxonomic groups relative to various environmental factors. Distribution information is derived from acquisitions at the East African Herbarium, Nairobi.

Table 3. Generalized comparisons of C_3 and C_4 systems derived from numerous literature sources, principally those dealing with grasses.

	C_3	C_4
A. BIOCHEMICAL CHARACTERISTICS		
1. Early stable products	C_3 acids (Phosphoglycerate)	C_4 acids (Oxaloacetate, asparate, malate)
2. Carboxylation substrate	RuBP	PEP + RuBP
3. Primary carboxylating enzyme	RuBP carboxylase/ oxygenase	PEP carboxylase
4. Carbonic anhydrase	High in mesophyll	High, location not certain
B. ANATOMICAL CHARACTERISTICS		
1. Leaf anatomy	One type of photosynthetic cell, diffuse mesophyll	Two types of photosynthetic cells, mesophyll usually compact around vascular bundles
2. Interveinal distance	Large (more than 5 chlorenchyma cells)	Small (around 4 chlorenchyma cells)
3. Parenchymatous Bundle Sheath cells	Poorly developed	Extensively developed (usually with thick walls and numerous organelles)
4. Chloroplasts	Granal	Granal or agranal (at least modified)
C. PHYSIOLOGICAL CHARACTERISTICS		
1. Photorespiration	Present	Absent from leaf gas exchange measurements
2. O_2 inhibition	Present	Absent from leaf gas exchange measurements
3. CO_2 compensation point	50 (15-150) ppm	<5 ppm
4. CO_2 evolution in light	High	None
D. LEAF PHOTOSYNTHESIS		
1. Maximum photosynthetic rate	15 to 35 mg CO_2 $dm^{-2}hr^{-1}$	>35 mg CO_2 $dm^{-2}hr^{-1}$
2. Irradiance required for saturation	Low	Very high
3. Temperature optima (photosynthesis and growth)	Low to high	High (to low rarely)
4. Leaf conductance (maximum)	Similar	Similar
5. Mesophyll conductance	Low	High
6. Water use efficiency	Low	High
7. Nitrogen use efficiency	Low	High

Table 3 - continued

	C_3	C_4
E. PHOTOSYNTHETIC EFFICIENCY		
1. Quantum yield	Higher at low temperatures	Temperature independent
2. Canopy conversion rates (maximum)	Lower (35 g $m^{-2}d^{-1}$)	Higher (50 g $m^{-2}d^{-1}$)
3. Canopy conversion effi encies (maximum)	3 to 3.4%	3 to 4.5%
4. Growing season efficiencies	1.4%	2.0%
F. ENZYMATIC CHARACTERISTICS		
1. Km (CO_2, HCO_3^-)	RuBPcase around 15μM	PEPcase similar?
2. Activity	Lower	Higher
3. Size	RuBPcase very large	PEPcase smaller
4. Regulation	RuBPcase complex	PEPcase complex
G. OTHER PHYSIOLOGICAL CHARACTERISTICS		
1. Translocation rate	Slow	Rapid
2. Starch accumulation	Normal in mesophyll	In PBS cells
H. CARBON DISCRIMINATION		
1. $\delta^{13}C$ value	-28 (-38‰ to -23‰)	-12.5 (-15‰ to -9‰)
I. ECOLOGICAL FEATURES		
1. Distribution		
Water	Hydric = mesic > xeric	Xeric > mesic
Irradiance	Low to high	High
Temperature	Low to high	High to moderate
Canopy	Closed	Open
2. Grazing		
Nutrient value	Variable	Lower?
Digestibility	Variable	Lower?

cells usually possess an abundance of organelles which are often centripetally or centrifugally located, thereby creating a dense concentric zone next to a transparent one, that is, a halo (='Kranz') effect. These PBS cells are surrounded by mesophyll cells, often radially arranged, which contain PEP carboxylase and no or very little RuBP carboxylase. This spatial arrangement places a highly active carboxylase enzyme, which is not inhibited

by oxygen, in contact with atmospheric pools of CO_2 and O_2 and isolates the RuBP carboxylase, which is sensitive to O_2, in a deep internal milieu. This arrangement allows a pumping system to create a CO_2-rich environment in the PBS cells.

Although Kranz anatomy, as defined above, is present in most C_4 plants, it is not essential for C_4 systems. But all C_4 plants do possess a spatial arrangement as described above. Among dicots this may take various forms. Additionally, C_4 plants possess short interveinal distances (Hattersley and Watson, 1975), with only two to four mesophyll cells between adjacent bundle sheaths, in contrast to C_3 plants with commonly as many as 12 intervening mesophyll cells. Close proximity to vascular tissue may facilitate transport of photosynthate, which is rapid in C_4 plants, or may simply reflect a requirement for effective CO_2 trapping and pumping.

It should also be pointed out that the C_4 system is differentiated into three subtypes based on the dominant mechanism of 4-carbon decarboxylation, that is via NADP malic enzyme (a malate former), NAD malic enzyme (aspartate former), or PEP carboxykinase (aspartate former). Each subtype has anatomical correlates although these are not consistent between grasses and dicots. The consequences of subtypes are not clear, although grasses possessing NADme dominate the most arid areas whereas those possessing NADPme dominate with increasing rainfall (Ellis *et al.*, 1980). Furthermore, there is some evidence supporting the hypothesis that certain subtypes are adapted to nutrient poor conditions (Tew *et al.*, 1974); and it is now known that RuBP carboxylases from the subtypes differ in Km values (Yeoh *et al.*, 1980), suggesting different selection pressures.

Physiological characteristics

Light response. Most C_4 plants possess a photosynthetic light response curve in which CO_2 uptake continues to increase to irradiances which exceed the solar constant. Thus C_4 plants appear not to become saturated with naturally occurring levels of light (Ludlow and Wilson, 1971) in contrast to C_3 plants which generally saturate at lower irradiances (Black, 1971). This generalization is clearly supported by studies of grasses. Tieszen (1970) compared light responses of C_4 and C_3 grasses in a mixed grass prairie of North America. The C_3 species saturated at lower irradiances even though they grew in the same open canopy as the C_4 grasses which tended not to saturate (see also El-Sharkawy and Hesketh, 1965; Hesketh and Baker, 1967). This generalization is supported by other data on grasses. However, when other environmental factors limit photosynthesis, for example, leaf temperature (Pearcy *et al.*, 1981) C_4 leaves do saturate; and their responses to irradiance become more similar to those of C_3 species. The effectiveness of the generally greater photosynthetic capacities in C_4 plants is realized, then, mainly under optimal growth conditions in an open canopy. It is also well established that the light response curve of many plants is strongly modified by the irradiance experienced during growth (Bjorkman *et al.*, 1972; Grahl and Wild, 1973); and some C_4 plants have dramatically lower maximum capacities, and saturation requirements (Ludlow and Wilson, 1972), when grown under low light conditions.

Because of the lower energetic requirements of C_3 photosynthesis, the efficiencies of CO_2 uptake at low irradiances are higher for C_3 plants. This is best illustrated by comparing the quantum yields (moles CO_2 taken up per Einstein absorbed). This quantum yield is greater than 0.052 moles CO_2 per Einstein in C_3 grasses at 30°C and lower temperatures. It is temperature dependent (Ehleringer and Bjorkman, 1977), however, and at higher temperatures the quantum yield of C_4 plants is greater. These differences apparently result because of the greater energetic requirement for CO_2 reduction in C_4 plants and the temperature stimulated photorespiration in C_3 plants. Thus, as temperatures increase, the loss of carbon by photorespiration becomes more important than the lower energetic requirements of C_3 reduction, and the quantum yield decreases to values below those of C_4 plants.

Temperature responses. Species which possess the C_4 pathway generally also possess higher temperature requirements for growth and photosynthesis with optima of 30 to 45°C (Black, 1971, 1973; Ludlow, 1976) in contrast to the 15 to 25°C optima characteristic of many C_3 grasses. This difference is not always clear-cut, however, since both C_3 and C_4 species show adaptations to the thermal environments they inhabit. Thus, the ability to photosynthesize and grow at high temperatures is not a unique characteristic of C_4 plants (Caldwell *et al.*, 1977a, b; Bjorkman, 1976) although most do respond favourably up to 35° or well beyond (Imbamba and Tieszen, 1977). The generalized difference between the response curves of C_3 and C_4 plants is believed to be largely due to the oxygen inhibition of CO_2 uptake and the temperature effect on oxygen inhibition (Bjorkman, 1976; Pearcy, 1977; Tieszen, 1973). The general ability of many tropical plants (C_3 or C_4) to tolerate high temperatures is not related to differences in the temperature characteristics of carboxylating enzymes (Tieszen and Sigurdson, 1973; Bjorkman and Badger, 1977). It is unclear, however, to what extent major differences in the temperature response curves result from basic differences engrained in the photosynthetic systems. They may simply reflect a general adaptation to tropical and subtropical temperature regimes rather than a unique feature of the pathways.

CO_2 concentration. The net effect of PEP carboxylase serving as the primary carboxylase enzyme and of decarboxylation in the PBS cells is to create a system capable of high rates of photosynthesis even at low intercellular CO_2 concentrations (Bjorkman *et al.*, 1976). Thus, photosynthesis as a function of CO_2 concentration shows a different response curve in C_4 plants than in C_3 plants. C_4 plants possess a net positive uptake of CO_2 down to concentrations approaching 0 ppm. The slope is independent of O_2 concentrations, as we would expect, in the absence of photorespiration. The slope is also greater in C_4 plants. In most species so far examined C_3 and C_4 plants saturate with respect to CO_2 at different concentrations. Most C_3 plants retain a linear response to concentrations much higher than ambient CO_2 levels, for example, 1000 to 2000 ppm. C_4 plants, however, become saturated at CO_2 concentrations only slightly higher than ambient levels. Thus, at higher CO_2 levels, C_3 plants photosynthesize at rates

greater than C_4 plants due to a reduction in photorespiration and an enzyme system which does not saturate.

Water requirements. The availability of water affects plant growth and productivity by affecting stomatal and mesophyll conductances as well as by its influence on growth and dry matter distribution. It is now clearly established that C_4 plants have higher water use efficiencies (g CO_2 taken up per g H_2O lost) as Schantz and Piemeisel's (1927) production data from many years ago illustrate. This has led to the suggestion that C_4 plants have lower stomatal conductances. However, the difference in water use efficiency is due nearly entirely to the higher photosynthetic rates of C_4 plants (Ludlow and Wilson, 1972; Ludlow, 1975). Körner *et al.* (1979) have recently reviewed maximum conductance values among a wide range of C_3 and C_4 growth forms. They indicate that maximum conductances are equal in C_4 grasses and C_3 grasses. Thus, it appears that both C_3 and C_4 plants have the capability of reducing stomatal resistance to equivalent levels. Total water loss per unit of leaf area, then, under similar conditions should be the same for both photosynthetic types. The higher water use efficiencies of C_4 plants result only from their high mesophyll conductances. The data of Ludlow and Wilson (1972) suggest that this relationship holds even for mature stands although this comparison was between C_4 grasses and C_3 legumes. In a closed canopy water use efficiencies should become comparable, since the higher potential photosynthetic rates of C_4 plants are not achieved as self-shading becomes sufficient.

Ludlow (1975) provides a general review of water potentials in C_3 and C_4 plants. In essence, variations in the response of growth, stomatal conductance, and so on are related more to environmental conditions in which species are found than they are to photosynthetic systems. Ludlow indicates that *Panicum maximum* at moderate leaf water potentials (-6 to -8 bars) behave much like C_3 plants and possess low photosynthetic capacities and low light requirements for saturation. On the basis of biochemical evidence, however, it appears that as gross photosynthesis decreases in water-stressed C_4 plants there is a relative increase in photorespiratory losses. This is also detected at the physiological level as an increase in non-stomatal resistance. In C_4 plants, however, the decrease of net photosynthesis with water stress appears due mainly to an increased stomatal diffusion resistance.

Mineral nutrient requirements. Nutrient quality of vegetation varies greatly for many reasons. Literature comparisons (for example, Crampton and Harris, 1969) often suggest that the nutrient quality of C_3 plants is inferior to that of C_4 plants. This led Caswell *et al.* (1973) to suggest the hypothesis that C_4 herbage was of lower nutrient quality than C_3 herbage and tended to be avoided by insect herbivores. Although many of the broad comparisons of nutrient quality support this generalization, it must be accepted with caution since the comparisons are rarely made with developmentally equivalent plant structures or under comparable environments. Wilson and Ford (1971), for example, showed that varieties of ryegrass have nitrogen contents at low growth temperatures similar to those of *Panicum* and *Setaria*.

Only at higher temperatures did the C_4 species possess significantly lower N concentrations. This reduction, however, may have been caused by a dilution effect of the growth and leaf turnover in the C_4 grasses.

From a physiological or biochemical basis, lower N requirements for C_4 grasses are not surprising, since the high carboxylating activities of C_4 plants require less investment in RuBP carboxylase. Lower concentrations of P and other soluble nutrients could also be associated with the C_4 system. The situation with respect to other nutrients, however, is not as clear. Calcium, mainly a constituent of the wall, might be expected in equivalent or even higher concentrations in C_4 plants.

C_4 plants appear to differ qualitatively from most C_3 plants by virtue of what appears to be an obligate requirement for sodium (Brownwell and Crossland, 1972) as a micronutrient. Although few species have been tested, this requirement pervades all families. It is not known if Na has an intimate role in specific biochemical reactions of the C_4 systems, or if Na represents a general requirement reflecting an arid (and high Na) origin.

The best indications of a nutritional difference is that provided by direct experimental comparisons. Brown (1978) has shown that C_4 grasses have a higher nitrogen use efficiency than C_3 grasses. Furthermore, his analysis illustrates that C_3 grasses possess greater N stresses at equivalent N concentrations than do C_4 grasses. Comparisons among dicots, however, do not illustrate marked differences among photosynthetic types (see Brown, 1978). In Kenya, Imbamba (1973) indicates that a number of C_4 dicots have high N contents and are, in fact, used as leafy vegetables. It is not clear, however, if these species were selected as vegetables because of high protein levels or if this characteristic developed later.

Isotope discrimination. Differences in the discrimination against ^{13}C between C_3 and C_4 plants are consistent and of fundamental importance. C_4 plants are richer in the stable isotope, ^{13}C, than C_3 plants (Hatch and Slack, 1970; Lerman, 1975). This difference is now well established and stems mainly from the different discrimination of the primary carboxylase enzymes (Whelen *et al.*, 1973; Deleens *et al.*, 1974; Deleens, 1976). Both PEP and RuBP carboxylase discriminate against ^{13}C but PEP carboxylase discriminates less. In a C_4 plant the RuBP utilizes a closed pool of CO_2 (provided by PEP carboxylase) and therefore cannot discriminate further in this system.

The magnitude of the discrimination is represented by $\delta^{13}C$ values as determined mass spectrometrically from combustion and collected CO_2 samples.

$$\delta^{13}C(‰) = \left| \frac{^{13}C/^{12}C \text{ (sample)}}{^{13}C/^{12}C \text{ (standard)}} - 1 \right| \times 1000$$

Atmospheric CO_2 has a $\delta^{13}C$ value around -7‰ (all relative to the PBD standard). C_3 plants discriminate against ^{13}C to produce a $\delta^{13}C$ value around -28 and C_4 plants, which discriminate less, cluster around a $\delta^{13}C$ of -12.5 (Smith, 1976; Smith and Brown, 1973; Smith and Turner, 1975). These values are generally similar

for each photosynthetic type regardless of taxonomic group. The major exception to these two clusters results from species with CAM metabolism or, in a few cases, from so-called intermediates.

To be of substantial ecological use, however, it must be demonstrated that the $\delta^{13}C$ is relatively independent of environmental factors (or that its dependence is known and quantified) and that subsequent fractionation (as in secondary production) is minor. Lerman (1975) stresses that caution must be exercised when comparing literature $\delta^{13}C$ ratios, since greenhouse experiments may recycle CO_2 and result in artificial ratios. Smith *et al.* (1976) further indicate that there are environmental effects on the $\delta^{13}C$ values, but these are minor. We would expect secondary fractionation to be minor, since the isotopic effect on mass is small. This predictability has been verified by DeNiro and Epstein (1978a, b) and Teeri and Schoeller (1979). Thus, isotopic analyses can be used to assess, quantitatively, (Tieszen, 1978a; Tieszen *et al.*, 1979b; Tieszen and Imbamba, 1980) dependence of herbivores on C_3 or C_4 plants or the relative contributions of each system to above-ground or below-ground productivity.

CONSIDERATIONS FOR AGROFORESTRY

The selection of species to be used in agroforestry must be based on cultural and economic as well as environmental and biological factors. There are some general principles related to photosynthetic pathways to be considered in selecting species for incorporation in agroforestry systems. They can provide some perspectives when developing long-term programmes of research and application and are not intended to supplant normal criteria of adaptation and appropriateness.

Once again it is important to recognize that agroforestry systems may require species, or complementary associations of species, which possess different adaptive responses or environmental requirements from those characteristic of energy intensive agricultural systems. The North Temperate zone heritage is largely based on C_3 grass cereals and has emphasized production or yield at the expense of high nutrient and water requirements and, in fact, perhaps at low energetic efficiencies. Agroforestry systems may place less emphasis on yield and more on efficient resource utilization (see Vose, 1981) as well as sustainability.

Most agroforestry systems will likely rely on local species already somewhat adapted to local environmental conditions. And they may be selected not only on the basis of their production or yield but also on the efficiency of energy conversion or resource utilization. Thus, each situation will be different and needs to be evaluated in its own context. This makes generalizations difficult.

Photosynthetic rates, production, and yield

It is clear that the photosynthetic capacity or potential is only one of many plant characteristics which determine ultimate production or yield. As such, however, we would expect C_4 dominated systems to be more productive in habitats where their potential can be realized. Monteith's (1978) recent evaluation of production data and review of earlier comparisons confirm higher short-term maximum growth rates for C_4 crops in their

environments compared to C_3 crops in more temperate zones (Table 4). This difference results from the greater availability of light and the higher 'efficiency' of energy conversion by the C_4 canopy. These data suggest that under good agronomic conditions in the tropics or subtropics, C_4 monoculture systems should be more productive than C_3 monoculture systems.

I should point out, however, that high photosynthetic capacities are not exclusively the domain of C_4 plants. High photosynthetic capacities in C_3 plants demand large investments in protein (RuBP carboxylase, for example) and hence, may have high resource demands. They may also, then, be especially attractive to herbivorous pests.

Table 4. Production (dry weight) comparisons of C_3 and C_4 systems. (From Monteith, 1978.)

Group	Mean maximum growth rate		Mean seasonal growth rate	
	$g\ m^{-2}d^{-1}$	% efficiency	$g\ m^{-2}d^{-1}$	% efficiency
C_4	50 to 54	3 to 4.5	22 ± 3.6	2.0
C_3	34 to 39	3 to 3.4	13 ± 1.6	1.4

Growing season

A further examination of Table 4 reveals that the advantage of a C_4 system is still greater than a C_3 system when the production is relative to total season length. This may reflect the ability of C_4 plants to utilize the high leaf irradiances in younger developing canopies (of low LAI). When self-shading is minimal in tropical environments, C_4 plants should show substantially higher crop growth rates than C_3 plants. This consideration could be of great significance since often tropical growing seasons are initiated and terminated by moisture availability.

Our (Tieszen, 1978b) simulation studies in other short growing season systems clearly indicate that production is highly dependent on two things: the length of the growing season, and the rate of allocation (or of development) of carbon to leaf material. With all other things (for example, seed size, germination rate, leaf angle, and so on) equal, a C_4 canopy should develop faster and begin to utilize light more completely than a C_3 canopy.

Canopy relationships

We would expect C_4 plants, then, to be more productive under canopy conditions which expose leaves to high irradiances. Under conditions of subdued light, however, as in cloudy areas or with canopies of high LAI, we might expect C_3 and C_4 performances to be comparable. Ehleringer and Bjorkman's (1977) simulations suggest that differences in quantum yield account for the replacement of C_4 grasses by C_3 grasses as latitude increases. However, we have clear quantum yield data for relatively few species. And their simulations included other variables which operated simultaneously.

Field observations are clear. Under low irradiance conditions, C_3 plants predominate. In Kenya, for example, even at low altitudes, nearly all understorey grasses are C_3 . And in open areas where canopies of high leaf area can develop, for example in swamps, sedges and grasses (like *Phragmites*) again are often C_3. This relationship is likely the factor which is largely responsible for the near absence of C_4 species among tree growth forms. With a closed canopy, C_3 species, in fact, may be both more efficient and more productive. Certainly, during successional stages efficient and productive systems at low irradiances would be important.

This explanation, however, does not account for the absence of C_4 forms from woody species in more open systems such as savanna. Why are all legumes C_3? We don't know enough about the physiology of these species to really compare them to other C_3 or C_4 plants. The absence of C_4, however, may be explained by ultimate evolutionary pressures.

Water availability

Both C_3 and C_4 plants can show similar adaptations to water stress. Yet the high occurrence of C_4 species under warm and arid conditions (for example, Mulroy and Runderl, 1977) argues in favour of a competitive advantage for this pathway. This is also suggested by the higher water use efficiencies shown by C_4 grasses. This is accounted for, however, at the physiological level by an increase in mesophyll conductance. Thus C_4 plants, grasses at least, do not appear to conserve water by reducing maximum leaf conductances. Their greater water use efficiency stems entirely from a higher rate of CO_2 uptake for equivalent rates of water loss.

This non-conservative strategy is not unexpected in areas of high water demand, brief water availability, or only near-surface wetting. Conservation of water could result in increased water loss directly by evaporation thereby decreasing plant production. If a subsurface water source is tapped, however, a conservative approach with decreased leaf conductances (and, therefore, reduced production rates) could be exploited. The woody desert forms described by Winter (1981) are suggestive of this pattern, but nothing is known of their physiological responses or, for that matter, their productivities. Their high biomass suggests a reasonable productivity. If this proves correct some of these species may be very significant as overstorey plants in water limited systems.

Salt accumulation areas

Similarly, C_4 plants should be given serious consideration in any system where salt accumulation is a problem. We do not know whether all C_4 plants tolerate saline environments, but many certainly do. A more systematic screening of potentially useful species might be advised.

Mineral nutrients

The relationships between C_3 and C_4 systems and nutrients is highly important but least clearly known. As our earlier review indicated, C_4 grasses may have lower requirements for nutrients

Table 5. Protein contents, where available, of local C_3 and C_4 leafy vegetables in Nairobi. (From Imbamba, 1973; Imbamba and Papa, 1979.)

Species	Type	Family	% protein
Amaranthus lividus	C_4	Amaranthaceae	26.7
Amaranthus hybridus	C_4	Amaranthaceae	27.8
Gynandropsis gynandra	C_4	Capparaceae	35.8
Vigna unguiculata	C_3	Leguminosae	28.5
Crotalaria brevidens	C_3	Leguminosae	32.5
Corchorus olitorius	C_3	Tiliaceae	22.5
Brassica intergrifolia	C_3	Cruciferae	28.9
Solanum nigrum	C_3	Solanaceae	29.3
Trianthema ceratocepala	C_4	Aizoaceae	
Aerva lanata	C_4	Amaranthaceae	
Alternanthera peploides	C_4	Amaranthaceae	
Gomphrena globosa	C_4	Amaranthaceae	
Atriplex halimus	C_4	Chenopodiaceae	
Kochia scoparia	C_4	Chenopodiaceae	
Boerhavia diffusa	C_4	Nyctaginaceae	
Portulaca quadrifida	C_4	Portulacaceae	
Tribulus terrestris	C_4	Zygophyllaceae	

than C_3 grasses. In our mixed prairie system in the United States of America, this results in different microdistributions for these two groups. C_3 grasses occupy resource rich areas (Tieszen *et al.*, 1981) and C_4 grasses occupy resource limited areas; especially dry sites low in N and P. This results in the seemingly incongruous situation in which our communities dominated by C_4 grasses have lower productivities than those dominated by C_3 grasses.

The lower nutrient requirements make C_4 grasses the species of choice where nutrients may be scarce. Obviously, however, fewer nutrients are then available in the ensuing forage. Comparisons among seeds or other useful parts have not been made. The expected low nutrient status of leaves decreases their value for human or animal consumption. But it may increase their value if used for fuel either directly or indirectly, since nutrient losses from the system are minimized.

The situation with dicot vegetables is not at all clear. Imbamba has shown that a number of local vegetables are in fact C_4 (Table 5) and some of these have very high protein or N contents. If C_4 dicots do depart from the grass generalizations, they may be more important as high quality and highly productive vegetable components in agroforestry systems. We must remember, however, that these analyses were performed on plants which may have experienced considerable selection pressure. Regardless, they do then reveal the potential for increasing nutrient levels.

It is tempting to consider greater exploitation of C_4 dicots as leafy vegetables. Their value, however, will likely be greatest in open or semi-open situations. Under closed canopies, our more traditional C_3 forms should be exploited.

Perhaps one other feature related to nutrient status should

be mentioned. The generally inferior nutrient quality may result in reduced herbivore pressure on C_4 plants, especially in mixed systems. This has been demonstrated in some instances (Boutton *et al.*, 1980) as Figure 4 shows.

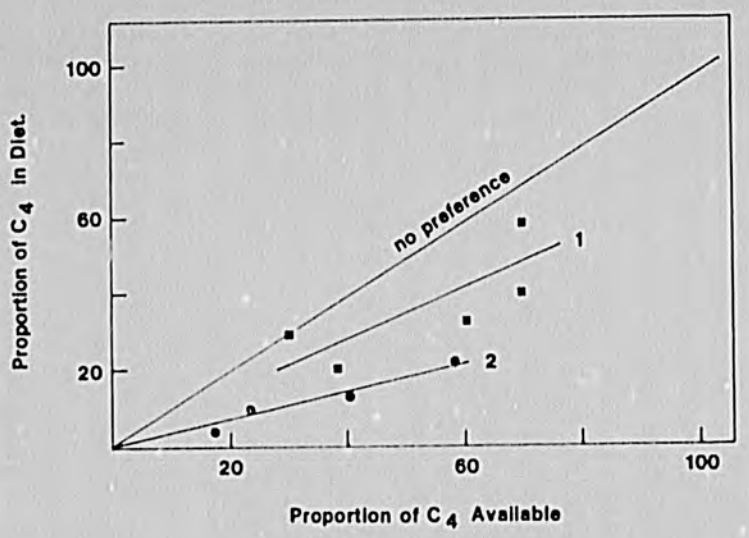


Fig. 4. Dietary selection among C_3 and C_4 species of grass as a function of availability by two species of grasshopper. Data points to the right of no preference indicate preference for C_4. A slope less than 1 indicates that preference is greater as the abundance of C_4 increases.

Mixed agroforestry systems

In considering appropriate combinations of species, from the point of view of their photosynthetic system, we need to distinguish the annual or seasonal canopy type from the 'permanent' overstorey type. In the annual or seasonal type it is usually imperative to establish a high LAI as quickly as possible and C_4 plants should be included in suitable environments. Maize, sorghum, millets, sugarcane and other grass cereals are likely candidates. In the understorey, C_4 annuals should perform well in the early stages of canopy development, especially as leafy vegetables. In later stages C_3 dicots would likely need to replace C_4 dicots, although we do not know much about C_4 dicot responses. When available C_4 species could, with advantage, also form the upper levels of the canopy where high irradiances can be utilized more effectively.

If resources are strongly limiting, or available for only a brief period, it may not be possible to attain a high LAI. Physiologically, a C_4 system should outperform C_3 plants by a substantial margin under these conditions. Therefore, we should try to incorporate C_4 plants of whatever growth form under these conditions.

In conditions with a permanent woody overstorey our options seem more limited. Very few of the families with woody species of interest possess any C_4 species. Members of the Fabaceae, for

example, all appear to be C_3. Thus, under reasonably mesic conditions our overstorey species will be C_3. And, if shading is significant, our understorey options may be foreclosed as well; C_3 plants will be required. If, however, the overstorey is open C_4 types, including both dicots and some grasses, could be interspersed in the understorey.

When resources are more limiting, we should consider the use of C_4 woody species as overstorey forms even though only few are available. Nevertheless, as Winter (1981) indicates, where these forms occur a number serve very important economic functions. Since one of our objectives is to develop appropriate agroforestry systems, and since these may be especially important in resource limited areas, we need to know more about these woody forms. If they retain the general features of low nutrient content, relatively high productivity and water use efficiency, enhanced herbivore avoidance, and so on, they should become especially important in systems using them for fuel or biomass.

Realities of C_4 exploitation

It is now well known that many grass cereals in the tropics are C_4, and these and other grasses (for example, maize, sugarcane, sorghum and millets) will certainly play an important role in future development. We should not ignore, however, the large number of local grains which are not receiving international support but which are of great local importance. In Eastern Africa finger millet (*Eleusine coracana*) and tef (*Eragrostis tef*) are excellent examples of well-adapted varieties of economic importance and often of cultural preference. Other important species are (Portères, 1976); fonio millet (*Digitaria exillis*), black fonio (*Digitaria iburua*), animal millet (*Brachiaria* spp.), and various species of *Paspalum* and *Pennisetum*. It is unlikely, however, that more C_4 species will be developed or are necessary.

The situation with respect to C_4 dicots is again quite different. With the possible exception of *Amaranthus* I know of no C_4 vegetable of widespread use. Yet in East Africa a number of species are of local importance; and this local dependency may be of more general occurrence in other tropical areas. These species appear often to be annuals and to be derived from open, perhaps disturbed, habitats. Many are certainly from, or close relatives of, species adapted to arid or semi-arid areas. Thus, their greatest potential is likely in similar environments.

Relatively few of the woody shrubs or trees are C_4 and I suspect that further searches will reveal few C_4 species with the exception of those families already known to possess C_4 species and occupying desert environments (Winter, 1981). Further studies will likely reveal a few more woody species adapted to desert or saline environments and these need to be considered for exploitation.

RECOMMENDATIONS

We might, therefore, summarize some recommendations as follows.

- Catalogue all known woody C_4 forms and describe their environmental requirements and potential economic importance.
- Document all known C_4 dicot vegetables or other economically

important forms.

- Establish the photosynthetic capacities, productivities, nutrient contents, and water requirements of C_4 dicot vegetables and related species.
- Summarize the local uses of C_4 grasses as cereals or for other economic purposes.
- Prepare lists of appropriate C_3 and C_4 species for various roles in agroforestry systems in various environments.
- Identify important grass micro-organism associations for potential exploitation as nitrogen fixers.

ACKNOWLEDGMENTS

The work on which this paper is based was supported by research grants from the NSF (DEB-7819552 and INT76-82012) and by a William and Flora Hewlett Foundation Grant of Research Corporation. The Kenya work was made possible by close co-operation with Dr Simeon K. Imbamba, University of Nairobi.

REFERENCES

Bjorkman, O. (1976). Adaptive and genetic aspects of C_4 photosynthesis. *In* "CO_2 Metabolism and Plant Productivity" (R.H. Burris and C.C. Black, eds), pp.287-309. Univ. Park Press, Baltimore, Md, USA.

Bjorkman, O. and Badger, M. (1977). Thermal stability of photosynthetic enzymes in heat and cool adapted C_4 species. *Carnegie Inst. Washington Yearbook* 75, 346-354.

Bjorkman, O., Boardman, N.K., Anderson, J.M., Thorne, S.W., Goodchild, D.J. and Pyliotis, N.A. (1972). Effect of light intensity during growth of *Atriplex patula* on the capacity of photosynthetic reactions, chloroplast components and structure. *Carnegie Inst. Washington Yearbook* 71, 115.

Bjorkman, O., Mooney, H. and Ehleringer, J. (1976). Photosynthetic characteristics of plants from habitats with contrasting thermal regimes: comparisons of photosynthetic responses of intact plants. *Carnegie Inst. Washington Yearbook* 74, 743-748.

Black, C.C. (1971). Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. *Adv. Ecol. Res.* 7, 87-114.

Black, C.C. (1973). Photosynthetic carbon fixation in relation to net CO_2 uptake. *Ann. Rev. Plant Physiol.* 24, 253-286.

Boutton, T.W., Smith, B.N. and Harrison, A.T. (1980). Carbon isotope ratios and crop analyses of *Arphia* (Orthoptera: acrididae) species in southeastern Wyoming grassland. *Oecologia* 45, 299-306.

Brown, R.H. (1978). A difference in N use efficiency in C_3 and C_4 plants and its implications in adaptation and evolution. *Crop Sci.* 18, 93-98.

Brown, W.V. (1975). Variations in anatomy, associations, and origins of Kranz tissue. *Amer. J. Bot.* 62, 395-402.

Brown, W.V. (1977). The Kranz syndrome and its subtypes in grass systematics. *Mem. Torrey Botan. Club* 23 (January).

Brownwell, P.F. and Crossland, C.J. (1972). The requirement for sodium as a micronutrient by species having the C_4 dicarboxylic photosynthetic pathway. *Plant Physiol.* 49, 794-797.

Caldwell, M.M., Osmond, C.B. and Nott, D.L. (1977a). C_4 pathway photosynthesis at low temperature in cold tolerant *Atriplex* species. *Plant Physiol.* 60, 157-164.

Caldwell, M.M., White, R.S., Moore, R.T. and Camp, L.B. (1977b). Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species. *Oecologia* 29, 275-300.

Caswell, H., Reed, F., Stephenson, S.N. and Werner, P.A. (1973). Photosynthetic pathways and selective herbivory: a hypothesis. *Am. Nat.* 107, 465-481.

Crampton, E.W. and Harris, L.E. (1969). "Applied Animal Nutrition." W.H. Freeman and Co., San Francisco.

Deleens, E. (1976). Discrimination of ^{13}C and three types of metabolism of plants C_3 and C_4, crassulacean acid metabolism. *Physiol. Veg.* 14, 641-656.

Deleens, E., Lerman, J.C., Nato, A. and Moyse, A. (1974). Carbon isotope discrimination by the carboxylating reactions in C_3, C_4 and CAM plants. *Proc. 3rd Intern. Congress Photosyn.* (A.M. Rehovof, ed.), pp.1267-1276. Elsevier, Amsterdam.

DeNiro, M.J. and Epstein, S. (1978a). Carbon isotopic evidence for different feeding patterns in two Hyrax species occupying the same habitat. *Science* 201, 906-908.

DeNiro, M.J. and Epstein, S. (1978b). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42, 495-506.

Ehleringer, J. and Bjorkman, O. (1977). Quantum yields for CO_2 uptake in C_3 and C_4 plants: dependence on temperature, CO_2 and O_2 concentrations. *Plant Physiol.* 59, 86-90.

Ellis, R.P., Vogel, J.C. and Fuls, A. (1980). Photosynthetic pathways and the geographical distribution of grasses in Southwest African Namibia. *S. Afr. J. Sci.* 76, 307-314.

El-Sharkawy, M. and Hesketh, J. (1965). Photosynthesis among species in relation to characteristics of leaf anatomy and CO_2 diffusion resistances. *Crop Sci.* 5, 517.

Grahl, H. and Wild, A. (1973). Lichtinduzierte Veränderungen im Photosyntheses-Apparat von *Sinapis alba*. [Light induced changes in the photosynthetic apparatus of *Sinapis alba*.] *Ber. Deut. Bot. Ges.* 86, 341.

Hatch, M.D. and Slack, C.R. (1970). Photosynthesis CO_2-fixation pathways. *Ann. Rev. Plant Physiol.* 21, 141.

Hattersley, P.W. and Watson, L. (1975). Anatomical parameters for predicting photosynthetic pathways of grass leaves: the 'maximum lateral cell count' and the 'maximum cells distant count'. *Phytomorphology* 25, 325-333.

Hesketh, J. and Baker, D. (1967). Light and carbon assimilation by plant communities. *Crop Sci.* 7, 285.

Imbamba, S.K. (1973). Leaf protein content of some Kenya vegetables. *East Afr. Agric. & Forestry J.* 38, 246-251.

Imbamba, S.K. and Papa, G. (1979). Distribution of the Kranz type anatomy in some dicotyledonous families of Kenya. *Photosynthetica* 13, 315-322.

Imbamba, S.K. and Tieszen, L.L. (1977). Influence of light and temperature on photosynthesis and transpiration in some C_3 and C_4 vegetable plants from Kenya. *Physiol. Plant.* 39, 311-316.

Kennedy, R.A., Eastburn, J.L. and Jensen, K.G. (1980). C_3-C_4

evolution of intermediate characteristics. *Amer. J. Bot.* 67, 1207-1217.

Körner, C.H., Scheel, J.A. and Bauer, H. (1979). Maximum leaf diffusive conductance in vascular plants. *Photosynthetica* 13, 45-82.

Lerman, J.C. (1975). How to interpret variations in the carbon isotope ratio of plants: biologic and environmental effects. *In* "Environmental and Biological Control of Photosynthesis" (R. Marcelle, ed.), pp.1267-1276. W. Junk, The Hague.

Long, S.P., Incoll, L.C. and Woolhouse, H.W. (1975). C_4 photosynthesis in plants from cool temperate regions, with particular reference to *Spartina townsendii*. *Nature* 257, 622-624.

Ludlow, M.M. (1975). Effect of water stress on the decline of leaf net photosynthesis with age. *In* "Environmental and Biological Control of Photosynthesis" (R. Marcelle, ed.), pp. 123-134. W. Junk, The Hague.

Ludlow, M.M. (1976). Ecophysiology of C_4 grasses. *In* "Ecological Studies, Analysis and Synthesis", Vol. 19 (O.L. Lange *et al.*, eds), pp.364-386. Springer Verlag.

Ludlow, M.M. and Wilson, G.L. (1971). Photosynthesis of tropical pasture plants. I. Illuminance, carbon dioxide concentration, leaf temperature, and leaf - air vapour pressure difference. *Aust. J. biol. Sci.* 24, 449-470.

Ludlow, M.M. and Wilson, G.L. (1972). Photosynthesis of tropical pasture plants. IV. Basis and consequences of differences between grasses and legumes. *Aust. J. biol. Sci.* 25, 1113-1145.

May, R.M. (1981). The world's worst weeds. *Nature* 290, 85-86.

Monteith, J.L. (1978). Reassessment of maximum growth rates for C_3 and C_4 crops. *Expl Agric.* 14, 1-5.

Mulroy, T.W. and Rundel, P.W. (1977). Annual plants: adaptations to desert environments. *BioScience* 27, 109-114.

Ode, D., Tieszen, L.L. and Lerman, J.L. (1980). The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. *Ecology* 61, 1304-1311.

Pearcy, R.W. (1977). Acclimatization of photosynthetic and respiratory carbon dioxide exchange to growth temperature in *Atriplex lentiformis* (Torr.) Wats. *Plant Physiol.* 59, 795-799.

Pearcy, R.W. and Troughton, J. (1975). C_4 photosynthesis in tree form *Euphorbia* species from Hawaiian rainforest sites. *Plant Physiol.* 55, 1054-1056.

Pearcy, R.W., Tumosa, N. and Williams, K. (1981). Relationships between growth, photosynthesis and competitive interactions for a C_3 and a C_4 plant. *Oecologia* 48, 321-326.

Portères, R. (1976). African cereals: *Eleusine*, 'Fonio', 'Black Fonio', 'Teff', *Brachiaria*, *Paspalum*, *Pennisetum*, and African Rice. *In* "Origins of African Plant Domestication" (J.R. Harlan, J.M.J. de Wet and A.B.L. Stemler, eds), pp.409-452. Mouton Publishers, The Hague.

Rundel, P.W. (1980). The ecological distribution of C_4 and C_3 grasses in the Hawaiian Islands. *Oecologia* 45, 354-359.

Shantz, H.L. and Piemeisel, L.N. (1927). The water requirement of plants at Akron, Colorado. *J. Agric. Res.* 34, 1093.

Smith, B.N. (1976). Evaluation of C_4 photosynthesis. *In* "The Fractionation of Stable Carbon Isotopes by Plants. Symposium

of the Southern Section of ASSP." (C.R. Benedict, ed.), pp.5-21. Texas A.&M. Univ., College Station, Texas, USA.

Smith, B.N. and Brown, W.V. (1973). The Kranz syndrome in the Gramineae as indicated by carbon isotopic ratios. *Am. J. Bot.* 60, 505-513.

Smith, B.N. and Turner, B.L. (1975). Distribution of Kranz syndrome among Asteraceae. *Am. J. Bot.* 62, 541-545.

Smith, B.N., Oliver, J. and McMillan, C. (1976). Influence of carbon source, oxygen concentration, light intensity and temperature on $^{13}C/^{12}C$ ratios in plant tissues. *Bot. Gaz.* 137, 99-104.

Takeda, T., Ueno, O. and Agata, W. (1980). The occurrence of C_4 species in the genus Rhynchospora and its significance in Kranz anatomy of the Cyperaceae. *Bot. Mag. Tokyo* 93, 55-56.

Teeri, J.A. and Schoeller, D.A. (1979). Delta ^{13}C values of an herbivore and the ratio of C_3 to C_4 plant carbon in its diet. *Oecologia* 39, 197-200.

Teeri, J.A. and Stowe, L.G. (1976). Climatic patterns and the distribution of C_4 grasses in North America. *Oecologia* 23, 1-12.

Tew, J., Grossman, E.S., Fair, P. and Cresswell, C.F. (1974). A study of the fine structure, enzyme activities and pattern of $^{14}CO_2$ incorporation of high yield grasses from different successional stages. *Proc. Grassld Soc. Sth Afr.* 9, 95-104.

Tieszen, L.L. (1970). Photosynthetic properties of some grasses in eastern South Dakota. *Proc. S.D. Acad. Sci.* 49, 78-89.

Tieszen, L.L. (1973). Photosynthesis and respiration of arctic tundra grasses: field light intensity and temperature responses. *Arct. Alp. Res.* 5, 239-251.

Tieszen, L.L. (1978a). Carbon isotope fractionation in biological material. *Nature* 276, 97-98.

Tieszen, L.L. (1978b). Photosynthesis in the principal Barrow, Alaska, species: a summary of field and laboratory response. *In* "Vegetation and Production Ecology of an Alaskan Arctic Tundra" (L.L. Tieszen, ed.), pp.241-268. Springer-Verlag, New York.

Tieszen, L.L. and Imbamba, S.K. (1980). Photosynthetic systems, carbon isotope discrimination and herbivore selectivity in Kenya. *Afr. J. Ecol.* 18, 237-242.

Tieszen, L.L. and Sigurdson, D.C. (1973). Effect of temperature on carboxylase activity and stability in some Calvin Cycle grasses from the Arctic. *Arct. Alp. Res.* 5, 59-66.

Tieszen, L.L., Senyimba, M.M., Imbamba, S.K. and Troughton, J.H. (1979a). The distribution of C_3 and C_4 grasses and delta ^{13}C values along an altitudinal gradient in Kenya. *Oecologia* 37, 337-350.

Tieszen, L.L., Hein, D., Qvortrup, A.A., Troughton, J.H. and Imbamba, S.K. (1979b). Use of delta ^{13}C values to determine vegetation selectivity in East African herbivores. *Oecologia* 37, 351-359.

Tieszen, L.L., Ode, P.J., Barnes, P.W. and Bultsma, P.M. (1983). Seasonal variation in C_3 and C_4 biomass at the Ordway Prairie and selectivity by bison and cattle. *Proc. 7th North Amer. Prairie Conf.* (in press).

Vose, P. (1981). Crops for all conditions. *New Scientist* 89, 688-690.

Whelan, T., Sackett, W.M. and Benedict, C.R. (1973). Enzymatic fractionation of carbon isotopes by phosphoenolpyruvate carboxylase from C_4 plants. *Plant Physiol.* 51, 1051-1054.

Wilson, J.R. and Ford, C.W. (1971). Temperature influences on the growth, digestibility, and carbohydrate composition of two tropical grasses, *Panicum maximum* var. *trichoglume* and *Setaria sphacelata*, and two cultivars of the temperate grass *Lolium perenne*. *Aust. J. Agric. Res.* 22, 563-571.

Winter, K. (1981). C_4 plants of high biomass in arid regions of Asia: occurrence of C_4 photosynthesis in Chenopodiaceae and Polygonaceae from the Middle East and USSR. *Oecologia* 48, 100-106.

Yeoh, H., Badger, M.R. and Watson, L. (1980). Variations in K_m (CO_2) of Ribulose-1,5-bisphosphate carboxylase among grasses. *Plant Physiol.* 66, 1110-1112.

Ziegler, H., Batanouny, K.H., Sankhla, N., Vyas, O.P. and Stichler, W. (1981). The photosynthetic pathway types of some desert plants from India, Saudi Arabia, Egypt and Iraq. *Oecologia* 48, 93-99.

DISCUSSION

LAMPREY - Is it likely that a particular, highly salt tolerant forb (not named) in Northern Kenya could be a C_4 plant?

TIESZEN - As I indicated, C_4 systems are adaptive under conditions in which internal leaf CO_2 becomes limiting. These conditions occur when light is abundant and stomatal closure occurs. This is common in water stressed plants, and therefore in plants growing in areas of salt accumulation. This includes members of the Chenopodiaceae. Your species would have to be tested.

ALVIM - Can any shade tolerant species be C_4 plants?

TIESZEN - Both C_3 and C_4 species show varying degrees of shade tolerance but in East Africa all the grasses examined from open canopy systems at low altitude were found to be C_4. In closed forest systems all the grass species were C_3, although some C_4 grasses grow at the forest edge (for example, some species of *Setaria*).

BUDOWSKI - Is the capacity for leaf movement an important factor in considering photosynthetic systems?

TIESZEN - Solar tracking by leaves is a very common phenomenon in both C_3 and C_4 species. It is highly developed among some annual species which occur in habitats characterized by short growing seasons and low leaf area indices. In water stressed systems leaves often minimize the interception of solar radiation.

LEDIG - Data from Pearcy related to Calvin's[1] work suggest that

---

1. Calvin, M., Nemetry, E.K., Redenbaugh, K. and Otvos, J.W. (1981). Plants can be a direct fuel source. *Petroculture J.* 2, 26-28. (Reprinted in *Biologist* 29, 145-148, 1982.)(*Ed.*)

some tree euphorbias in Hawaii are C_4. These may be important for the production of secondary compounds ('fuel' plants).

LOOMIS - The values of output reported by Calvin from these plants cannot be theoretically accounted for.

TIESZEN - I am unable to account for Calvin's production data from CAM euphorbias either.

DRY MATTER PRODUCTION AND EFFICIENCY IN VARIOUS TYPES OF PLANT CANOPIES

*T. KIRA and †A. KUMURA
*Department of Biology, Osaka City University, Osaka, Japan
†Department of Agronomy, University of Tokyo, Tokyo, Japan.

ABSTRACT. Different types of plant canopy are compared with respect to their dry matter productivity, with an emphasis on forest canopies. Properties such as the type of photosynthetic metabolism, rate of net photosynthesis in leaves, leaf area density, the aggregated arrangement of leaves, evergreenness and stand age are considered.

Limited available data suggest that forest communities tend to have not only a larger leaf area index but a higher efficiency of solar energy conversion to gross production than natural herbaceous communities. The ratio of net to gross production is, however, greater in herbaceous communities, so that the efficiency of net production may differ little between the two canopy types, being mostly between 0.5 and 1 per cent. Net production efficiency can be raised to 1.5 per cent in intensively managed crop fields, although the net to gross production ratio is likely to remain more or less the same. C_4 crops tend to have much higher efficiencies for both net and gross production.

The poverty of existing knowledge about the characteristics and performance of mixed multispecies canopies needs to be remedied if agroforestry systems are to be designed and managed optimally. Meanwhile we have to fall back on a more theoretical approach to the behaviour of crop mixtures and a brief account of Ogawa's yield diagrams for these is given.

INTRODUCTION

Information on the photosynthetic performance of plant canopies is now available due, especially, to the concentrated efforts made during the period of the International Biological Programme from 1965 to 1974 (Eckardt, 1968; Duvigneaud, 1971; Cooper, 1975; Lieth and Whittaker, 1975; Murata, 1975; Numata, 1975; Shidei and Kira, 1977; Kira *et al.*, 1978; Monsi and Saeki, 1978).

However, our present knowledge is still limited in both quality and quantity, giving only a general idea about the distribution of organic matter productivity among different kinds of plant canopies. Furthermore, reports are often based on different techniques, making exact comparisons difficult. Tropical examples are poorly documented even though the information is keenly needed to establish new ways of land use, including agroforestry.

This paper is a tentative review of the comparative productivity of different plant canopies, based on the limited, available information. It is oriented more to general trends than to detailed considerations. Emphasis is laid on the study of arboreal canopies, which is still much behind the study of herbaceous crop canopies.

FACTORS AFFECTING THE PRODUCTIVITY OF PLANT CANOPIES

Types of photosynthetic process

The advantage of C_4 plant canopies over C_3 canopies in their photosynthetic production is widely accepted, though not without some doubts. According to Gifford (1974), there is a wide difference between C_4 and C_3 plants in the efficiency of biochemical carbon fixation (see also Tieszen, this volume), but the difference tends to be less pronounced in the performance of single leaves, and is said to disappear almost completely when the dry matter production by a whole canopy is compared. He ascribed this trend mainly to the greater gas phase resistance in C_4 leaves and their low carbon fixation capacity under the low light levels that may prevail in field conditions. Though Gifford's point contains considerable truth, there is concrete evidence that C_4 canopies can produce more organic matter than C_3 canopies.

Ishii and Murata (1978), for instance, compared the maximum production of various crops in terms of the mean crop growth rate (CGR = rate of dry matter production) over the whole growing period to obtain the result shown in Figure 1. Apparently C_4 crops are much more productive than C_3 crops as far as their maximum yield records are concerned. The same conclusion may be drawn from the Japanese IBP experiments (Murata, 1975), in which maize (C_4, Gramineae) always proved to have a higher CGR and efficiency of solar energy utilization than rice (C_3, Gramineae) under the same conditions at various locations in Japan.

The maximum net production rate for C_3 canopies of 40 to 50 tonnes $ha^{-1}yr^{-1}$ is most probably reached by plantations of so-called 'fast growing trees' in the tropics, though few exact estimates are available. Corresponding maxima for C_4 canopies are twice as large; for example, 96 t $ha^{-1}yr^{-1}$ in napier grass (*Pennisetum purpureum*) (Puerto Rico) and 78 t $ha^{-1}yr^{-1}$ in sugar cane (Hawaii).

However, this does not mean that C_4 canopies are always highly productive. Certain C_3 plants such as sunflower are often as productive as C_4 plants. In some cases, genetic differences in other physiological characters than photosynthetic pathways may become more important.

Interspecific difference in photosynthetic rates

Remarkable differences in leaf photosynthetic rates do exist not

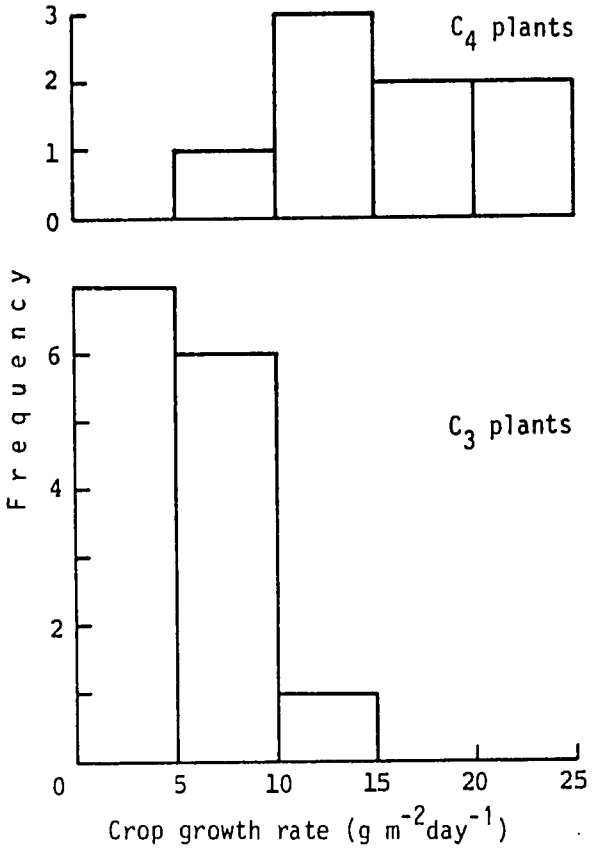


Fig. 1. Frequency distribution of crop growth rate averaged over the whole growing season in various crops. Maximum yield records for respective crops were used for the calculation. Drawn from the table by Ishii and Murata (1978).

only in well-known cases of herbaceous plants but also in trees, which are all C_3 plants. In his study on the photosynthetic rate of trees in a lowland rainforest of peninsular Malaysia, Koyama (1978) found remarkable differences among the species tested in the rate of net photosynthesis of sunleaves at light saturation. Typical large trees of the top layer of undisturbed forest stands, such as *Dipterocarpus* spp. and *Shorea* spp., had rates of 10 to 15 mg CO_2 dm^{-2} (leaf area) hr^{-1}, which are approximately equivalent to those of temperate trees (Larcher, 1980). On the other hand, higher rates ranging between 20 and 25 mg CO_2 dm^{-2} hr^{-1} were obtained in such small pioneer trees as *Macaranga hypoleuca*, *Mallotus paniculatus* and *Glochidion* sp. that colonized bare grounds immediately after tree felling. These species are the ecological equivalents of the American *Cecropia* spp., also known for their high photosynthetic rates (Stephens and Waggoner, 1970), and the African *Musanga cecropioides*. These species grow very rapidly, although they are very short-lived and have light wood of little economic value.

It is interesting to note that the highest rate of 25 to 30 mg CO_2 $dm^{-2}hr^{-1}$ was measured in leaves of *Shorea leprosula*. This

is also a light demanding secondary forest species, characterized by a high growth rate in its initial growth stages, but it lives much longer and is frequently found as a large tree in mature rainforest stands.

The secondary succession in tropical rainforest districts starts usually with a dense growth of short-lived pioneer trees, and passes through a long, intermediate stage or stages of mixed secondary forest before the final stationary phase is reached. There seems to be a general trend along this course of secondary succession toward bigger tree size, heavier wood, longevity, slower growth rate and lower assimilation rate. As shown by the example of *S. leprosula*, certain species of the intermediate stage may have both high rates of photosynthesis and growth, and large stems of good timber quality. Most of the so-called fast growing species used for tropical tree plantations appear to belong to this ecological group, except for Australian *Eucalyptus* spp. A vast extent of secondary jungle in the humid tropics thus offers a valuable gene pool from which more suitable species for agroforestry use may be found in the future.

Canopy structure

The average inclination of leaves has been recognized as an important factor influencing the efficiency of solar energy utilization in plant canopies since the classical study by Monsi and Saeki (1953; Saeki, 1960). It may also, by encouraging leaf production and/or retention in the lower part of the canopy, increase the leaf area index (LAI). Canopies consisting of erect leaves (erectophile canopies; de Wit, 1965) thus have smaller values for light extinction coefficients, greater leaf area indices and higher rates of canopy photosynthesis than planophile canopies (those with horizontally situated leaves) (Fig. 2).

Some other structural attributes are also important in the case of forest canopies. The leaf area density (LAD) is much smaller in forest than in herbaceous canopies owing to the greater plant height and resultant larger canopy depth in the former. Mean LAD values in most forest canopies range between 0.2 and 0.4 m^2m^{-3}, whereas those for herbaceous canopies amount to 2 to $4^2m\ m^{-3}$ in general (Kira *et al.*, 1969). A low LAD may favour the penetration of light into a canopy due to diffraction and result in an increase in the total LAI, and hence the total photosynthesis of the canopy. It may also serve to increase canopy photosynthesis by reducing the midday depression of atmospheric carbon dioxide concentration. The CO_2 concentration within dense herbaceous canopies is known to drop to a very low level of around 250 ppm at midday on a clear, windless day, while the daytime concentration observed in a luxuriant rainforest of Malaysia was rarely less than 300 ppm (Aoki *et al.*, 1975).

In fact, the LAI of forest canopies tends to be greater than that of herbaceous canopies. Broadleaved forests in the temperate zone of Japan show a range of LAI of 6 to 7 m^2m^{-2}, including that of undergrowth, while that of planophile herbaceous canopies rarely exceeds 5 to 6 m^2m^{-2}, even in densely planted crop fields. The aggregated distribution of tree leaves within the three-dimensional canopy space seems to play a significant role in increasing the LAI of forest canopies in addition

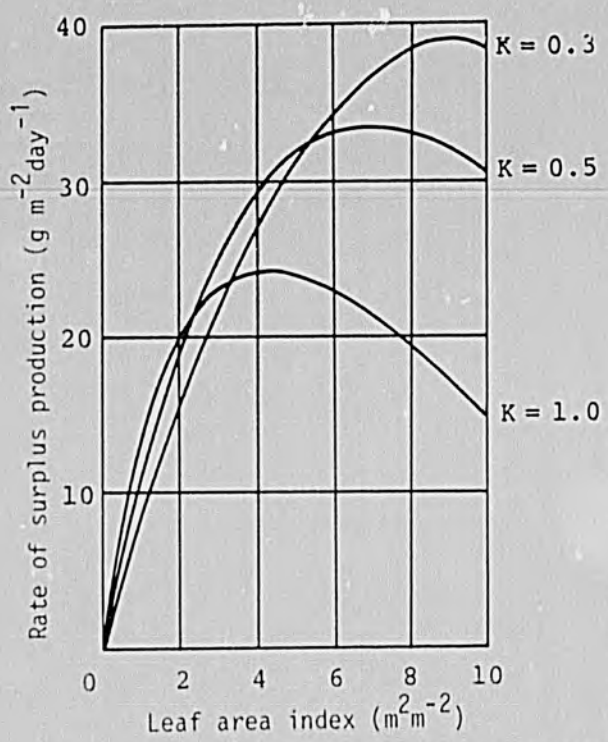


Fig. 2. Relationship between the leaf area index of a plant canopy and the rate of surplus production (gross canopy photosynthesis minus leaf respiration) for different values of light extinction coefficient (K). Redrawn from Saeki (1960).

to their small LAD. Tree leaves tend to form dense clusters on twigs, which in turn assemble to make up tree crowns and the whole forest canopy. Shinozaki developed a theory (Kira *et al.*, 1969; Shinozaki and Kira, 1977) to show that such a cluster structure could increase the total LAI held by a forest canopy to a considerable extent.

Evergreen versus deciduous leaves

Growing in the same habitat, evergreen forests almost always prove to be more productive than deciduous forests (Ovington, 1962; Kira, 1975). Summarizing the above-ground net production data in Japanese forests, Kira (1976) arrived at an average production rate of 11.15 ± 3.75 t ha^{-1}yr^{-1} (mean of 88 stands) for boreal and subalpine coniferous forests, while the corresponding average for cool, temperate deciduous broadleaved forests was 8.74 ± 3.47 t ha^{-1}yr^{-1} (55 stands) (Table 1). The evergreenness of the former forest type appears to be advantageous for its primary production in spite of the thermal climate being less favourable than that of the cool, temperate zone. The length of growing season for deciduous trees is substantially shortened, both at its beginning and end, owing to the time needed for the unfolding of new leaves and the coloration period before leaf-fall. Both times which can be utilized for positive production by evergreen leaves. This is probably the reason for the higher productivity of evergreen forests. The same relationship may

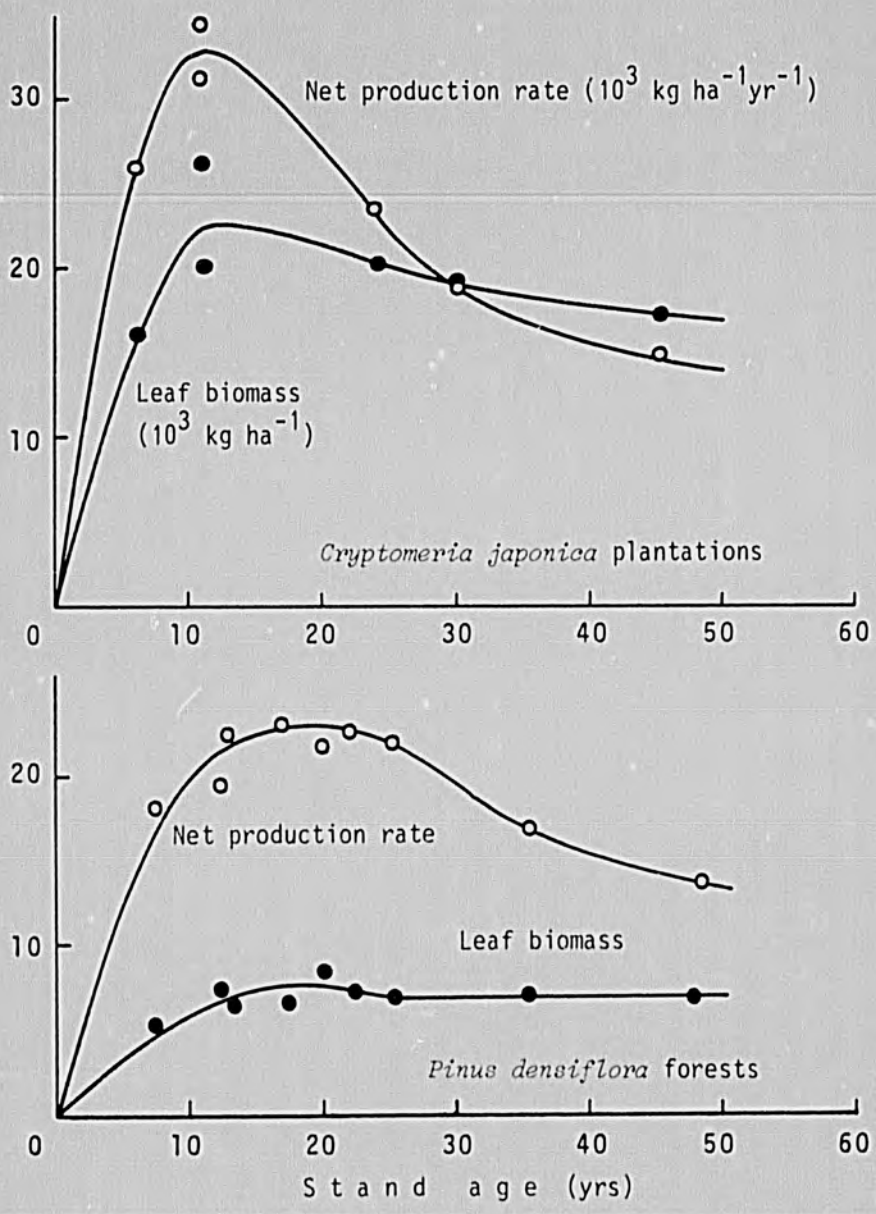


Fig. 3. Age dependent changes in leaf biomass and net production rate in even-aged forests. The leaf biomass in *Cryptomeria* includes the mass of green twigs (Kira, 1976).

also exist between drought deciduous and evergreen forests in the tropics as well as among herbaceous canopies.

Age of forest stands

A peculiar feature of forest canopies is the remarkable dependence of their net production rate on stand age. Age dependent changes in the rate of current annual growth of stem wood biomass are well known in even-aged tree plantations, and the time trend of net production rate also follows more or less the same

Table 1. Mean rates of above-ground net production (10^3 kg $ha^{-1}yr^{-1}$) in Japanese and Euro-American forests (Kira, 1976).

Forest type	Japan		Europe and N. America	
	No. of stands	Mean rate	No. of stands	Mean rate
Boreal and subalpine conifer forest	88	11.15 ± 3.75	19	9.01 ± 3.47
Cool, temperate deciduous broadleaved forest	55	8.74 ± 3.47	57	10.17 ± 2.26
Temperate conifer forest	96*	14.25 ± 5.78	5	14.96 ± 9.01
Temperate pine forest	44	13.64 ± 5.00	15	10.41 ± 5.72
Warm, temperate evergreen broadleaved forest	33	20.65± 7.21	1**	7.0

* Mostly plantations of *Cryptomeria japonica*, with some *Abies* and *Tsuga* stands. Pine forests are excluded.
**Mediterranean sclerophyll forest.

pattern. In even-aged forests and plantations, the net production rate increases at first with stand age until a maximum value is reached at the time when the canopy becomes fully closed, but thereafter it undergoes a gradual decline, as illustrated in Figure 3, although the leaf biomass tends to maintain a more or less constant level for quite a long time. The time of maximum net production rate depends on the density of trees initially planted. If the initial tree density was very high, the production rate would be maximal within only a few years. Ordinary planted stands in the temperate regions, on the other hand, may reach the stage of maximum production in 10 to 30 years unless the stands are artificially thinned.

This time trend has not yet been explained in terms of exact quantitative models. One of the main causes may be found in the increase of total community respiration due to the progressive accumulation of stems, branches and other supporting organs, as suggested by Kira and Shidei (1967). In any case, the net production rate in young forest stands may sometimes be twice as large as that in older stands of the same tree species, even where environmental conditions are not different. This is at least partly responsible for the wide variability of the net production rate within the same forest type as shown in Table 1.

The time and duration of the highest productivity stage are important points in the management of tree plantations and in agroforestry systems. An artificial time control may be possible through the change of planting density and appropriate thinnings. In this connection, however, basic studies on the time trends of net production and community respiration rates are especially needed, preferably by means of an age series of fast growing tree plantations.

ENERGY EFFICIENCY OF PRIMARY PRODUCTION IN DIFFERENT CANOPY TYPES

The efficiency of solar energy utilization offers the most reasonable measure for comparing primary productivity in different plant communities and different environments. The number and reliability of available efficiency estimates are, however, not enough to allow detailed comparisons. In addition to the difficulty involved in the exact assessment of production rates, simultaneous observations of incident solar radiation is not always available in studies on forests and other natural communities. Thus the mean solar radiation observed at a nearby meteorological station has often been used as the basis of efficiency calculation instead of synchronous *in situ* radiation data. For the time being, therefore, we have to be contented with a rough comparison between major canopy types.

The solar energy efficiency of primary production is defined here as the ratio of the energy content of organic matter produced during the growing period in a year on a unit area of land to the total short-wave solar radiation falling on the area in the same period. From the ecological standpoint, it may be more pertinent to adopt incident radiation than actually absorbed or net radiation. Using the photosynthetically active radiation as the basis approximately doubles the calculated efficiency value.

Table 2 enumerates the estimates of energy efficiency of net and gross production which we considered to be most reliable. The term gross production is used here to mean the sum of net production and dark respiration of the whole community. Since the authors used different methods for assessing community respiration rates, and none of the methods seemed technically complete, the gross production efficiencies in the table are regarded as less accurate than the net production values.

The efficiency of net production in forests ranges from 0.6 to 1.0 per cent, with the exception of a very young fir stand on Mount Fuji. Higher values up to 1.5 per cent have been reported for dense young stands, for example of *Cryptomeria japonica* (Tadaki and Kawasaki, 1966), but 1 per cent appears to be the practical upper limit of net production efficiency in fully grown forest stands. The efficiency of gross production is also very low in the same young fir stand. It is also the case with the old secondary forest of mixed oak and pine studied by Whittaker and Woodwell (1969), where they estimated the community respiration rate indirectly from the accumulation of carbon dioxide in the lower layer of atmosphere during the temperature inversion at night. When these two cases are excluded, the efficiency of gross production in forests falls within a relatively limited range of 2.4 to 3.4 per cent.

The ratio of net production to gross production differs appreciably between forest and herbaceous communities. The mean value of the ratio is 0.33 ± 0.09 for forests and 0.55 ± 0.08 for herbaceous communities. An enormous accumulation of supporting organs in forests may be responsible for the greater loss of produced organic matter due to respiratory consumption as compared with the case of herbaceous communities.

A large value of the ratio seems to be common to both natural and cultivated herbaceous communities, although the information on gross production rates in natural communities is scanty

(for example, Midorikawa, 1959; Golley, 1965). If such really is the case, the gross production is expected to be less efficient in natural herbaceous communities than in forests, since the range of observed net production efficiency does not differ between the two community types, being between 0.5 and 1 per cent.

We may then characterize the primary production processes in the two community types as follows. Forest communities tend to have greater gross production rates than their herbaceous counterparts in the same natural environment, owing to the greater leaf area held by their canopies. Smaller LAIs and lower rates of gross production are characteristic of natural herbaceous communities, but this drawback is counterbalanced by larger values of net production : gross production ratios which are the outcome of the smaller portion of supporting tissues in the total community biomass. As a result, there is little difference in the efficiency of net production between woody and herbaceous communities growing under natural conditions as far as overall averages are concerned. *There is no reason to consider that a tree crop is fundamentally more productive than a herbaceous crop, or vice versa.*

The production efficiencies in herbaceous communities are considerably raised in intensively managed crop fields as Table 2 shows. The net production efficiency is generally around 1.5 per cent in C_3 crops, while the gross production efficiency may be as high as 3 per cent. The very high efficiencies observed in a maize field are probably an indication of the high photosynthetic capacity of C_4 canopies.

PRODUCTIVITY OF MIXED CANOPIES

Various types of mixed cropping are common among native agriculture in both the old and the new tropics. It is common to find several different kinds of crops sown or planted in the same field as a mixture. These traditional cropping systems may be interpreted, at least partly, as a safeguard against disasters such as drought, for which different crops have different tolerances, but the occurrence of complicated interactions among crops in mixed culture may sometimes result in a significantly increased overall yield. The behaviour of component species in a multispecies community, and the productivity of a mixed species canopy, offer important themes for both theoretical and applied ecology, but little has yet been done along this line. De Wit's (1960) and Ogawa's (1961, 1980; Suehiro and Ogawa, 1980) formulations of the effect of plant density on the yield of mixed, two-species stands contributed much to this aspect of plant ecology; although their theories could cover only some of the simplest cases.

Consider a simple mixed cultivation experiment in which two plant species, respectively called D and S species, are grown together in homogeneous mixture. The number of D plants per unit land area (ρ_d) and that of S plants (ρ_s) varies in different plots, while the total plant density ($P = \rho_d + \rho_s$) is kept constant. The effect of the mixing ratio (ρ_d/ρ_s) on the yields or standing crops of total plants ($y = y_d + y_s$), D plants (y_d) and S plants (y_s), can then be expressed in a compact form called the 'yield diagram' (Ogawa, 1961) as shown in Figure 4.

Table 2. Efficiency of solar energy utilization (total short-wave radiation basis) in various plant communities. Net production : gross production ratio is given on a dry matter basis.

	Growing season	Efficiency of net production %	Efficiency of gross production %	Ratio net prod. / gross prod.	Source of data
Lowland rainforest, Negeri Sembilan, West Malaysia	12 months	0.97	3.4	0.27	Kira, 1978; Yoda, 1981
Evergreen seasonal forest, SW Kampuchea	-	-	2.8	-	Hozumi *et al.*, 1969
Evergreen oak (*Castanopsis - Quercobalanopsis*) forest, S. Kyushu, Japan	12 months	1.0	2.7	0.35	Kira, 1978
Beech (*Fagus crenata*) forest, C. Honshu, Japan					Maruyama, 1977; Kakubari, 1977
Alt. 700 m	173 days	0.62	2.5	0.23	
Alt. 1500 m	143 days	0.68	2.4	0.26	
Oak - pine forest, New York, USA	5 months	0.75	1.8	0.45	Whittaker and Woodwell, 1969
Fir (*Abies mariesii*) forest, Mount Fuji, Japan					Tadaki *et al.*, 1970
4 to 5-yr-old stands	6 months	0.5	1.1	0.48	
ca 25-yr-old stands	6 months	0.95	2.7	0.34	
ca 60-yr-old stands	6 months	0.75	2.5	0.28	

Table 2 continued

Solidago altissima community, near Tokyo, Japan.	7 months	0.71	1.6	0.45	Iwaki *et al.*, 1966
*Miscanthus sacchariflorus** community near Tokyo, Japan	7 months	0.79	-	-	Mutoh *et al.*, 1968
Phragmites communis community, Osaka, Japan	7 months	0.95	-	-	Mihara, unpubl. data
Aconitum japonicum community NE Honshu, Japan	-	-	-	0.63	Midorikawa, 1959
*Miscanthus sinensis** community, NE Honshu, Japan	5 months	0.52	-	-	Midorikawa *et al.*, 1975
Soya bean, Tokyo, Japan	82 days	0.97	1.7	0.56	Ishii *et al.*, 1973
Italian ryegrass - sorghum* rotation culture, Tokyo, Japan	12 months	1.0	2.2	0.46	Kumura, 1977
Paddy rice, N Kyushu, Japan					Suzuki and Murata, 1975
normal culture	109 days	1.5	2.2	0.67	
early culture	104 days	1.5	2.2	0.66	
Paddy rice, Tokyo, Japan	4.5 months	1.3	2.7	0.49	Yamagishi *et al.*, 1979
Barley, UK	77 days	1.4	2.9	0.48	Biscoe *et al.*, 1975
Maize*, Tokyo, Japan	82 days	2.8	4.6	0.56	Ishii *et al.*, 1973

*C_4 plants

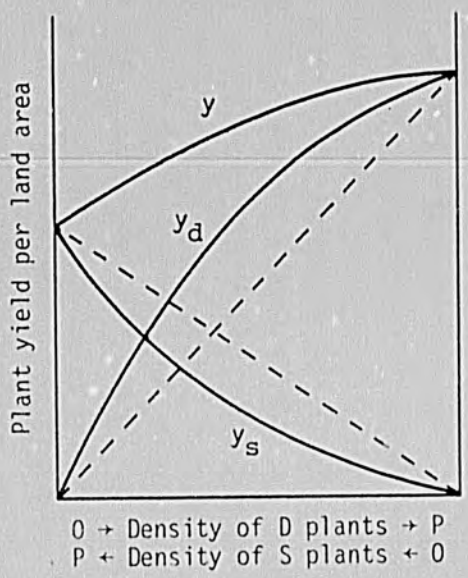


Fig. 4. 'Yield diagram' that represents the plant yield-density relations in mixed cultures of D and S species in which the total plant density (P = density of D plants (ρ_d) + density of S plants (ρ_s)) is kept constant. Symbols y_d, y_s and y refer to the yields of D plants, S plants and total plants. Density is plant population per unit area.

According to Ogawa, the shape of the species curves in the yield diagram depends on the relative dominance between the species.

When D plants are grown in pure stands, the mean plant weight (w_d) decreases with increasing plant density (ρ_d), following a hyperbolic curve as shown in Figure 5 (Shinozaki and Kira, 1956). The point A on the curve (Fig. 5) shows that a mean

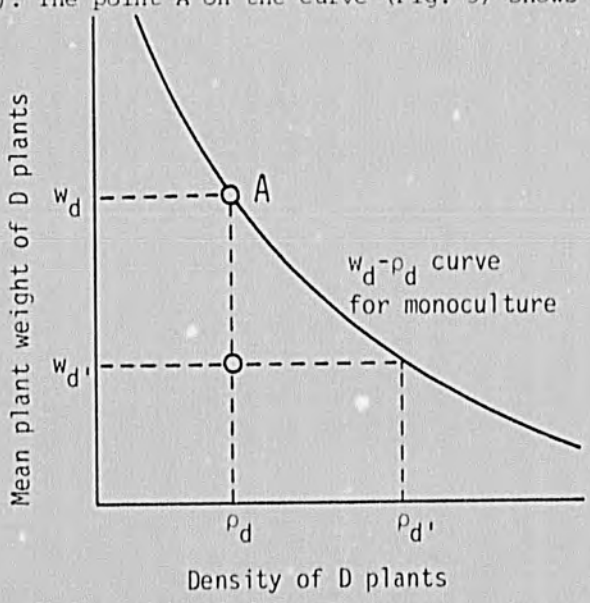


Fig. 5. Diagram showing the derivation of a density conversion factor. For further explanation see text.

plant weight of w_d is realized in a pure culture plot with a plant density of ρ_d. Suppose, then, that a certain number (ρ_s) of S plants has existed in the same plot in mixture with D plants. In this case, the mean weight of D plants is normally expected to decrease from w_d to $w_{d'}$, because they have been subject to the influence of both ρ_d and ρ_s. When the density of D plants corresponding to $w_{d'}$ on the pure culture curve is denoted by $\rho_{d'}$ the quotient

$$q_d = \frac{\rho_{d'} - \rho_d}{\rho_s}$$

gives the number of S plants which is equivalent to a single D plant with respect to their influence on the growth of D plants. Ogawa (1961) called q_d the S → D density conversion factor. If q_d is smaller than 1, the D species is evidently dominant over the S species. In a similar way, we can obtain q_s as the D → S density conversion factor, by which the density of D plants is converted to that of S plants equivalent in their effect on the growth of S plants. In normal cases, if $q_d < 1$, q_s is generally greater than 1 indicating the suppression of S species by D species. If both pure and mixed culture experiments are carried out with the two species simultaneously, we can estimate the values of density conversion factors for a given sampling time.

In many cases the density conversion factors tend to remain more or less constant and independent of the changes in P and the ρ_d/ρ_s ratio. The interrelationships among y_d, y_s, ρ_d and ρ_s can be expressed by relatively simple formulations for this particular case. Based on the formulation Ogawa (1961) proved that a convex species curve such as the y_d curve in Figure 4 always corresponded to a value of q_d smaller than 1, while a concave y_s curve corresponded to the cases where $q_s > 1$. If $q_d = q_s = 1$, the plants of both species have behaved as if they belonged to one and the same species, and the three yield curves become linear as shown by broken lines in Figure 4.

On the other hand, the shape of the total yield (y) curve is determined by a complex of factors such as q_d, q_s and the relative size of the yields of D and S species in pure culture (at $\rho_d = P$ or $\rho_s = P$). A noteworthy fact is that the total plant yield (y) curve sometimes reaches a maximum or a minimum value at a certain mixing ratio as seen in the examples of Figures 6B and 6C. In the former case, a greater harvest is expected by growing two species in a mixture than by the monoculture of either one of the species. Experimental data are still too scanty to predict which pairs of species will meet such expectations.

The density conversion factors may vary with time even in the same pair of species. Furthermore, there are cases in which the density conversion factors change as a function of the mixing ratio (Ogawa, 1961), or because of certain growth factors other than plant density (Suehiro and Ogawa, 1980). Therefore, almost all conceivable patterns of yield diagram that can be met with in experimental results are as indicated by the examples given in Figure 6. Even the behaviour of the 'simple' mixed two-species community is thus extremely complicated, to say nothing of where mixtures of three or more species are found. The very wide gap in our knowledge of how plants interact in

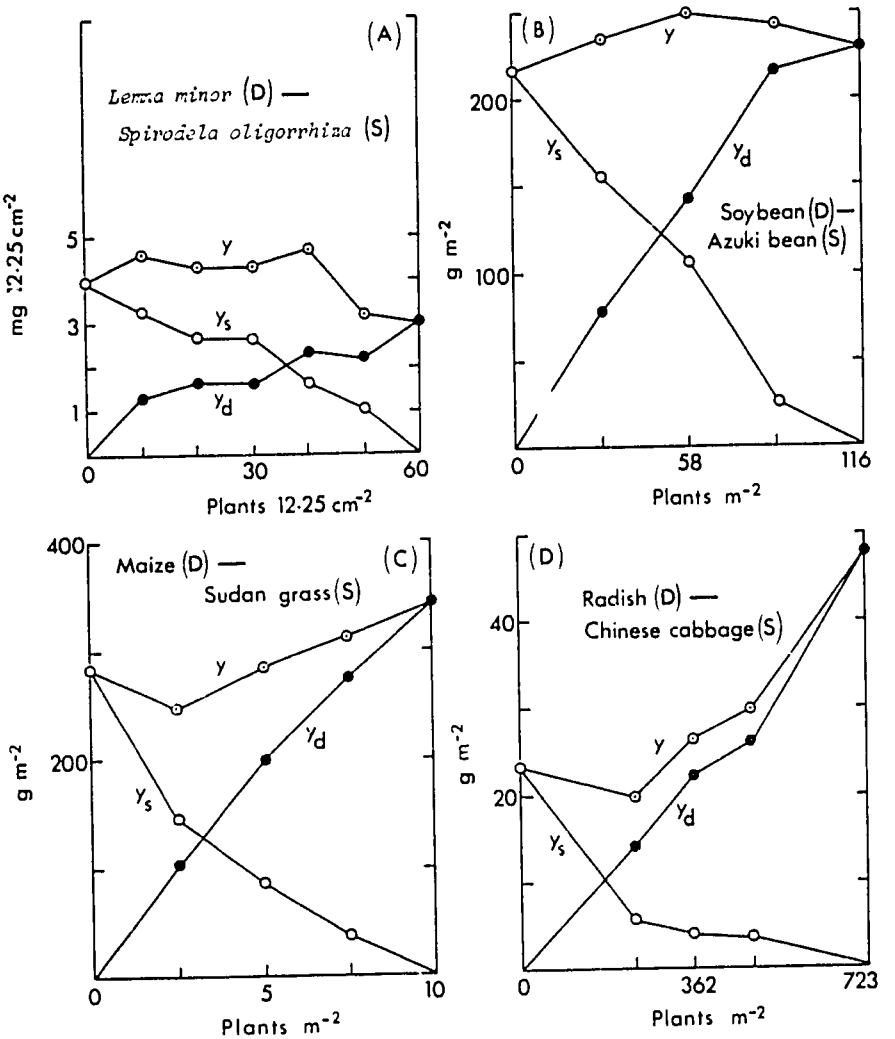


Fig. 6. Examples of yield diagrams for two-crop mixtures.

mixed crop communities, especially in agroforestry where the species can be so very different, is a challenge to plant scientists in the years to come.

A PLATE illustrating this paper is elsewhere in this volume.

REFERENCES

Aoki, M., Yabuki, K. and Koyama, H. (1975). Micrometeorology and assessment of primary production of a tropical rainforest in West Malaysia. *J. agr. Met.* (Tokyo) 3, 115-124.

Biscoe, P.V., Scott, R.K. and Monteith, J.L. (1975) Barley and its environment. III. Carbon budget of the stand. *J. appl. Ecol.* 12, 269-295.

Cooper, J.P. (Ed.) (1975). "Photosynthesis and Productivity in Different Environments". IBP 3. Cambridge University Press, Cambridge, UK.

Duvigneaud, P. (Ed.) (1971). "Productivity of Forest Ecosystems". Proc. Brussels Symposium 1969. UNESCO, Paris, France.

Eckardt, F.E. (Ed.) (1968). "Functioning Terrestrial Ecosystems at the Primary Production Level". Proc. Copenhagen Symposium. UNESCO, Paris, France.

Gifford, R.M. (1974). A comparison of potential photosynthesis, productivity and yield of plant species with differing photosynthetic metabolism. *Aust. J. Plant Physiol.* 1, 107-117.

Golley, F.B. (1965). Structure and function of an old-field broomsedge community. *Ecol. Monogr.* 35, 113-137.

Hozumi, K., Yoda, K. and Kira, T. (1969). Production ecology of tropical rainforests in southwestern Cambodia. II. Photosynthetic production in an evergreen seasonal forest. *Nature and Life in Southeast Asia* 6, 57-81.

Ishii, R. and Murata, Y. (1978). Photosynthesis in C_3 and C_4 plants. *Jap. J. Crop Sci.* 47, 165-188. (In Japanese with English summary.)

Ishii, R., Kumura, A. and Kariya, K. (1973). Measurement of the efficiency of solar energy utilization by maize and soybean populations. *Jap. J. Crop Sci.* 42, 89-90. (In Japanese.)

Iwaki, H., Monsi, M. and Midorikawa, B. (1966). Dry matter production of some herb communities in Japan. Pre-print 11th Pacific Science Congress, Tokyo. 15 pp.

Kakubari, Y. (1977). Beech forests in the Naeba Mountains. II. Distribution of primary productivity along the altitudinal gradient. *In* "Primary Productivity of Japanese Forests" (T. Shidei and T. Kira, eds), pp.201-212. Univ. of Tokyo Press, Tokyo, Japan.

Kira, T. (1975). Primary production of forests. *In* "Photosynthesis and Productivity in Different Environments" (J.P. Cooper, ed.), pp.5-40. IBP 3. Cambridge Univ. Press, Cambridge, UK.

Kira, T. (1976). "Terrestrial Ecosystems - a General View". Handbook of Ecology Vol.2. Kyoritsu Shuppan, Tokyo, Japan. (In Japanese.)

Kira, T. (1978). Community architecture and organic matter dynamics in tropical lowland rainforests of Southeast Asia with special reference to Pasoh Forest, West Malaysia. *In* "Tropical Trees as Living Systems" (P.B. Tomlinson and M.H. Zimmermann, eds), pp.561-590. Cambridge Univ. Press, Cambridge, UK.

Kira, T. and Shidei, T. (1967). Primary production and turnover of organic matter in different forest ecosystems of the Western Pacific. *Jap. J. Ecol.* 17, 70-87.

Kira, T., Shinozaki, K. and Hozumi, K. (1969). Structure of forest canopies as related to their primary productivity. *Plant & Cell Physiol.* 10, 129-142.

Kira, T., Ono, Y. and Hosokawa, T. (Eds) (1978). "Biological Production in a Warm Temperate Evergreen Oak Forest of Japan". JIBP 18. Univ. of Tokyo Press, Tokyo, Japan.

Koyama, H. (1978). Photosynthesis studies in Pasoh Forest. *Malay. Nat. J.* 30, 253-258.

Kumura, A. (1977). Dynamics in the turnover of organic matter, some nutrient elements and energy in a cultivated land ecosystem. *In* "Environment and Human Survival" (M. Monsi, ed.), pp.131-146. Ministry of Education, Science and Culture, Tokyo, Japan. (In Japanese with English summary.)

Larcher, W. (1980). "Physiological Plant Ecology". Revised 2nd

edition. Springer-Verlag, Berlin.
Lieth, H. and Whittaker, R.H. (Eds) (1975). "Primary Productivity of the Biosphere". Springer-Verlag, Berlin.
Maruyama, K. (1977). Beech forests in the Naeba Mountains. I. Comparison of forest structure, biomass and net productivity between the upper and lower parts of the beech forest zone. *In* "Primary Productivity of Japanese Forests" (T. Shidei and T. Kira, eds), pp.186-201. Univ. of Tokyo Press, Tokyo, Japan.
Midorikawa, B. (1959). Growth analytical study of altherbosa on Mount Hakkoda, northeast Japan. *Ecol. Rev. (Sendai)* 15, 83-117.
Midorikawa, B., Shimada, Y., Iwaki, H. and Ohga, N. (1975). Root production in seminatural grassland community dominated by *Miscanthus sinensis* in the Kawatabi area. *In* "Ecological Studies in Japanese Grasslands with Special Reference to the IBP Area" (M. Numata, ed.), pp.114-122. JIBP 13. Univ. of Tokyo Press, Tokyo, Japan.
Monsi, M. and Saeki, T. (1953). Über den Lichtfaktor in den Pflanzengesellschaften und ihre Bedeutung für die Stoffproduktion. [On the light factor in plant communities and its meaning for dry matter production.] *Jap. J. Bot.* 14, 22-52.
Monsi, M. and Saeki, T. (Eds) (1978). "Ecophysiology of Photosynthetic Productivity". JIBP 19. Univ. of Tokyo Press, Tokyo, Japan.
Murata, Y. (Ed.) (1975). "Crop Productivity and Solar Energy Utilization in Various Climates in Japan". JIBP 11. Univ. of Tokyo Press, Tokyo, Japan.
Mutoh, N., Yoshida, K.H., Yokoi, Y., Kimura, M. and Hogetsu, K. (1968). Studies on the production processes and net production of a *Miscanthus sacchariflorus* community. *Jap. J. Bot.* 20, 67-92.
Numata, M. (Ed.) (1975). "Ecological Studies in Japanese Grasslands with Special Reference to the IBP Area". JIBP 13. Univ. of Tokyo Press, Tokyo, Japan.
Ogawa, H. (1961). "Experimental studies on the density effect in mixed communities of higher plants". D.Agr. Thesis, College of Agriculture, Kyoto University, Japan. (In Japanese.)
Ogawa, H. (1980). "Structure and Function of Plant Populations". Asakura Publ. Co., Tokyo, Japan. (In Japanese.)
Ovington, J.D. (1962). Quantitative ecology and the woodland ecosystem concept. *Adv. ecol. Res.* 1, 103-192.
Saeki, T. (1960). Interrelationships between leaf amount, light distribution and total photosynthesis in a plant community. *Bot. Mag. Tokyo* 73, 55-63.
Shidei, T. and Kira, T. (Eds) (1977). "Primary Productivity of Japanese Forests". JIBP 16. Univ. of Tokyo Press, Tokyo, Japan.
Shinozaki, K. and Kira, T. (1956). Intraspecific competition among higher plants. VII. Logistic theory of the C-D effect. *J. Inst. Polytech. Osaka City Univ. Ser. D.* 7, 35-72.
Shinozaki, K. and Kira, T. (1977). Canopy structure and light utilization. *In* "Primary Productivity of Japanese Forests" (T. Shidei and T. Kira, eds), pp.75-86. JIBP 16. Univ. of Tokyo, Tokyo, Japan.
Stephens, G.R. and Waggoner, P.E. (1970). Carbon dioxide exchange of a tropical rainforest. I. *Bioscience* 20, 1050-1053.

Suehiro, K. and Ogawa, H. (1980). Competition between two annual herbs, *Atriplex gmelini* C.A. Mey and *Chenopodium album* L., in mixed cultures irrigated with seawater of various concentrations. *Oecologia* 45, 167-177.

Suzuki, M. and Murata, Y. (1975). Measurement of the efficiency for photosynthetic light energy conversion of rice population under field conditions. *Jap. J. Crop Sci.* 44, 109-113. (In Japanese with English summary.)

Tadaki, Y. and Kawasaki, Y. (1966). Studies on the production structure of forests. IX. Primary productivity of a young *Cryptomeria* plantation with excessively high stand density. *J. Jap. For. Soc.* 48, 55-61.

Tadaki, Y., Hatiya, H., Tochiaki, H., Miyauchi, H. and Matsuda, U. (1970). Studies on the production structure of forests. XVI. Primary productivity of *Abies veitchii* forests in the subalpine zone of Mount Fuji. *Bull. Gov. For. Exp. Stn* (Tokyo) 229, 1-22.

Whittaker, R.H. and Woodwell, G.M. (1969). Structure, production and diversity of the oak-pine forest at Brookhaven, New York. *J. Ecol.* 57, 155-174.

Wit, C.T. de (1960). On competition. *Versl. Landbouw. Onderz.* 66, 1-82.

Yamagishi, T., Okada, K., Hayashi, T., Kumura, A. and Murata, Y. (1979). Studies on the carbon cycling in paddy ricefields. III. Dry matter production and solar energy utilization in irrigated rice. *Jap. J. Crop Sci.* 48, Suppl. issue 2.

Yoda, K. (in press). Community respiration in a lowland rainforest of Peninsular Malaysia. *Jap. J. Ecol.*

DISCUSSION

LEYTON - Have the photosynthetic light responses of leaves been measured at different places in the canopy?

KIRA - Leaves were detached from the uppermost point of the trees and measurements were taken under controlled conditions.

TIESZEN - Usually what the 'average' leaf in a canopy is doing is not close to that of the 'ideal' leaf.

BRUNIG - Productivity data should be treated with great caution because of the great year-to-year variability. This could be even more pronounced in agroforestry systems as compared with the canopies of natural communities.

KIRA - Our data are from 5-year averages.

BUDOWSKI - Why is *Eucalyptus* which is one of the most efficient converters of energy into biomass classed as an intermediate plant in the serial succession?

KIRA - It comes from drier areas, and more studies are needed to understand why it has such high productivity.

ALVIM - Biological response is probably not the most interesting parameter because farmers are more concerned about economic returns. In this respect shade from agroforestry canopies can be

particularly important in reducing production costs in a number of ways.

KIRA - We are working on the biological values and these can, later, be incorporated into economic models.

OKIGBO - The figures shown were mainly concerned with maximum yields which is not always the farmer's objective. He may be looking for stability or risk avoidance.

RAINTREE - Under natural conditions, woody and herbaceous productivities were similar. Considering that the productivity of domesticated herbaceous species has been greatly increased, is there a similar potential to increase the canopy productivity of woody components useful in agroforestry?

COOMBS - Woody components should be expected to have lower productivities because chemical conversions of wood formation are less efficient, which could probably explain why they have higher net photosynthesis but equal net productivities.

LOOMIS - Five-year averages really are necessary to estimate forest productivity with reasonable accuracy.

OKIGBO - As an attempt to provide an answer to Dr Kira's question as to the reasons for intercropping I would like to observe that, generally speaking, intercropping gives higher total yields than sole cropping, although yields of individual component species may be reduced. It should, however, be observed that the total yields of economic products, even when they are higher than individual component species, may vary in their economic or nutritive value. The farmer benefits from intercropping in:

- reduction of risks that may be associated with failure of individual crop species;
- a facility for frequent harvesting of cash crops and other components, while waiting for the main crop; and
- ensuring that soil is kept covered and protected from erosion.

It should be noted that limited attention has been given to research in intercropping and, often, too much emphasis has been placed on difficulties in mechanization and the application of certain inputs, such as fertilizers and pesticides, in intercropping systems. Unnecessary bias against intercropping should be overcome and more resources should be allocated to determine the potentials and limitations of intercropping, and to methods of improving such systems and realizing their potentials. Particularly as they are highly relevant for agroforestry research, where at least one of the intercrops will always be a woody species.

LIGHT CLIMATE AND CROP-TREE MIXTURES

J.E. JACKSON
Pomology Department, East Malling Research Station,
Maidstone, Kent, U.K.

ABSTRACT. In order to estimate the potential productivity of crops, whether growing alone or mixtures, it is first necessary to know how much photosynthetically active radiation (PAR) is intercepted. This can be done by defining the position of each leaf in three-dimensional space and estimating the light falling on it by means of a computer programme. Another method, outlined here in relation to multi-storey canopies, is to define the light transmission properties of whole units (trees, bushes) and build up a picture of the light being intercepted by the different plant layers. Irradiation above critical levels may be necessary for some plant processes. To estimate the within crop light climate of different multiple crop canopy designs leaf area index (LAI), the light extinction coefficient (K) and the maximum fraction of available light which can be intercepted by the trees (F_{max}) have to be known. F_{max} can be estimated using a physical model of the tree canopy on a panel of silicon cells or other light sensors under field conditions. Practical ways of increasing total light interception in multi-storey systems are discussed, and the need to consider the light responses of potential species or cultivars for multi-cropping systems is noted and some examples given. Although the balance of light distribution between upper and lower storey plant components has to be decided both by their light requirements and their economic values, knowledge of the ways in which changes in the structure of a multi-storey canopy can influence potential productivity is clearly useful in helping to design agroforestry systems.

INTRODUCTION

The yields of crops, whether tree crops or ground crops, are dependent on the radiant energy which they intercept. For many, ranging from apples to cereals, the relationship between dry-matter yield and intercepted energy is approximately linear (Monteith, 1977) and the fraction (F) of the photosynthetically

active radiation (PAR) which is intercepted by a crop sets the upper limit to its potential productivity under those climatic conditions. It does not follow either that all crops should be grown at the maximum possible foliage density or that crop yields will always be increased by increasing irradiance. Excessive canopy density may depress economic yield. For example, apple trees do not fruit on the current year's shoots and a very high density of the latter may so shade the potentially fruit-bearing zone that yield is reduced (Jackson, 1980). Excessive exposure to irradiation may also depress economic yield, as is the case when heat-sensitive apple varieties suffer from 'sunscald' of the fruits. It is, however, axiomatic that PAR which is not intercepted by the leaves of a crop plant cannot be directly used by it. In order to estimate the potential productivity of crops, whether growing alone or mixtures, it is first necessary to know how much PAR is intercepted.

In considering the potential productivity of multiple cropping systems, especially intercropping systems involving trees, shrubs and ground-cover crops, it is essential to be able to estimate the PAR intercepted by each of the component crops at any given time and to integrate this over the time they occupy space. There is now a very substantial body of theory which enables calculation of the photosynthetic productivity of a crop given knowledge of its leaf area index, the light transmission coefficients of the canopy, the angles of the leaves and the photosynthetic response curves of individual leaves. This theory is, however, essentially based on the concept of random leaf distribution in a canopy which is effectively continuous. Allen *et al.* (1976) in a review of work on radiation and microclimate relationships stated 'Since the dominant species in polycultures or intercropping systems seldom develop complete canopy closure, it is difficult to apply the previous material (i.e. the general linking theory) on radiation quality, photosynthesis, evapotranspiration and radiation fluctuation to these systems.' The present paper outlines an approach whereby this can be done.

SOLAR ENERGY INTERCEPTION

This section discusses solar energy interception by different components of a multi-layered canopy with large gaps between its constituent units and, in particular, the distribution of PAR within these units. At least two techniques can be used to calculate energy interception and distribution in discontinuous canopies of any form.

The first is the Monte-Carlo method used by Oikawa and Saeki (1977) and Oikawa (1977). In this the position of each leaf is defined in three-dimensional space in a computer simulation and the penetration of beams of light of similar angular distributions to those occurring in nature are calculated. Such a technique requires access to a powerful computer and would, even then, be very laborious if applied to canopies of complex and irregular geometries with varying leaf characteristics in their different components.

The second (Jackson and Palmer, 1979, 1981) defines the basic functional relationships at the varying hierarchical

levels rather than taking the individual leaf as the unit and building up from this. It is, therefore, capable of treating a row of trees, a single tree, or a bush as a unit with respect to some of its properties. Such an approach involves some simplifications and approximations. Nevertheless, it is easy to use, does not require expensive facilities, and provides a useful conceptual framework for the agronomist and crop physiologist because it deals in the entities such as tree size, shape, and arrangement which he manipulates in experiments and agricultural practice.

Energy interception by discontinuous and multi-storey canopies

With continuous-canopy crops such as wheat the calculation of light interception and distribution is governed by the equation

$$I_L/I_o = e^{-KL} \quad (1)$$

where I_o is the light intensity above the canopy, I_L the light intensity below a leaf area index of L where leaf area index is expressed as m^2 leaf per m^2 ground, and K is an extinction coefficient calculated after measuring I_o, I_L and L under relevant conditions.

This equation cannot be applied directly to a horizontally discontinuous two-layered canopy of trees and a ground-cover crop, but it can be applied, in a slightly modified form, after we have taken separate account of the light which reaches the ground-cover crop without passing through the canopy of any individual tree. Total transmission (penetration) to the ground-cover crop (T) is the sum of T_f (light which misses the trees completely and would reach the ground crop even if each tree were solid) and T_c, which is light which has passed through the canopy of the trees, that is

$$T = T_f + T_c \quad (2)$$

T_c will obviously relate to the depth of the tree canopy and the density with which leaves are arranged within it so it will be governed by an equation similar to (1). It would, however, be inappropriate to use L (leaf area per unit of total ground area) as the measure of depth of tree canopy penetrated. A more realistic measure, which can best be visualised with respect to direct light, although it is also relevant to diffuse light, is the tree leaf area per unit of ground surface which it potentially shades, that is the unit area enclosed by the outline of the projected cast shadows of the trees in direct light. This, defined as L', can be calculated with respect to both direct and diffuse light by equation (3)

$$L' = L/(1-T_f) \quad (3)$$

in which T_f is defined as in equation (2) and expressed as a decimal fraction of the light which would reach the ground-cover crop if there were no trees, that is of the irradiance per unit horizontal surface above the canopy.

The total light reaching the upper surface of the ground-cover crop after transmission through the tree canopy (T_c) is thus

$$T_c = (1-T_f)e^{-KL'} \quad (4)$$

and total transmission (T) to this 'undercrop' is

$$T = T_f + (1-T_f)e^{-KL'} \quad (5)$$

The radiant energy actually intercepted by the two crops is then derived. For the tree crop the maximum fraction of the available energy which it could intercept, given the tree dimensions and spacings, is $(1-T_f)$. If this is re-defined as F_{max} then

$$T = T_f + F_{max}e^{-KL'} \quad (6)$$

and the fraction (F) of the available energy actually intercepted by the trees will be as in equation (7)

$$F = F_{max} - F_{max}e^{-KL'}. \quad (7)$$

That is, the fraction which would be intercepted if the trees were non-transmitting minus transmission through trees of the given dimensions and leaf density.

T represents, for the ground-cover crop, the total radiant energy available above its canopy as a decimal fraction of that available above the trees. If this ground-cover crop forms a closed canopy over the surface of the ground then the energy intercepted by this crop can be calculated from equation (1) with I_o given the numerical value of I_o x T. This ignores the effect of the space taken up by tree trunks. If the ground-cover crop is markedly discontinuous with large gaps of bare soil then its energy interception can be calculated from an equation analogous to equation (7), bearing in mind that the value of F obtained relates to available energy at the upper surface of this crop (I_o x T) not total available energy above the multiple-crop canopy.

Distribution of radiant energy within the trees and the ground-cover crop

In view of the nonlinear relationships between sunlight intensity and important plant processes such as fruit bud formation and photosynthesis it is important to know not only how much solar radiation a canopy intercepts, but also how much of the canopy volume is irradiated above critical levels. Lower layers in the canopy frequently contribute little to photosynthesis (Allen *et al.*, 1974) and may contribute nothing to the economic yield of fruits so it is wasteful to grow canopies to more than a certain depth. For the continuous cover crop it can readily be shown from the Monsi and Saeki (1953) equation (1) that if we define L_I as the leaf area in that upper zone of the canopy within which irradiance as measured on a horizontal surface is I or more then

$$L_I = (\ln I)/(-K). \quad (8)$$

This leaf area can be visualised as being above an 'irradiance contour' which is at a given depth, in leaf area index terms, from a horizontal upper surface in the case of a continuous canopy. Clearly this argument does not apply in the same way, for example, to hemispherically shaped trees where the 'irradiance contour' will be influenced by distance not just from the

top but from the outside of the tree, and by the shade cast by neighbouring trees. It has, however, been shown (Jackson and Palmer, 1981) that in the discontinuous canopy

$$L_I = F_{max} [(\ln I)/(-K)]. \quad (9)$$

The volume of canopy (CV_I) within which the irradiance as measured using a horizontally held, cosine law sensor would be as great as, or greater than, I is then given by equation (10).

$$CV_I = L_I/(\text{leaf area density, } m^2 \text{ leaf } m^{-3} \text{ canopy volume}). \quad (10)$$

Measurement of the necessary parameters

In order to calculate the effect of a particular design of a multiple crop canopy on the light climate within it, and the energy interception by its components, we need to know the leaf area index (LAI), K and F_{max}.

LAI is laborious to measure but special techniques can reduce the labour involved in its measurement on some tree crops because leaf area is usually related to trunk girth. Because of the exponential relationship between LAI and light penetration errors of measurement at high LAIs (where the work is greatest) are relatively unimportant.

K, the light extinction coefficient, can be calculated by using the Monsi and Saeki equation (1) following measurement of radiant energy by cosine law sensors with appropriate wavelength response held horizontally above and below a sector of canopy of measured LAI. For the calculations to be valid the sector of canopy must be fairly continuous, and large relative to the sensors so that the radiant energy falling on the lower sensor has actually passed through the measured canopy. Determination of K must be over a time period appropriate to that over which the equations are to be used. For example, it should be based on daily or even weekly integrals of radiation if applied to crop physiological, agronomic or ecological studies. Serious errors occur if either the sensor has an inappropriate wavelength or angular response, or if the K value is measured over an inappropriate period so that it cannot validly be used with the leaf area and climatic data relevant to the agronomic questions being asked (Jackson, 1980; Jackson and Palmer, 1981).

F_{max} (that is $1-T_f$) can be calculated, as long as the shapes of the discontinuous canopy elements are simple, over any desired period of time by using simple computer or desk calculator routines based on known distributions of sun and sky irradiance (Cain, 1972; Jackson and Palmer, 1972). If the sizes, shapes or spacings of the trees are highly variable, or the daily pattern of angular distribution of direct and diffuse radiation is either complex or unknown, then it may be better to use a physical system to estimate F_{max} directly. We are currently testing very compact ones (Fig. 1) based on small solar panels made up of silicon cells. These are bought as units and encased so as to give a cosine law response so that the electrical output is proportional to the irradiance. F_{max} is determined by subtracting the output from one of these panels with model trees *in situ* on it from that of a corresponding panel (or calibrated silicon photocell) without any such shading. Silicon cells are robust and give a high

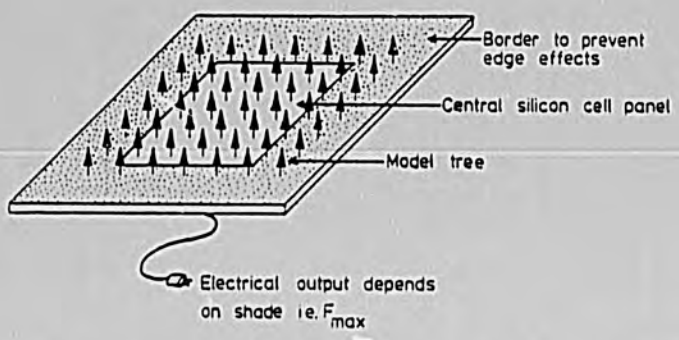


Fig. 1. Photocell (solar panel) system for measuring F_{max} (where $F_{max} = (1-T_f)$).

output; moreover, their wavelength response, which causes difficulties for many purposes, is irrelevant for such use with totally opaque models.

PRACTICAL ASPECTS OF ECOSYSTEM LIGHT CLIMATE

Given that we can measure, or estimate, irradiance levels and light interception in the different strata of a multicrop system we need, next, to consider the physiological implications of the ecosystem light climate and the use to which this knowledge can be put with regard to the choice of mixed tree and ground crop systems, and to their subsequent management.

Increasing cropping system light interception

Major advantages will accrue in growing a ground cover crop in addition to a tree crop only where the latter fails to intercept a high proportion of the available light. Any potential advantage will be small where the trees intercept most of the light.

Having said this we should appreciate that many tree crops are inefficient in interception of radiant energy in two main ways. First, they take many years to reach full canopy and, second, this full canopy may still be incomplete for management and access reasons or it may, in the case of deciduous trees, be very inefficient in light interception at particular times of the year. These sources of failure to intercept available radiation not only result in underutilisation of radiant energy resources but they also carry the positive penalty that energy which is not used by the trees and crop plants is available for the growth of weeds.

In their early years tree crops are, therefore, frequently intercropped with ground-cover crops. In the United Kingdom, for example, strawberries are often planted with apples. The apple trees are grown in rows with the minimum distance between the rows being such as to allow the movement of tractors and machinery for spraying. The minimum between-row spacing is about 3 m, the more usual spacing in England about 4.5 m. At this spacing the trees intercept only little of the available light in their early years. For example, a very high density apple planting of cv. Golden Delicious on M.9 rootstock, at a spacing of 2.9 m

between the rows and 0.9 m between trees within the row, was shown to intercept only 11 per cent of available PAR at the end of its first orchard year. One using more vigorous trees planted at 4.3 x 2.9 m intercepted only 11 per cent at full leaf in the second orchard year, while a 5-year-old orchard of Cox and Worcester on M.26 rootstock intercepted only 30 per cent of available PAR (Jackson, 1980).

Under such circumstances the intercrop is actually using the greater part of the available radiation. The dominant factor in the choice of intercrop is then its actual value over a relatively few years. Strawberries often fill this role in apple orchards, as do field vegetables in some temperate fruit growing areas. Coconut, oil palm and young rubber trees in Malaysia are often intercropped in their early years with annual crops. For example, cassava, soybeans, peanuts, maize etc. (Blencowe, 1969) and upland rice and maize are grown in young mango and coconut plantations in the Philippines (Harwood and Price, 1976). It should be noted that intercrops in this open-tree-canopy situation do not need to be particularly shade tolerant, or even to have strategies enabling them to grow at the time of season when the trees have least leaf. Although, no doubt, such characteristics can prolong their years of profitable use.

Some tree crops show systematic changes in LAI over the year. This is so in an extreme form in deciduous temperate trees which may not attain full canopy until after midsummer, and thus may have little or no foliage at times of high incident energy in the early summer and late autumn (Jackson and Landsberg, 1972). It is, however, also so in evergreen trees in the tropics (see Huxley, page 503 in this volume). In either case the undercrop should be so rapid growing that it can exploit the relatively short period during which radiation penetration through the tree canopy is maximal. Bunting (1976) cites cucurbits, with their very effective production of leaf area per unit of dry matter, as being outstanding performers in this respect.

Optimisation of interception by the component tree and ground-cover crops

In natural forests the adaptation of the different plant species to their environmental niches permits a greater utilisation of resources than would be achieved by a closed canopy of a single genotype. In man-managed systems we can work towards a similar maximum exploitation of total light resources by matching the crops to the light climate to which they are subjected in the mixed cropping situation.

Light climate in this context is defined as intensity or, more correctly, flux density per unit area. Dry-matter production in a field crop growing under a given radiation regime increases with the proportion of available PAR which it intercepts, because light missing the leaves cannot be used in photosynthesis. However, increasing the *intensity* of solar radiation will not, necessarily, increase productivity. To achieve this it is necessary to have species which respond positively to a high intensity of PAR at the top of the canopy and those with light response curves flattening off at relatively low irradiation in the lower part. The key crop parameter in relation to light requirements is economic yield and the relationship between

light intensity and economic yield varies both between species and between cultivars. This makes generalisation difficult but adds to the flexibility with which the light climates of cropping systems can be exploited.

Tree crop light requirements. The apple, to take a well-studied example, exhibits characteristics which fit it very well to the role of an upper canopy crop in a mixed cropping system under some environmental conditions. For example, from North America to the United Kingdom, Poland and Italy it has been found that shade depresses the fruit quality of some important apple cultivars (Bassi *et al.*, 1980; Heinicke, 1966; Jackson, 1970, 1980; Jacyna, 1978). In the relatively high light intensity conditions of Summerland, British Columbia, Heinicke (1966) concluded that the best fruit colour was obtained where they were exposed to more than 70 per cent of full sunlight, and inadequate for sale under 40 per cent. In addition, fruit size and soluble solids content are reduced, as is fruit bud formation, at light intensities which are more than adequate for vegetative growth (Jackson, 1980). Shade has also been noted to affect adversely fruit bud formation in South Africa where a degree of shade otherwise benefits the cultivars grown by reducing the risk of sunscald. From such work it would appear that there is little to be gained by having any apple canopy which is not irradiated to at least 50 per cent of the above canopy level.

Citrus is usually grown in much denser plantations than apple but, even so, and although vegetative growth is vigorous under shaded conditions, a relatively high light intensity is required for maximum fruiting to the extent that thinning the trees in an overcrowded grove can increase yields by improving within canopy irradiance (Monselise, 1951).

Under some circumstances where irradiation levels are very high the tree crop may be primarily grown to provide shade for the economically more important ground crops. Such trees must be adapted to the potentially high heat load on their upper leaves. Brünig (1976) has reviewed appropriate adaptations in crown and leaf form, in particular the value of small xeromorphic leaves.

Understorey crop light requirements. Where the understorey crop is grown only in the first few years after planting the trees there is little interference in light interception. But this becomes more important as the trees utilize more of the available energy later. Again, the strawberry is an example of an intercrop species particularly used in the early years after planting with several species of tall, temperate fruit trees. Sturm (1961) considered that light was always the limiting factor for the strawberry intercrop and that this latter could only be grown satisfactorily for the first three years under closely spaced bush apple trees (at 3 x 3 m or 2.5 x 2.5 m spacing), and for nine years under wide-spaced trees (at 6 x 6 m or 10 x 10 m). Strawberry leaves require light intensities as high as apple to attain light saturation of photosynthesis. Lenz and Daunich (1975) cite 0.36 cal cm^{-2}, that is 44 k lux, which is very similar to the value for sun leaves of apple shown by Barden (1977). However, strawberries do show some adaptations to an

understorey role. They attain full leaf canopy earlier in the season than does apple (compare Arney, 1953, 1954 with Palmer and Jackson, 1977) and they are tolerant of some degree of shade. Yu, Park and Song (1971) reported that Pocohontas strawberries planted between 2-, 4- and 6-year-old vines, where the light intensity was 41.7, 31.4 and 19.9 k lux respectively during a three-month shading season, had similar flowering dates and yields, although the plants among the older vines had fewer leaves and fewer flowers.

More generally, C_4 plants have higher photosynthetic rates than C_3 plants at high PAR flux densities (Hesketh, 1963), so the latter should be less reduced in performance when grown as understorey crops. Leaves of maize (Hesketh and Musgrave, 1962) do not become light saturated in full sunlight whereas leaves of C_3 crops, such as sugar beet or soybean, may saturate at about half of full sunlight.

At the crop level the studies of Sale (1974) on the productivity of vegetable crops in a region of high solar input (the Murrumbidgee irrigation area of New South Wales where solar input is often up to 1000 Wm^{-2}) are of particular interest. He showed that the potato crop was unable to use a large part of this PAR, light saturation of the canopy occurring at about 450 Wm^{-2}. Using a technique of canopy enclosure he found that light saturation of a French bean crop occurred at 600-650 Wm^{-2}, and of cabbages at about 700 Wm^{-2} (Sale, 1975). On the face of it the crops with the lowest light saturation levels would appear to be most suited to being understorey crops, with some temperate crops of this type possibly being able to perform as well under a degree of moderate shade from a tree crop as they could in the open. Sale (1976) did, however, note some reduction in yield of potatoes at a shade level under which light was not considered limiting for photosynthesis.

The response of the tea plant to light climate, both in relation to shade trees and to artificial shading, has been studied in considerable detail and the results reviewed by Barua (1969). Several points of general relevance seem to have been shown in this work. First, that photosynthesis and potential growth of the tea plant are reduced by the very high temperatures (over 35°C) which can result from direct insolation, but that increased irradiation *per se* and an increase in leaf temperature up to 35°C are beneficial. Second, that those clones of tea with erect or semierect foliage (E-types) make better use of available energy for photosynthesis than do those with horizontal leaves (H-types); the latter being more likely to become excessively heated in full sun and so requiring light shade for maximum growth in the conditions of North East India. Moreover, there is a difference in light penetration between canopies with erect and horizontal leaves. Values of the extinction coefficient, K, in equation (1) tend towards unity with horizontal leaves and tend to be much lower with erect leaves. Thus the erect leaf type of tea bush develops a much higher LAI (5-7) than the H-types (3-4) and so surpasses the latter in potential productivity (Hadfield, 1968). It also seems that reduction of light intensity to about 60 per cent of full sunshine appears to divert a larger fraction of assimilates towards economic yield (leaf) as opposed to total net production.

Generalisations and arguments by analogy are frequently misleading, but it may well be that the greatest biological efficiency in a multi-crop, multi-tiered agricultural ecosystem will be achieved by having trees with small, erect or semierect leaves, and hence low K values, forming the upper storey and plants with large horizontal leaves, and high K values, at ground level. This would to some extent parallel the forest ecosystem situation.

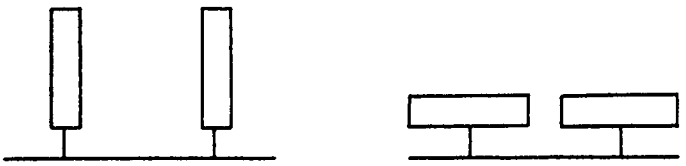
HORIZONTAL DIMENSIONS

As a generalisation the more uniformly a tree crop occupies the space in which it is planted the higher will its interception of PAR per unit of leaf area be (Jackson, 1980), and the more uniform the irradiance on the upper surface of the ground-cover crop with which it is associated. Whether this is desirable or not depends on the required distribution of intercepted light between the two crops which, in turn, will be greatly influenced by their relative economic values and light requirements. If the tree crop is grown in discrete rows its shade on the ground-cover crop will be a function of row orientation, solar altitude and solar azimuth; the latter two, and hence the effect of row orientation, being dependent on latitude and time of year and day. The relevant mathematics are discussed by Usher (1970) and Jackson and Palmer (1972). The physical model system discussed earlier in this paper for measuring F_{max} would, of course, give a result directly proportional to shadow length at any given time, or integrated over any chosen time period. If H is the height of the trees then at 50°N the cast shadows are probably unimportant at more than 1 to 2 heights distant, and much less at lower latitudes.

In general, arrangement of the tree canopy so as to maximize its occupancy of space in the horizontal plane maximizes F_{max}, and hence total light interception. In this, the effect of tree form and arrangement is essentially similar, at a different hierarchical level, to the well-known effects of leaf angle with horizontal leaves giving greater interception per unit LAI (higher K values) than vertical leaves. This effect of tree canopy arrangement is, of course, more pronounced the less transmission there is through the trees so it is greater at high rather than at low LAIs. Figure 2 shows extreme examples of the effect of arranging the same volume of tree canopy in different ways at 51°N.

CHANGES IN LIGHT QUALITY

There are appreciable changes in the spectral composition of radiation with depth in the canopy, leaves transmitting less of the PAR than the far red and infra-red parts of the spectrum. Typical values for a tree leaf transmission (apple) have been given by Palmer (1977) and the changes in 730 nm to 660 nm irradiance at different depths in tree and ground crop canopies have been reviewed by Allen *et al.* (1976). The importance of light quality (wavelength) with respect to such factors as seed germination and morphogenesis is well established. It might therefore be unwise to assume that simple shading trials with screens which do not influence the spectral composition of light under



F_{max} = 0.696 F_{max} = 0.924

LAI	L'	$F_{max}e^{-KL'}$	F	L'	$F_{max}e^{-KL'}$	F
0.5	0.72	0.45	0.24	0.54	0.67	0.26
1.0	1.44	0.29	0.40	1.08	0.48	0.44
2.0	2.87	0.13	0.57	2.16	0.25	0.67
3.0	4.31	0.05	0.64	3.25	0.13	0.79
4.0	5.74	0.02	0.67	4.33	0.07	0.86

Calculated for K = 0.6

Fig. 2. Tree form effects on fraction of light intercepted (F) where $F = F_{max} - F_{max}\, e^{-KL'}$.
N.B. Effects of tree outline parallel to those of leaf angle at a different hierarchical level.

their shade give results which are fully relevant to the under-crop situation. More detailed research is, however, needed on this point before its practical significance can be ascertained.

REFERENCES

Allen, L.H. Jr, Sinclair, T.R. and Lemon, E.R. (1976). Radiation and microclimate relationships in multiple cropping systems. *In* "Multiple Cropping", pp.171-200. ASA Special Publication No.27. American Society of Agronomy, Madison, Wisconsin.

Allen, L.H. Jr, Stewart, D.W. and Lemon, E.R. (1974). Photosynthesis in plant canopies: effect of light response curves and radiation source geometry. *Photosynthetica* 8, 184-207.

Arney, S.E. (1953). The initiation, growth and emergence of leaf primordia in *Fragaria*. *Ann. Bot.* 17, 477-492.

Arney, S.E. (1954). Studies of growth and development in the genus *Fragaria*. III. The growth of leaves and shoot. *Ann. Bot.* 18, 349-365.

Barden, J.A. (1977). Apple tree growth, net photosynthesis, dark respiration and specific leaf weight as affected by continuous and intermittent shade. *J. Amer. Soc. Hort. Sci.* 102, 391-394.

Barua, D.N. (1969). Light as a factor in the metabolism of the tea plant (*Camellia sinensis* L.). *In* "Physiology of Tree Crops" (L.C. Luckwill and C.V. Cutting, eds) pp.307-322. Academic Press, London, New York.

Bassi, D., Sansavini, S. and Giunchi, L. (1980). Tree efficiency and fruit quality of high density apple orchards. *Obstbau Weinbau* 17, 236. Südtiroler Beratungsring, Lana.

Blencowe, J.W. (1969). "Crop Diversification in Malaysia." Incorporated Society of Planters, Kuala Lumpur.

Brünig, E.F. (1976). Tree forms in relation to environmental conditions: an ecological viewpoint. *In* "Tree Physiology and Yield Improvement" (M.G.R. Cannell and F.T. Last, eds)

pp.139-156. Academic Press, London, New York.
Bunting, A.H. (1976). Inaugural lecture. *In* "Tree Physiology and Yield Improvement" (M.G.R. Cannell and F.T. Last, eds) pp.1-20. Academic Press, London, New York.
Cain, J.C. (1972). Hedgerow orchard design for most efficient interception of solar radiation. Effects of tree size, shape, spacing and row direction. *Search Agr.* 2, 1-14.
Hadfield, W. (1968). Leaf temperature, leaf pose and productivity of the tea bush. *Nature* London 219, 282-284.
Harwood, R.R. and Price, E.C. (1976). Multiple cropping in tropical Asia. *In* "Multiple Cropping", pp.11-40. ASA Special Publication No.27. American Society of Agronomy, Madison, Wisconsin, USA.
Heinicke, D.R. (1966). Characteristics of McIntosh and Red Delicious apples as influenced by exposure to sunlight during the growing season. *Proc. Am. Soc. Hort. Sci.* 89, 10-13.
Hesketh, J.D. (1963). Limitations to photosynthesis responsible for differences among species. *Crop Sci.* 3, 493-496.
Hesketh, J.D. and Musgrave, R.B. (1962). Photosynthesis under field conditions. IV. Light studies with individual corn leaves. *Crop Sci.* 2, 311-315.
Jackson, J.E. (1970). Aspects of light climate within apple orchards. *J. appl. Ecol.* 7, 207-216.
Jackson, J.E. (1980). Light interception and utilization by orchard systems. *In* "Horticultural Reviews" (J. Janick, ed.) pp.208-267. AVI Publishing Co. Inc., Westport, Conn., USA.
Jackson, J.E. and Landsberg, J. (1972). The value of research in orchard climatology. *Span* 15, 63-65.
Jackson, J.E. and Palmer, J.W. (1972). Interception of light by model hedgerow orchards in relation to latitude, time of year and hedgerow configuration and orientation. *J. appl. Ecol.* 9, 341-357.
Jackson, J.E. and Palmer, J.W. (1979). A simple model of light transmission and interception by discontinuous canopies. *Ann. Bot.* 44, 381-383.
Jackson, J.E. and Palmer, J.W. (1981). Light distribution in discontinuous canopies: calculation of leaf areas and canopy volumes above defined 'irradiance contours' for use in productivity modelling. *Ann. Bot.* 47, 561-565.
Jacyna, T. (1978). Influence of light penetration on the quality of McIntosh apple fruits. *Fruit Science Rpt* 5, 7-17.
Lenz, F. and Daunich, H.J. (1975). Photosynthesis in strawberry plants. *Erwerbobstbau* 17 148-152. (Horticultural Abstracts, CAB, Slough, UK. Abstract No.6578, 1976.)
Monselise, S.P. (1951). Light distribution in citrus trees. *Bul. Res. Council of Israel* 1, 36-53.
Monsi, M. and Saeki, T. (1953). Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. [On the light factor in plant communities and its significance for dry matter production.] *Jap. J. Bot.* 14, 22-52.
Monteith, J.L. (1977). Climate and the efficiency of crop production in Britain. *Phil. Trans. R. Soc. Lond. B.* 281, 277-294.
Oikawa, T. (1977). Light-regime in relation to plant population geometry. II. Light penetration in a square-planted population. *Bot. Mag. Tokyo* 90, 11-22.

Oikawa, T. and Saeki, T. (1977). Light-regime in relation to plant population geometry. I. A Monte Carlo simulation of light microclimates within a random distribution foliage. *Bot. Mag. Tokyo* 90, 1-10.

Palmer, J.W. (1977). Light transmittance by apple leaves and canopies. *J. appl. Ecol.* 14, 505-513.

Palmer, J.W. and Jackson, J.E. (1977). Seasonal light interception and canopy development in hedgerow and bed system apple orchards. *J. appl. Ecol.* 14, 539-549.

Sale, P.J.M. (1974). Productivity of vegetable crops in a region of high solar input. III. Carbon balance of potato crops. *Aust. J. Plant Physiol.* 1, 283-296.

Sale, P.J.M. (1975). Productivity of vegetable crops in a region of high solar input. IV. Field chamber measurements on French beans (*Phaseolus vulgaris* L.) and cabbages (*Brassica oleracea* L.). *Aust. J. Plant Physiol.* 2, 461-470.

Sale, P.J.M. (1976). Effect of shading at different times on the growth and yield of the potato. *Aust. J. Agric. Res.* 27, 557-566.

Sturm, M. (1961). The influence of fruit trees on the light growth factor for intercrops. *Erwerbsobstbau* 3, 201-203.

Usher, M.B. (1970). An algorithm for estimating the length and direction of shadows with reference to the shadows of shelter belts. *J. appl. Ecol.* 7, 141-145.

Yu, I.C., Park, S.K. and Song, K.W. (1971). The effect of shade from vines on the growth and yield of strawberries grown in vineyards. *Rep. Rptr Office Rural Dev., Hort. Expt Stn, Suwon, S. Korea* 14, 19-23. (Horticultural Abstracts, CAB, Slough, UK. Abstract No.544, 1973.)

DISCUSSION

LOOMIS - There are two problems with your model. First, it assumes a constant K; second, its validation under diffuse light conditions should not have involved use of the Monsi-Saeki equation which is only valid for direct light.

JACKSON - I think it reasonable to assume a constant K under discontinuous canopy conditions. For example, if you have a continuous canopy with vertical leaves K will obviously be much lower at midday than when solar angles are lower, but in the case of a tree, where K is probably determined more by clustering of leaves due to branches, a very similar arrangement is presented to light throughout the day: the high angle sun shines down on vertical branches; the low angle sun laterally into horizontal branches. The equation used in validating the model was essentially Beer's Law, which applies to both direct and diffuse light, not a more complex equation. Validation was under diffuse light conditions because it is easier to obtain a whole day which is cloudy with only diffuse light than a whole day with bright sunshine under UK conditions.

LOOMIS - If there is shade the biological productivity of all crops, including potatoes, will be decreased because it will decrease the time period during which the leaves are light saturated.

JACKSON - Sale's results still showed hardly any effect of heavy shading on potato yields in Australia.

NAIR - Sun elevation is important. In coconuts 55 per cent of the light may be intercepted between 10.00 and 16.00 hours.

JACKSON - We have computed light interception for all sun elevations in all seasons at our latitude and used these integrated values in our modelling.

TIESZEN - We must remember that there are plants in which the leaves change angle - both solar trackers and solar avoiders.

HUXLEY - We also have to remember effects of incoming solar radiation on other processes. For example, many tropical plants close their stomata during the midday period. For this, and other reasons, shade can be beneficial.

CROP WATER USE: PRINCIPLES AND SOME CONSIDERATIONS FOR AGROFORESTRY

L. LEYTON
Department of Forestry, University of Oxford, South Parks Road, Oxford, UK.

ABSTRACT. The concept of using seasonal water balances to provide both a description of climate and a relevant guide to the choice of cultivated plant species is now well established. The paper outlines some commonly used approaches to estimating evaporation and points out that account must be taken in calculating water balances of the interception losses that can occur especially where woody perenials are grown. Aspects of some factors affecting crop water consumption, and the effects of water depletion, are noted and the need to know more about rooting and competition for water in agroforestry situations is stressed. The complexity of the water balance situation when trees or bushes are grown in association with agricultural crops provides a challenge to agroforesters to define, clearly, the situations which should now be investigated. Only then can the information, ideas and methodologies relating to plant - soil water relationships, which have been amassed over the last few decades, be applied effectively.

RAINFALL

The type of crop or crops it is practical to grow in much of the warmer parts of the world is often determined by the rainfall, especially its seasonal distribution. Clearly, this also affects the choice of management system.

Depending on the nature and extent of the vegetative cover some rain will fall directly onto the ground surface through gaps in the plant canopy. The rest will be intercepted by foliage and branches, either to be re-routed to the ground via branches and main stem (stemflow), and by dripping from the crown or, in the case of wetted foliage, to be lost back into the air by evaporation.

Interception

Stemflow is important in so far as it concentrates rainwater around the base of the plant, hence not only affecting soil moisture distribution but also the degree of leaching. Both factors are of importance for understorey vegetation. For most trees and shrubs stemflow only amounts to about 5 to 10 per cent of the gross rainfall, but with certain species it is very much higher. Slatyer (1965) noted over 40 per cent of the gross rainfall as stemflow in *Acacia aneura*, for example.

Although water on the surface of leaves may reduce transpiration, it can evaporate about 5 to 6 times faster than water passing through the plant so that the result is a net loss to soil water known as the 'interception loss' (Rutter, 1975). The amount of this loss will depend on the amount of water that can be retained on the vegetation (the interception storage capacity) and the nature of the rainfall. Measurements on temperate vegetation indicate interception storage capacities of about 1 to 2 mm for conifer stands, about 1 mm for deciduous stands and from about 0.5 to over 2 mm for herbaceous covers (Rutter, 1975; Sinke, 1967; Leyton *et al.*, 1967). Few data are available for tropical vegetation, but they would be expected to be of the same order; Cooper (1980) quotes a value of 2.5 mm for tea. Continuous rain, as compared to short rainshowers leading to repeated wetting and drying of the foliage, will give relatively smaller or larger interception losses, respectively. Again data for tropical and subtropical vegetation are wanting. In temperate regions, losses of 15 to 40 per cent have been reported for conifers, and of 10 to 25 per cent for deciduous stands (Rutter, 1975). For 4-year-old Eucalyptus coppice in Israel, Karschon (1971) found an annual interception loss of about 96 mm, amounting to 15 per cent of the total rainfall of 644 mm. Ringoet (1952) reported an annual interception loss of 152 mm in an oil palm plantation at Yangambi with a total water income of 1950 mm.

Occult precipitation

It is evident that with a fairly dense vegetative cover and light, but frequent, rainshowers the amount of water actually reaching the ground may be substantially less than the gross rainfall. To some extent this loss may be compensated for by the condensation of mist or fog (occult precipitation). This is particularly prevalent in mountainous and coastal areas. According to Nicholson (1936) it accounts for up to 25 per cent of the total 'rainfall' in the montane forests of East Africa (for general reviews see Penman, 1963; Kerfoot, 1968; Rutter, 1975).

Drainage and soil evaporation

Water reaching the ground may be lost by deep drainage, ultimately to reappear as streamflow, or it may be retained in the soil, eventually either to be evaporated from the surface or taken up by plant roots and transpired. Under a reasonably dense plant cover the amount lost by evaporation from the soil surface is probably small, but it can be substantial from exposed bare soil, especially when irrigated (Hillel and Rawitz, 1972). In the oil palm plantation mentioned above Ringoet (1952) estimated

an annual loss of 307 mm by soil evaporation; almost as much as that lost by transpiration (400 mm). When water is in short supply it is essential to minimize soil evaporation, for example by regular hoeing of exposed soil (dry mulching).

POTENTIAL EVAPORATION AND THE WATER BALANCE

The highest possible yield of a crop can only be assured under conditions leading to maximum photosynthesis per unit area of land. In the case of C_3 and C_4 plants this means, among other things, that the stomata remain open as long as possible during the day to ensure maximum CO_2 uptake. This can only occur when the leaves are not waterstressed so that, other factors apart, the soil water supply must not be limiting, that is, it must be at or near field capacity.

Empirical estimates of evaporation

Using a combination of meteorological data. Under such circumstances, and assuming a complete crop cover, transpiration (evaporation) occurs at a rate, the potential rate (E_T), determined largely by the evaporative conditions of the air. Essentially, three factors are involved.

(1) The vapour pressure deficit of the air (VPD). That is the difference between the vapour pressure of saturated air (e_s), at the prevailing air temperature, and the existing vapour pressure (e). Thus,

$$E_T \propto (e_s - e).$$

(2) Windspeed. Increasing the windspeed leads to greater turbulent transport of water vapour from the leaves to the bulk air above. The taller the plant, and the rougher and larger the crown, the greater will be the rate of turbulent transport at a given windspeed (Fig. 1). This is one of the reasons why, under

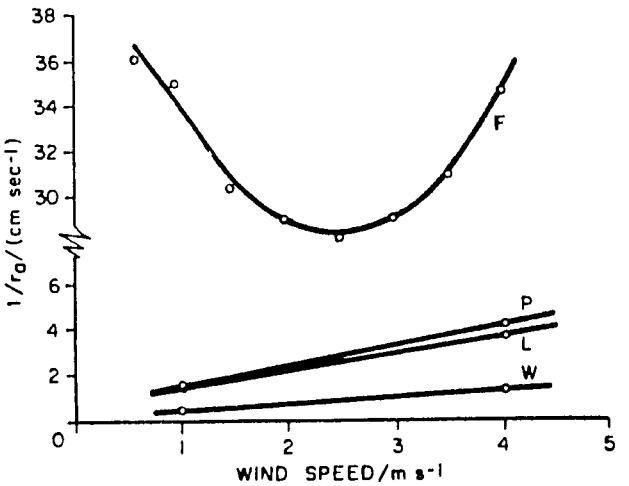


Fig. 1. Relation between eddy conductivity and windspeed for different crops. F - conifer stand; P - potato; L - lucerne; W - open water surface. From Szeicz *et al.* (1969). Copyright American Geophysical Union.

the same conditions, tree crops transpire faster than shrubs and herbs, and why water intercepted on tree foliage evaporates more rapidly than an open water surface at ground level. For a given crop at a given windspeed E_T can be expressed as a simple function of the windspeed (U).

(3) Heat energy. In order to convert liquid water to water vapour heat energy (latent heat) is required and, normally, this comes directly from solar radiation. Allowance has to be made for the reflection of solar radiation from the surface of the foliage (the reflection coefficient, or albedo) and for long wave thermal radiation exchange between the foliage and environment. At any one moment in time the balance, that is the rate at which energy is being absorbed by the foliage, is known as the net radiation (R_N). Ignoring the small fraction used in photosynthesis, and allowing for a certain amount of heat stored in the foliage and ground (G), the remainder, $R_N - G$, is dissipated by heat loss to the air (H), and as latent heat in evaporation (λE where λ = latent heat of evaporation). Thus,

$$R_N - G = H + \lambda E.$$

In his well-known and probably most widely used evaporation equation, Penman (1963) combined the aerodynamic factors (VPD, U) with the energy factor ($R_N - G$). His original equation related to the rate of evaporation from an open water surface (E_O), and an empirical coefficient (average about 0.7) was used to convert E_O to E_T. Later, by taking into account the reflection coefficient of the crop, and its extra roughness, he produced a second equation which could be applied directly to the crop:

$$E_T = \frac{(\Delta/\gamma)(R_N - G) + 0.35\ (1 + U/100)(e_s - e)}{\Delta + \gamma}$$

where Δ = the slope of the saturation vapour pressure/temperature curve at the mean air temperature, and γ = the psychrometric constant.

Although originally based on a complete short grass cover, this equation, with minor modifications to the empirically derived coefficients, has been found to apply with reasonable accuracy to other crops, including deciduous forest, over a wide range of climates. Air humidity, air temperature and windspeed are regular meteorological measurements in many countries, but R_N is not; although it can be measured directly using a net radiometer. In order to estimate this, Penman used published data on solar radiation income above the atmosphere (R_C), mean air temperature, and daily hours of bright sunshine (n) so as to allow for absorption of radiation by cloud. During the day G is usually so small, compared with R_N, that it can be ignored.

In the United Kingdom, the Meteorological Office has computerized the calculations and produces monthly estimates of E_T for almost every part of the country. The practical importance of these is that when the rainfall is below E_T the difference provides a quantitative measure of the water deficiency and therefore a far better guide to the water status of crops than rainfall alone; thus it serves as a guide to irrigation requirements. When water is in short supply, this is of considerable economic importance.

In their intensive hydrological investigations, the East African Agricultural and Forestry Organization (EAAFRO) used Penman's first equation to calculate E_O for various catchment areas in East Africa (Blackie, 1980a; Edwards and Blackie, 1980). Their data for Kericho and Atumatak in Kenya are illustrated in Figure 2, and even though in terms of E_O and not E_T clearly reflect differences between the water balances of the two areas. Except perhaps in December and January the balance is always positive at Kericho, but that at Atumatak, almost always negative. It should be noted, however, that these are mean values over periods of 10 years or more; in some years, the water balances were very different.

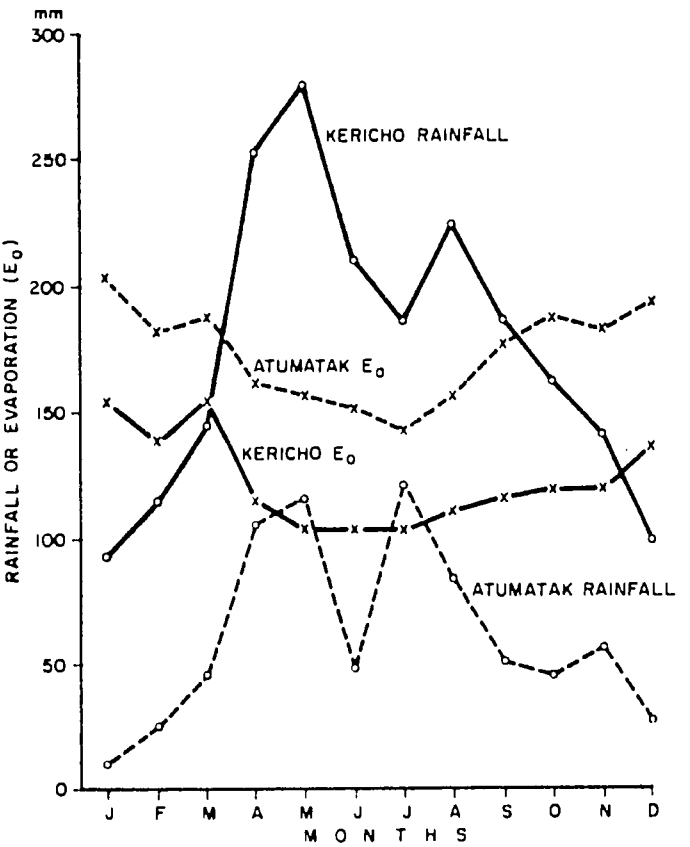


Fig. 2. Mean monthly rainfall and potential evaporation (E_O) for Kericho and Atumatak catchments. Redrawn from Table 5 in Blackie, 1980a and Fig. 1 in Edwards and Blackie, 1980.

Using net radiation. Apart from EAAFRO's studies, few such detailed measurements have been made in the tropics or subtropics, largely because of the absence of the necessary meteorological data. Several short cuts have therefore been tried. Since R_N is by far the most important climatic factor concerned, attempts have been made to estimate this from measurements of solar radiation incident on the crop (S_i) according to a simple relationship of the form $R_N = a + bS_i$. Although the coefficients a and b vary from crop to crop, all

agree to within ± 20 per cent (Denmead, 1976). However, even incident solar radiation measurements are relatively scarce in the tropics, so recourse is commonly made, as in Penman's approach, to estimating R_N from incoming radiation above the atmosphere (R_c, obtained from published data for different latitudes and times of year) and allowing for cloud by using daily hours of bright sunshine. For the African continent, Davies and Robinson (1977) have worked out a simpler relation, $R_N = 0.617\ R_c - 24$ which incorporates a vegetation reflection coefficient of 0.25. Assuming a negligible contribution from humidity and wind factors, and that all the net radiation is used for evaporation, it is then only a matter of dividing R_N by λ (2.45 MJ/kg) to obtain the equivalent rate of potential evaporation. Davies and Robinson have produced maps of Africa showing average rainfall, estimated average potential evaporation and the difference between the two for each month. These show how widespread and severe are the rainfall deficiencies. In fact, only about 10 per cent of the continent has a positive water balance in any one month.

According to Monteith (1977) the approximation $E_T = R_N$ can be accepted provided that it is not applied to irrigated plantations surrounded by dry land where there is an 'oasis effect'. That is advection of hot dry air into the area. The approximation does not apply to CAM crops, such as pineapple, which close their stomata during the day. The net daily income of radiation in the tropics ranges from about 7 MJ/m² during the cloudiest part of the year near the equator to about 12 MJ/m² at the margins of subtropical deserts. These give an E_T range of about 3 to 5 mm per day, but much higher values, of the order of 10 to 15 mm per day have been reported for irrigated crops.

Using mean air temperature. Several more empirical evaporation equations have been used in practice (for example, Thornthwaite, 1948; Blaney and Criddle, 1950) all depending to a greater or lesser extent on mean air temperature, which is related to R_N. Among the simplest and crudest is that of Khosla for India (Jaiswal, 1980) which gives monthly E_T (cm) = 0.461 × mean monthly temperature (°C). A somewhat similar approach has been used by Walter and Lieth (1960) in their *World Climate Atlas*; this is based on the assumption that a rise in mean air temperature of 10°C is equivalent to an extra 20 mm precipitation requirement. Some examples of their seasonal water balance diagrams for South America are reproduced in Figure 3. Though caution must be exercised in making practical judgements from data of this kind, they provide a better basis for the classification of climates than rainfall alone. Various indices of aridity have been proposed in the past (Moreau, 1938). One of these is De Martonne's index, $i = P_a/T_a + 10$, where P_a, T_a represent, respectively, the mean monthly precipitation and air temperature. Although superficially attractive, equations of this kind are far too crude to be of real practical or ecological value.

Direct measurement

The direct measurement of evaporation using evaporation pans is a common meteorological practice and, although the heat balance

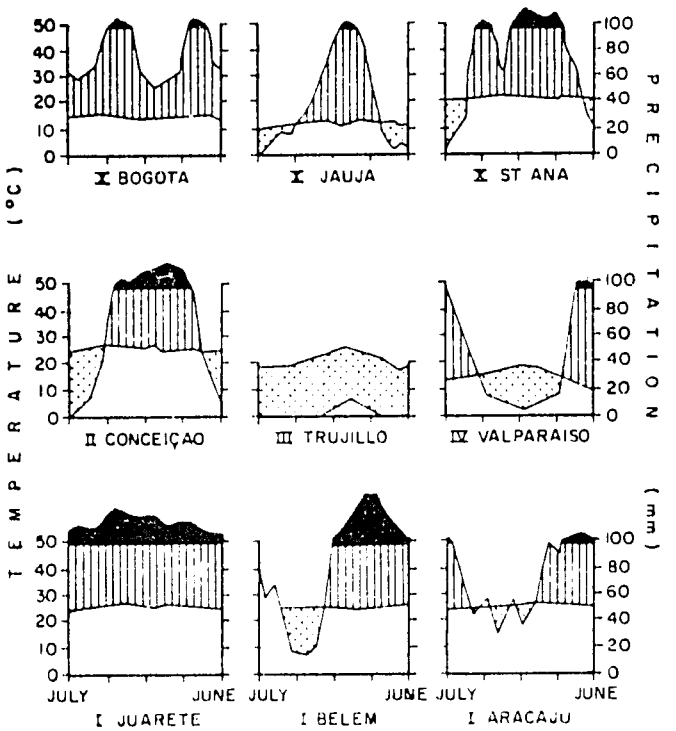


Fig. 3. Climatic diagrams for selected regions of South America. Drought periods - dotted lines; humid periods - vertical hatching; precipitation exceeding 100 mm - black. Reproduced from Walter and Lieth (1960), with permission of the publishers Gustav Fischer Verlag.

and aerodynamic properties of pans are very different from those of a crop, the simplicity of this measurement may appeal to those unwilling or unable to undertake more sophisticated measurements. Edwards and Blackie (1980) found that, during the wet season at Atumatak, the ratio between Penman's E_0 and Class A pan evaporation lay between 0.9 and 1.0. However, during the hot, dry period, when Penman's E_0 was 6 to 8 mm per day, pan evaporation was over 10 mm per day; probably because the Penman formula does not allow for advected energy. Usually, the ratio between potential evaporation (E_p) and Class A pan evaporation ranged from 0.7 to 0.8, being in good agreement with Penman's findings. It seems, therefore, that in the absence of other climatic data, Class A pan evaporation is a useful substitute for assessing the water balance of an area. In Malawi (Anon., 1963) yields of sugar cane were greatest when irrigated according to the difference between pan evaporation and rainfall, but during the driest period the water supply had to be increased to 1.4 times pan evaporation to maintain good yields.

Classifying climate on seasonal water balance

Classifying the climate in terms of the seasonal water balance between rainfall and potential evaporation has considerable advantages over more descriptive schemes as far as crop

selection and management are concerned. Indeed, it makes possible a simple distinction between wet equatorial regions, where rainfall exceeds E_T in every month of the year; monsoon regions, with one marked wet season in which rainfall exceeds E_T and there is a dry season in which it is less; and savanna regions, with one or two very dry seasons separated by very wet seasons in which rainfall substantially exceeds E_T (Monteith, 1977).

It must be appreciated that rainfall in many of the areas concerned is often quite unreliable and varies from year to year to a much greater extent than E_T. A feature of Indian agriculture, for example, is to arrange intercropping so that, if the dry period is unusually prolonged, at least one crop will survive. However, although there is considerable agricultural potential in assessing and analysing rainfall reliability, particularly in relation to planting dates, relatively little of this has been done outside East Africa (Gregory, 1969).

CROP WATER CONSUMPTION

Water use and the soil

Even when soil moisture is plentiful there are often occasions when, because of excessively high water demands, leaves develop water deficits, the stomata close and, with the exception of CAM plants, photosynthesis virtually ceases. Such events are unavoidable, especially when the foliage is exposed directly to sunlight, but they are usually of short duration. The situation is more serious when rainfall ceases for any length of time. When this occurs, plants must rely on water stored in the soil. How long this will suffice to maintain active growth will depend largely on the physical nature of the soil and on rooting depth. For each metre depth a sandy soil can only store about 6 cm of available water, whereas a clay soil may store 20 cm, or more if organic matter is present (Salter and Williams, 1965). At a potential evaporation rate of 5 mm per day plants rooting to a depth of 1 m will continue to transpire for about 10 days in a sandy soil, but for over a month in clay. Deep rooting is therefore a considerable advantage to plants during dry periods unless they can be irrigated.

Physiological effects of water stress

As soil moisture becomes depleted, but high evaporative conditions persist, leaves will experience an increasing degree of water stress. Besides a reduction in transpiration, many other physiological processes are adversely affected. As shown in Table 1, even moderate stress will slow down or stop cell division; this leads to a reduction in leaf area and in transpiration which, although delaying the onset of more severe stress, will not prevent it. As moisture stress increased, photosynthesis is further reduced as a result of stomatal closure, increasing mesophyll resistance and enzyme inactivation. However, the response varies with species (Table 2). C_4 plants, which are typically associated with semi-arid habitats, adapt to water stress by closing their stomata at higher potentials (less stress) than C_3 plants. CAM plants avoid stress by closing their stomata during the day and opening them at night.

Table 1. Generalized sensitivity to water stress of plant processes or parameters

SENSITIVITY TO STRESS[a]

Very sensitive → Relatively insensitive

REDUCTION IN TISSUE Ψ REQUIRED TO AFFECT PROCESS[b]

Process or parameter affected	0 bar	10 bars	20 bars	Remarks
Cell growth	————			
Protein synthesis	————			Fast growing tissue
Stomatal opening	---- ————	————	———	Depends on species
CO_2 assimilation	---- ————	————	———	Depends on species
Respiration	-----	————		
Sugar accumulation		————		

a) Length of the horizontal lines represents the range of stress levels within which a process becomes first affected. Dashed lines signify deductions based on more tenuous data.
b) With Ψ of well-watered plants under mild evaporative demand as the reference point.

From Hsiao (1973).

Table 2. Maximum and minimum leaf water potentials at which stomata close. (From Ludlow, 1980).

C_3 plants	*Glycine max*	-16 to -29
	Gossypium hirsutum	-30 to -43
	Eucalyptus socialis	-25 to -43
	Larrea divaricata	-40 to -58
C_4 plants	*Zea mais*	-11 to -28
	Sorghum bicolor	-15 to -28
	Panicum maximum	-17 to -30

Water consumption

Because of stomatal closure for shorter or longer periods, actual water consumption of a crop is generally less than E_T. Theoretically, it can be calculated from Monteith's (1965) modification of the Penman formula in which the degree of stomatal closure is quantitatively represented by a crop diffusion resistance, and the effect of wind by an air diffusion resistance.

The problem in applying this formula is the difficulty in measuring these diffusion resistances in the field without sophisticated micrometeorological techniques. Perhaps the simplest alternative is to measure the change i soil moisture content down to the lowest limit of the root system during dry periods when drainage losses are minimal. Some results obtained by EAAFRO for mountain evergreen forest, bamboo forest and a tea plantation at Kericho during the 1971 drought (Eales, 1980) are shown in Figure 4.

Data of this kind are of considerable importance to foresters and agronomists, not so much in respect of total moisture consumption, but as a guide to rooting and moisture uptake with depth, and hence the degree of competition that might be expected in intercropping systems. We see from Figure 4 that under all three types of plant cover the greatest depletion occurs in the top metre or so of soil, probably due to both surface evaporation and superficial roots. Lower down, the evergreen forest causes greater depletion between 2 and 3 m, bamboo between 3.5 and 4 m whereas tea, presumably more shallow rooted on this site, takes up relatively little water below 2 m. Of the total water depletion down to 4.5 m, tea extracted 73 per cent from the top 2.7 m and evergreen forest about 69 per cent, but bamboo less than 50 per cent, in spite of its overall lower water consumption. These moisture contents were largely determined using a neutron moisture meter, but useful data can be obtained, though more tediously, by augering and gravimetric sampling.

Over large areas serving as catchments the water consumption of vegetation may be determined from the difference between rainfall and streamflow (R - Q), if necessary after making allowance for changes in soil moisture storage. Numerous such measurements have been made in East Africa by EAAFRO, allowing for comparisons between Penman E_o and actual evaporation losses (Blackie, 1980a, b; Edwards, 1980). At Kericho and Kimakia, where the annual rainfall is relatively high and reasonably well distributed over the year (see Figure 2), the actual water

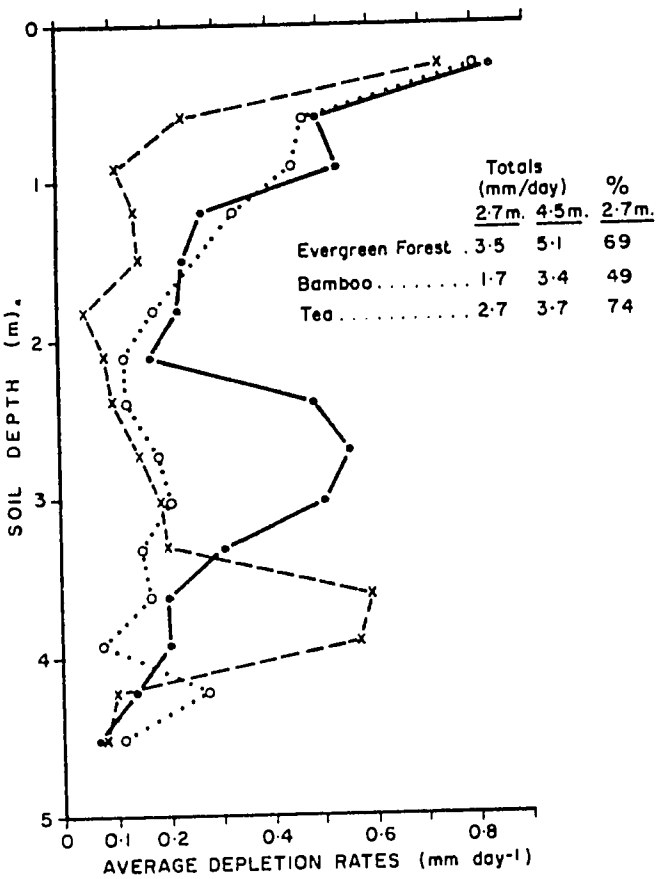


Fig. 4. Soil moisture profiles in evergreen and bamboo forest, and in a tea plantation at Kericho. Redrawn from data of Eales (1980).

consumption generally approached the potential level (around 0.7 to 0.8 E_o, see Table 3). In a newly cultivated area at Mbeya and with a greater seasonal variation in rainrall, water consumption also approached the potential level during the wet season, but it was very much less during the dry season, thus giving a lower measurement value (0.65).

In cropping practice determining the actual water consumption is often of less interest than monitoring the moisture status of the crop throughout the growing season by means of, for example, measurements of stomatal diffusion resistance. Modern automatic leaf diffusion resistance porometers, which are transportable, make this a relatively simple procedure.

Water use efficiency

Clearly, it would be of considerable value when selecting crops to know whether one species is more efficient in using water than another, especially where water is scarce. Much attention has been given to the transpiration ratio, that is the amount of water lost by transpiration per unit of dry matter production. Some published values for tropical crops are given in Table 4.

Table 3. Summary of EAAFRO catchment studies (mean annual values). (From Blackie, 1980a, b; Edwards, 1980.)

		mm R	mm R - Q	mm E_o	$(R-Q)/E_o$	Range
Kericho 1962-73	Forest control	2105	1316		0.92	(0.76 - 0.84)
	Cleared for tea	2021	1215	1474	0.84	(0.74 - 0.96)
	Bamboo	2036	1239		0.86	(0.79 - 0.97)
Kimakia 1967-73	Bamboo/evergreen	2140	1165		0.76	(0.74 - 0.82)
	Pine plantation	1993	1163	1514	0.77	(0.69 - 0.84)
	Mixed bamboo/pine	2062	1054		-	
Mbeya 1958-68	Tall evergreen	1899	1381*	1484	0.92 ± 0.06	
	Newly cultivated	1657	970*	1510	0.65 ± 0.03	

* Corrected for soil moisture changes

R = rainfall, Q = streamflow, E_o = evaporation

Table 4. Transpiration ratios of tropical crops (g water per g dry matter).

Species	Mean ratio	Authority
Oil palm	294	Ringoet (1952)
Upland rice	413	"
Robusta coffee	578	"
Cacao	866	"
C_3 plants	450 - 950	Black (1973)
C_4 plants	250 - 350	"
CAM plants	50 - 55	"

These values must not be taken too seriously. Transpiration is difficult to measure in the field so that most, if not all, data are derived from pot cultures and therefore under very different conditions. Furthermore, much depends on the water available. Ringoet (1952) found that as soil moisture was increased from 11 to 19 per cent, the transpiration ratio of oil palm increased from 164 to 337 and that of Robusta coffee from 515 to 613. There are also several other factors such as soil fertility and temperature which may influence yield more or less independently of water supply.

CROP WATER REQUIREMENTS

The enormous literature on tropical and subtropical agriculture and forestry provides a wealth of guidance as to the selection of crops and their management. Comprehensive publications such as the Indian *Handbook of Agriculture* (Jaiswal, 1980) and the French *Mémento de l'Agronomie* and *Mémento du Forestier* (République Française, 1974, 1976) include information on the water requirements of different species and give detailed guidance on cultural practices including irrigation. Webb *et al.* (1980) have recently produced a comprehensive guide to the selection of over 120 tree species based on an attempt to equate conditions at the trial site with known and reported characteristics. The guide is adapted for punched card or computer, and it incorporates site factors (climatic, edaphic) as well as product objectives (whether for sawn timber, pulp, fuelwood, etc.).

Valuable as these publications undoubtedly are, the final test of a species or system of management must be made on site and, where the rainfall varies from year to year, over a period of years. The question that must now be asked is: in the light of our increasing knowledge of the ecophysiology of crops, especially of their water relations, can we improve on existing recommendations?

Overcoming the effects of water deficiency

In the wet equatorial regions, with a positive water balance throughout most if not all the year, there are no water deficiency problems. On the contrary, it may be that where the forest is cleared for shifting cultivation excess rainfall may prove disadvantageous. The constant, humid climate allows a wide variety of crops to be grown, either temporarily, or

permanently as in the cases of cacao, oil palm or rubber.

The real problems occur in those areas in which a negative water balance persists for some length of time. One of three strategies may then be adopted depending on the length of the dry period: irrigation; growing those crops which complete at least most of their growth cycle during the period when moisture is available; or the cultivation of drought resistant crops.

Where it is practicable and economically feasible to do so by far the best solution is to irrigate. The additional water requirements can be determined with reasonable confidence from the difference between potential evaporation and the rainfall. Where irrigation water is scarce it may only prove necessary to irrigate during specific periods. There is considerable evidence that most annual crops exhibit a particular sensitivity to moisture stress from the time of flower initiation, during flowering and, to a lesser extent, during fruiting and seed development (Salter and Goode, 1967). Maize, during tasselling and silking and during early grain formation, sorghum at the end of tillering, rice just before flowering, and cotton before flowering and boll formation, are all critically affected by moisture stress. If water is in short supply during these stages the yield may be irreversibly harmed. It appears that during the flowering and fruiting stages, root growth is retarded or ceases completely, so worsening the situation (Leonard, 1962).

Perennial crops are also sensitive to water stress during the same reproductive stages, though probably no more so than during early vegetative growth. Perhaps the most critical stage for perennials is during the period when leaf area, and hence water demand, is increasing most rapidly. As this period does not appear to coincide with that of maximum root growth it is essential that there are no restrictions on moisture supply at this time if later growth and yield are not to be seriously diminished. Rapid vegetative growth is also an important requirement for high yields in those crops, such as sugar cane, that benefit from moisture stress just prior to harvesting. Mature mango trees may also be irrigated to encourage a particular growth flush so that they will flower and fruit at a desired time.

Since irrigation (or rainfall) at a particular growth stage may facilitate nutrient uptake by increasing nutrient availability and/or providing suitably moist conditions for root activity, it is possible that these drought sensitive stages are also times at which mineral nutrient uptake may be affected detrimentally. In the field, these two factors cannot easily be separated. There are also cases where restricted moisture supply can have a beneficial effect. For example, water stress during the early growth of an annual crop may promote early flowering which, in some cases, may be desirable.

It follows from the above that the cost-effectiveness of irrigation, in terms of yield, may be substantially improved by applying water only at those growth stages where the most beneficial responses are to be expected. However, if this is to be achieved in practice, attention must also be paid to previous weather conditions and to soil moisture. Fischer and Hagan (1965) have suggested that if the drought sensitive stages are of short duration, the temporary use of anti-transpirant sprays

may be justified. Many more comprehensive studies are necessary before this concept of drought sensitive stages can consistently be applied to economically important crops.

The method of irrigation also determines its cost-effectiveness. Drip irrigation, although involving higher initial costs and more maintenance than conventional channel techniques, is most economical in the long run because of smaller losses by deep percolation and surface evaporation.

Effect of shelterbelts

Because of the high water consumption of irrigated crops, especially when surrounded by arid areas, protection against hot, dry winds by shelterbelts is almost always essential. Comprehensive accounts, including practical details, are available in several reviews and texts (for example, World Meteorological Organization, 1964) and the scientific principles are described, among others, by Leyton (1975). It is important that shelter is provided down to the ground surface, and that the shelterbelt is partially permeable to air movement. The common use of Eucalypts and other fast growing trees, whilst often impressive, may eventually leave several metres above the ground surface unprotected except by stems. In such cases the tree belt must be underplanted with smaller trees or shrubs which are coppiced when necessary.

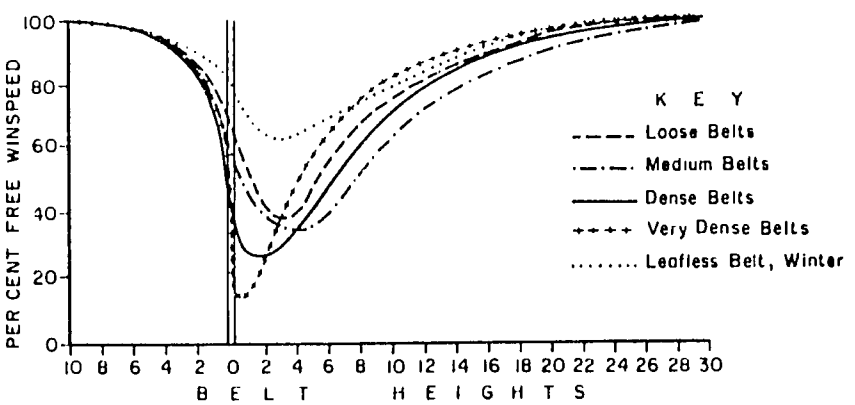


Fig. 5. Effect of shelterbelt permeability on relative windspeed pattern, 1.4 m above ground. Reproduced from Nägeli (1946) with permission of the Swiss Federal Institute for Forest Research.

Experiments have shown that the extent of the shelter effect, in terms of a reduction in windspeed, and therefore in evaporation, is proportional to the height of the belt. However, as is evident from Figure 5, there is a gradual increase in windspeed with distance behind the belt at a rate determined by its permeability. It is, therefore, common practice to define the sheltered zone as that over which the windspeed is reduced by at least 20 per cent. Depending on windspeed and permeability, this distance varies from about 15 to 20 times the height of the belt. Account must also be taken of the length of the belt and the wind direction. According to Nägeli (1946)

the length to height ratio should be at least 11.5 if it is to approximate to an infinitely long belt. With a ratio of only 2 the protected area will be about half the maximum.

ROOTING AND COMPETITION

Rooting depth

Competition for soil moisture between shelterbelts and crops, and between tree and crop components in agroforestry systems, raises the important issue of rooting depth. Deep rooting is an advantage to plants during dry periods. Many crop mixtures have been designed on the assumption that different crop plants root and take up water from different depths, hence minimizing competition. In the Indian *Handbook of Agriculture* (Jaiswal, 1980, p.182) the following examples are given, in relative terms, as maximum rooting depths in normal, well-drained soils:

medium - rice, millet, maize, groundnut, tobacco, cereals, banana;

deep - cotton, gram, sorghum, sugar cane, grain legumes, citrus;

very deep - fruit trees, forest trees.

Unfortunately, the situation is not nearly so straightforward as this classification suggests. Even between trees there are differences in moisture depletion rates with depth (Figure 4). Rooting depth is not solely determined genetically, but is also affected, and often much more so, by soil and climatic conditions. For example, Wallis (1963) found that in Kenya, unirrigated coffee rooted to a depth of about 3 m, whereas depths of only 0.3 m have been quoted for coffee in Uganda and in Central America (see Salter and Goode, 1967, p.118). These particular differences can probably be attributed largely to differences in rainfall. Unfavourable soil physical conditions and high water tables also restrict rooting depth.

Much of our difficulty in separating the various factors governing rooting depth arises from the paucity of objective experiments covering a wide range of environmental conditions, as distinct from just empirical observations. In some rhizotron experiments reported by Taylor (1980) all annuals tested, including groundnut, cotton, sweet potato, millet, sorghum and maize, had rooted by maturity to the maximum possible depth (1.68 m). The main differences between species lay in their rates of root growth, for example, whereas maize roots grew at a rate of 7.7 mm per day, with peanut it was only 3.7 mm per day.

Root activity

Rooting depth alone is not necessarily the best measure of root activity. Probably a better guide is the degree of exploitation of the soil as reflected in the root length density (RLD) expressed as rootlength (m) per m^3 of soil. This varies substantially between species (Kummerow, 1980). Generally, monocots have greater RLDs than dicots. For example, in the upper 1.3 m of soil, the RLD for maize was 0.22 but only 0.08 for soybean.

The RLD usually decreases with depth; in the case of sorghum from 4.0 to zero, at 5 and 95 cm soil depth, respectively. Kummerow draws attention to the importance of the fine roots (less than 1 mm diameter) which may comprise an important fraction of the total root biomass (50 per cent in southern Californian chaparral) but which are often ignored or overlooked in root studies. In the soil moisture depletion studies reported by Eales (1980) and illustrated in Figure 4, no bamboo roots were 'observed' below 2.4 m, yet over half the loss of water occurred between 2.4 and 4.5 m.

If we take into account variations in root growth and in moisture uptake according to the development stage of a plant, and also the effects of spacing, it is clear that much more research is necessary before the problems of rooting depth and competition for soil moisture can be clarified.

Root extension

Much the same confusion is apparent in relation to root extension growth. A generally cited adaptation to xeric conditions is a widespreading, shallow root system (Kummerow, 1980). This is, perhaps, understandable in view of the wide natural spacing of xerophytes in arid areas. In the case of trees under less arid conditions there is a general belief that roots do not extend much beyond the limits of the crown. However, measurements in the United Kingdom have shown that, on heavy clay soils at least, tree roots often extend as far as the height of the tree and, in certain cases (poplar and oak, for example), as far as twice their height. Few such measurements appear to have been published for tropical and subtropical trees, although this has an obviously important bearing on plant spacing and, in particular, on the effect of shelterbelts on the crops they are designed to protect. (For a more detailed discussion of rooting, see Huck, this volume.)

In recent years, evidence has been accumulating that the mycorrhizal habit (both ecto- and endotrophic) renders the host plant less susceptible to drought. Partly, it seems, through the greater effectiveness of the fungal hyphae in abstracting soil moisture, partly through an effect, not as yet completely understood, on the physiology of the host plant (Duddridge *et al.*, 1981; Hardie *et al.*, 1981). Since, in nature, most plants are mycorrhizal more attention must be paid to this feature, especially in the case of exotic crops in areas where the appropriate fungus may not be present. Besides affecting water relations the mycorrhizal habit invariably improves the phosphate status of the host plant. A particularly important factor where crops are grown on soils which fix phosphate.

THE COMPLEXITY OF MIXED AGROFORESTRY SYSTEMS

Where land is scarce, the simultaneous cultivation of tree and food crops may offer considerable economic advantages. However, in monsoon and savanna climates, with positive water balances during only part of the year, and even these subject to uncertainty from year to year, intercropping inevitably raises the question of below ground competition for water. This problem has already been discussed in relation to rooting depth and

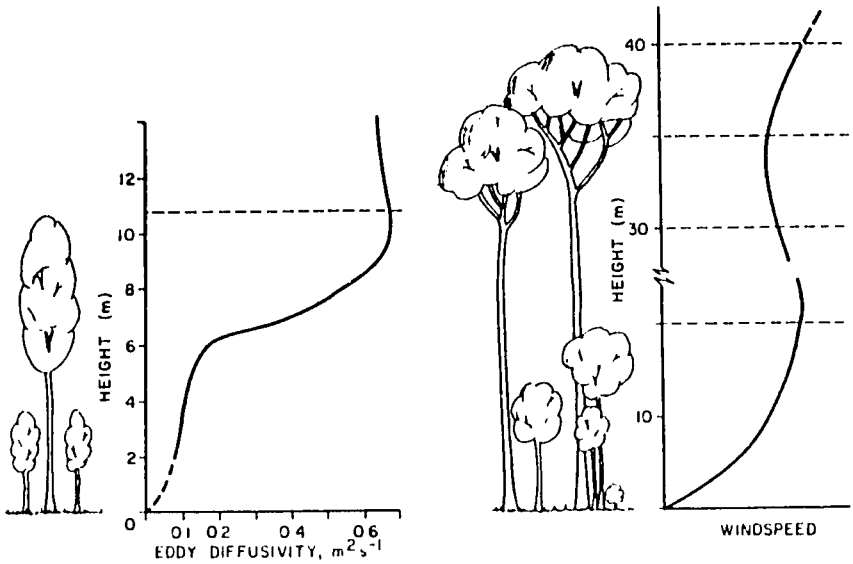


Fig. 6. Windspeed profiles in aspen stand in a temperate climate (redrawn from Rauner, 1975) and in a tropical rainforest (redrawn from Allen and Lemon, 1975).

spread. An additional consideration is to select combinations of crops which complete at least the most important part of their growth cycle during the period when adequate moisture is available. Although many woody perennial species may be assumed to be abstracting water from deeper regions of the soil than their companion agricultural crops their effects on the overall water balance are much more complex. For example, they will be responsible for changing the rainfall interception pattern (as discussed earlier), they may reduce (or enhance) windspeed over the agricultural crop, depending on their geometry, and they will cast shade on lower-storey crops.

An effect of reducing windspeed at lower levels, is clearly shown in Figure 6 for an aspen stand in a temperate climate (Rauner, 1975), and for a model tropical rainforest (Allen and Lemon, 1975). More widely spaced trees may have a different effect.

Since solar radiation accounts much more than wind for evaporation, except perhaps where an oasis effect is involved, the shading effect can be even more important. This of course will depend, again, on the density of the tree crowns (and see Jackson, this volume). Unfortunately, shading will also mean a reduction in photosynthesis, especially in the case of C_4 plants, so that often some compromise will be necessary, perhaps by regulating the overstorey canopy in relation to the light and water requirement of the understorey crops. Clearly, the outcome of such a complex situation will depend on many factors. A challenge for agroforesters now is to define clearly the situations which they wish to investigate.

REFERENCES

Allen, L.H. and Lemon, E.R. (1975). Carbon dioxide exchange and

turbulence in a tropical rainforest. *In* "Vegetation and the Atmosphere" (J.L. Monteith, ed.), pp.265-308. Academic Press, New York and London.

Alvim, P. de T. (1960). Moisture stress as a requirement for flowering in coffee. *Science* 132, 57-62.

Alvim, P. de T. and Kozlowski, T.T. (1977). "Ecophysiology of Tropical Crops". Academic Press, New York.

Anon. (1963). Irrigation studies - sugar cane. *Ann. Rep. Nyasaland Dept. Agric. 1961-62, Part 2*, pp.121-123.

Black, C.C. (1973). Photosynthetic carbon fixation in relation to net CO_2 uptake. *Ann. Rev. Plant Physiol.* 24, 253-286.

Blackie, J.R. (1980a). The water balance of the Kericho catchments. *In* "Final Report on the East African Research Project", Vol.II, chapter 2.2.1. Mimeo. Institute of Hydrology, Wallingford, UK.

Blackie, J.R. (1980b). The water balance of the Kimakia catchments. Ibid. Vol.III, chapter 3.2.1.

Blaney, H.F. and Criddle, W.D. (1950). Determining water requirements in irrigated areas from climatological and irrigation data. *U.S. Dept. Agric. Soil Conservation Service Tech. Pub.* 96 pp.

Cooper, I.D. (1980). Water use of a tea estate from soil moisture measurements. *In* "Final Report on the East African Research Project", Vol.II, chapter 2.2.3. Mimeo. Institute of Hydrology, Wallingford, UK.

Davies, J.A. and Robinson, R.J. (1977). A simple energy balance approach to the water balance climatology of Africa. *In* "Environment and Land Use in Africa" (M.F. Thomas and G.W. Whittington, eds), pp.23-56. Methuen, London.

Denmead, O.T. (1976). Temperate cereals. *In* "Vegetation and the Atmosphere" Vol.II (J.L. Monteith, ed.), pp.1-31. Academic Press, New York and London.

Duddridge, J.A., Malibari, A. and Reid, D.J. (1980). Structure and function of mycorrhizal rhizomorphs with special reference to their role in water transport. *Nature* 287, 834-836.

Eales, C.W.O. (1980). Soil moisture deficits under montane forest and tea. *In* "Final Report on the East African Research Project", Vol.II, chapter 2.2.5. Mimeo. Institute of Hydrology, Wallingford, UK.

Edwards, K.A. (1980). The water balance of the Mbeya catchments. Ibid. Vol.IV, chapter 5.2.1.

Edwards, K.A. and Blackie, J.R. (1980). Aspects of the hydrological regime of the Atumatak catchments. Ibid. Vol.III, chapter 4.2.1.

Fischer, R.D. and Hagan, R.M. (1965). Plant water relations, irrigation management and crop yield. *Expl Agric.* 1, 161-177.

Gregory, S. (1969). Rainfall reliability. *In* "Environment and Land Use in Africa" (M.F. Thomas and G.W. Whittington, eds), pp.57-82. Methuen, London.

Hardie, K. and Leyton, L. (1981). The influence of V-A mycorrhiza on growth and water relations of red clover. I. In phosphate deficient soil. *New Phytol.* 89, 599-608.

Hillel, D. and Rawitz, E. (1972). Soil water conservation. *In* "Water Deficits and Plant Growth" Vol.II (T.T. Kozlowski, ed.), pp.307-338. Academic Press, New York.

Hsaio, T.C. (1973). Plant responses to water stress. *Ann. Rev.*

Plant Physiol. 24, 519-570.

Jaiswal, P.L. (chief ed.) (1980). "Handbook of Agriculture". Indian Council of Agric. Res., New Delhi, India.

Karschon, R. (1971). The effect of coppice cutting on the water balance of *Eucalyptus camaldulensis* Dehn. *Israel J. agric. Res.* 21, 115-126.

Kerfoot, O. (1968). Mist precipitation on vegetation. *Forestry Abstracts* 29, 8-20.

Kummerow, J. (1980). Adaptation of roots in water-stressed mature vegetation. *In* "Adaptation of Plants to Water and High Temperature Stress" (N.C. Turner and P.J. Kramer, eds), pp. 57-73. John Wiley & Sons, New York, Chichester, Brisbane.

Leonard, E.R. (1962). Inter-relations of vegetative and reproductive growth with special reference to indeterminate plants. *Bot. Rev.* 28, 353-410.

Leyton, L. (1975). "Fluid Behaviour in Biological Systems". Clarendon Press, Oxford.

Leyton, L., Reynolds, E.R.C.R. and Thompson, F.B. (1967). Rainfall interception in forest and moorland. *In* "International Symposium on Forest Hydrology" (W.E. Sopper and H.W. Lull, eds), pp.163-178. Pergamon Press, Oxford and New York.

Ludlow, M.M. (1980). Adaptive significance of stomatal responses to water stress. *In* "Adaptation of Plants to Water and High Temperature Stress" (N.C. Turner and P.J. Kramer, eds), pp. 123-138. John Wiley & Sons, New York, Chichester, Brisbane.

Monteith, J.L. (1965). Evaporation and Environment. *In* "The State and Movement of Water in Living Organisms" (G.E. Fogg, ed.), pp.205-234. Cambridge University Press, Cambridge and New York.

Monteith, J.L. (1977). Climate. *In* "Ecophysiology of Tropical Crops" (P. de T. Alvim and T.T. Kozlowski, eds), pp.1-27. Academic Press, New York and London.

Moreau, R.E. (1938). Climatic classification from the standpoint of East African biology. *J. Ecol.* 26, 467-496.

Nägeli, W. (1946). Weitere Untersuchungen über die Windverhältnisse im Bereich von Windschutzanlagen. [Further investigations on wind conditions in the vicinity of shelterbelts.] *Mitt. Schweiz. Anst. Forstl. Versuchsw.* 24, 659-737.

Nicholson, J.W. (1936). The influence of forests on climate and water supply in Kenya. *East Afr. agric. J.* 2, 48-53; 164-170; 226-240.

Penman, H.L. (1963). Vegetation and hydrology. Tech. Comm. No.53. Commonwealth Bureau of Soils, Harpenden, UK.

Rauner, J.L. (1975). Deciduous forests. *In* "Vegetation and the Atmosphere" Vol.II (J.L. Monteith, ed.), pp.241-264. Academic Press, New York and London.

République Française, Ministère de la Coopération (1974). Techniques rurales en Afrique. *Mémento de l'Agronome*, 2nd edn, 1591 pp.

République Française, Ministère de la Coopération (1976). Techniques rurales en Afrique. *Mémento de l'Agronome*, 834 pp.

Ringoet, A. (1952). Recherche sur la transpiration et le bilan d'eau de quelques plantes tropicales. [Studies on transpiration and water balance of certain tropical plants.] *Pub. INEAC Sem. Sci.* 56, 139-154.

Rutter, A.J. (1975). The hydrological cycle in vegetation. *In*

"Vegetation and the Atmosphere" Vol.I (J.L. Monteith, ed.), pp.111-154. Academic Press, New York and London.

Salter, P.J. and Williams, J.B. (1965). The influence of texture on the moisture characteristics of soils. II. Available water capacity and moisture release characteristics. *J. Soil Sci.* 16, 310-317.

Salter, P.J. and Goode, J.E. (1967). Crop responses to water at different stages of growth. Res. Rev. No.2. Commonwealth Bureau Hort. Plant Crops, East Malling, UK.

Slatyer, R.O. (1965). Measurements of precipitation intercepted by an arid zone plant community. *Arid Zone Res.* 25, 181-192.

Szeicz, G. and Long, I.F. (1969). Surface resistance of crop canopies. *Water Resources Res.* 5, 622-631.

Szeicz, G., Endrödi, G. and Taschman, S. (1969). Aerodynamic and surface factors in evaporation. *Water Resources Res.* 5, 380-394.

Taylor, H.M. (1980). Modifying root systems of cotton and soybean to increase water absorption. *In* "Adaptation of Plants to Water and High Temperature Stress" (N.C. Turner and P.J. Kramer, eds), pp.175-184. John Wiley & Sons, New York.

Thornthwaite, C.W. (1948). An approach towards a rational classification of climate. *Geogr. Rev.* 38, 55-94.

Wallis, J.A.N. (1963). Physical aspects of water use by coffee in Kenya. Mimeo. 10th Meeting Spec. Ctee Agric. Bot., Nairobi, Kenya.

Walter, H. and Lieth, H. (1960). "Klimadiagramm Weltatlas". [World Climate Atlas.] Gustav Fisher Verlag, Stuttgart, W. Germany.

Webb, D.J., Wood, P.J. and Smith, J. (1980). A guide to species selection for tropical and substropical plantations. *Trop. For. Paper* No.16. Commonwealth Forestry Institute, Oxford, UK.

World Meteorological Organization (1964). Windbreaks and shelterbelts. Techn. Note 59. W.M.O., Geneva, Switzerland.

Zinke, P.J. (1967). Forest interception studies in the United States. *In* "International Symposium on Forest Hydrology" (W.E. Sopper and H.W. Lull, eds), pp.137-161. Pergamon Press, Oxford and New York.

DISCUSSION

KOZLOWSKI - Considering that water deficit is the resultant of the transpiration - absorption relationship, the problem can be tackled either by working on the leaf surface - root surface relationship, or by reducing transpiration through chemical or physical components. In this respect antitranspirants induce stomatal closure and can be harmful, particularly with gymnosperms.

LOOMIS - Plastic covers to decrease soil evaporation should be avoided because of their high cost and soil mulching effect which considerably reduces water loss.

Antitranspirants should not be used under practical conditions because: (*a*) they are very expensive; (*b*) they require skill to apply correctly; and (*c*) they cannot be removed (for example, when light rain falls). There are three alternative strategies to overcome water stress: (*a*) early maturation (trying to match

crop duration and water supply); (*b*) cropping in the cool season (reducing evapotranspiration); and (*c*) a non-uniform ground cover, either in space (low percentage cover), or in time (crop fallowing).

STEPPLER - Silvicultural managemant could be explored as a means to influence canopy structure and hence throughfall and stem-flow. Also, the observation and measurement of the root systems of mixed crops of woody and herbaceous components are likely to pose some difficulties.

BRUNIG - Measurements and calculations for different natural forest types in the Amazon Ecosystem MAB Project in San Carlos and in Borneo and Malaya have shown that soil depth and texture, and forest stature and structure have a strong effect on the evapotranspiration rates and water balance. In these areas, soil water depletes to very low levels during prolonged periods of bright, rainless weather and high saturation pressure deficits in spite of the seemingly ever-wet climate suggested by the climate diagrams of Walter Lieth. The structure, physiognomy and physiology of the natural vegetation are well adapted to these conditions, while in forest plantations these often are not. The interaction between climatic variation, soil water potential and tree crop properties must be carefully considered in designing agroforestry crops.

BUDOWSKI - The assumption that deep rooting plants should be always preferred in agroforestry systems is one to be challenged. Also, under certain conditions, nutrient cycling could be favoured by selecting plants and/or silvicultural management techniques which induce leaf and root shedding in stress situations.

PLANT STRESS FACTORS AND THEIR INFLUENCE ON PRODUCTION OF AGROFORESTRY PLANT ASSOCIATIONS

D.J. CONNOR
School of Agriculure, La Trobe University, Bundoora 3083, Australia.

ABSTRACT. An attempt is made to identify the interactions between plant and environment which will lead to the development of differential stress between the perennial and herbaceous components of agroforestry associations. On this basis suggestions are made concerning the preferred characteristics of the components of these associations and how they might be managed to maximize productivity and stability under stress.

It is explained that the resource pools of light, water and nutrient are not just different physically and chemically, but also with respect to the predictability with which suboptimal levels occur and are replenished. Predictability of replenishment and the behaviour of companion species are the important determinants in the development of adaptively successful responses. This is demonstrated by reference to the behaviour of natural vegetation, crops and pastures.

The components of agroforestry associations can be drawn widely from available plants so that their ability to handle stresses can be based upon different physiological or anatomical responses. It is important not only to understand the basis of their adaptation but also the extent to which the adaptations to stress of the potential components are competitive or complementary.

INTRODUCTION

In this paper we are directing attention towards that subset of agroforestry systems (Huxley, 1979) involving tall, woody, perennial trees or shrubs and short, herbaceous crops or pastures planted in such a way that there is considerable microclimatic interaction between the two components. In such systems the trees or shrubs will be distributed either singly, in small groups, or in rows, such that the interspecific perimeter is

long per unit land area.

This is an important restriction because if the aggregated sole units, trees or herbaceous species, are large in extent relative to the size of the trees then the system is one in which interaction during growth is dominantly intraspecific. For such systems the first step is to understand the behaviour of the individual components and to aggregate, with appropriate consideration of temporal rotational effects, a farm or region as the sum of the components. An appreciation of the interspecific interactions at the boundaries of the sole units becomes appropriate later, presenting a second level of precision.

The objective of this paper is to consider the ways in which nonoptimal levels of the environmental resources, water, light and nutrients, affect the growth and yield of the components of agroforestry associations and how in turn growth and resource use themselves contribute to the development of differential stresses. Differential stresses generated or intensified within communities are the potent forces that tend to destabilize the associations. An appreciation of the ways in which components interact in their procurement of environmental resources forms the basis for the selection of compatible components and of their management in stable, productive associations.

THE RESOURCE POOLS

For continued growth plants require continuous and balanced access to the resource pools of light, water and nutrients. Their growth responses must be adapted to the regional climate and to the behaviour of the cohabiting species. Growth implies resource use and hence a gradual diminution in the sizes of the pools. Opposing physical and chemical forces of the natural environment tend to replenish the pools although they may also, like plant growth, cause losses. A large part of the discussion that follows revolves around a consideration of preferential access and differential response to these environmental resources. For this reason it is important to establish their critical characteristics.

Light

A resource that is instantaneously available and if not used immediately in the photochemical reduction of CO_2 is lost to all plants in a community. There is no storage. The resource level varies widely with both strong diurnal and, except at equatorial locations, seasonal fluctuations. Its level changes rapidly, in the order of minutes or hours, but at any location its diurnal and seasonal levels are usually highly predictable. Preferential access relies upon canopy display in which *stature* is the most advantageous attribute. Differential response exists and can be quantified in leaf photosynthesis versus light response functions. Efficient utilization of both high and low intensities confer competitive advantage.

Water

This is available to plant roots from the soil within their root zone. If it is not used immediately it remains in the soil for

future use. Depending upon the soil depth and physical characteristics, the storage may be large (for example, 200 mm m^{-1} depth) relative to the rate of use by even actively transpiring and growing plants (for example, 8 mm day^{-1}). The storage is not perfect because losses may occur both upwards, by evaporation from the soil surface, and downwards to below the root zone even at nonsaturated water contents. Water below the root zone may become available by upward flow, when soil water potential gradients are appropriate, but more effectively by downward extension of the root zone. Changes in the level of soil water depend upon the pattern of rainfall but, by comparison with the hour by hour changes in the level of light, the changes are more appropriately measured in weeks. Preferential access relies upon the *relative root profiles* of the component species and differential access upon the *efficiency of extraction* per unit of rooting volume. High root density and low root water potential both contribute favourably to this. In drying soils the resistance to flow of water to and across the soil - root surface interface increases dramatically. Consequently high root density is likely to be the more effective basis of improved access to soil water.

Nutrients

These, like water, are located in the soil and also, like water, are available for immediate use or may remain stored for the future. Once again storage is not perfect with possible losses at the soil surface by volatilization and by erosion, and to depth by leaching. Additionally, nutrients may be rendered unavailable by chemical alteration. Nutrients located below the root zone can become available only by extension of the root system. In the absence of serious erosion, surface deposition, or fertilization changes in overall fertility are slow, are measurable in years, and rely upon continued weathering of the parent material both within and below the root profile and the redistribution of nutrients to the upper soil layers by recycling via the litter of deeply rooted species. This resource pool is thus at any site, like light and unlike water, highly predictable. Preferential access depends upon relative root profiles, principally *root depth*, whilst differential access is based upon *more efficient absorbing power* per unit rooting volume. Symbiotic dinitrogen fixation, or mycorrhizal associations effective in the uptake of other nutrients, provide extreme cases of differential ability in nutrient uptake.

RESPONSE TO STRESS

Our interest here lies in the response of plants when confronted with suboptimal levels of one or more of the growth resources at any stage in the phenological development of their biomass or yield. Stress describes a condition of the environment that causes a reduction in the growth of plants or damage to particularly sensitive meristematic activity that leads to a subsequent reduction in yield (Levitt, 1978). In the response to stress, the plant may or may not demonstrate changes in any of the various physiological indices, for example, water potential, nutrient content, enzyme activity. That is it may or may not be internally affected. The extent of its adaptation to stress is

measured by its growth or yield under stress relative to that in the absence of stress. This is an important relationship in the study of the growth response of a plant under stress although, in the development of productive systems, absolute yields under stress are likely to be more important than relative adaptability.

Since the growth resources have such different characteristics it is difficult to say a great deal about the nature of resource use which is generally appropriate. There are, however, some general points relevant to agroforestry associations which, in addition to their multispecific composition, are characterized by anatomically and physiologically diverse plants, and are intended to persist for at least tens of years.

Appropriate adaptations to stress depend not only upon the severity and duration of the stress, but also upon its predictability. Of the three resources to be discussed by far the most unpredictable is the level of available soil water. For light and nutrients the predictability at any site is high, although since the levels experienced by a particular component in an association depend also upon the growth of the cohabiting species, they may have an unpredictability entrained to the level of the water resource. Thus, for example, transient change in leaf area or display in the tree layer in response to water stress will alter the penetration of radiation to the lower canopy; or reduced growth in response to water stress will lower the current demand for nutrients.

Conservative use of the storable resources, water and nutrients, is a well-established component of successful adaptation for continued growth and for survival under stress (for example, Specht, 1972; Morrow and Mooney, 1974; Christie and Moorby, 1975). The value of this adaptation to an individual species clearly depends upon the behaviour of cohabiting species. It is this need to consider the co-ordination of stress responses between components that sets agroforestry apart from the bulk of the literature on plant response which arises from studies of sole crops. Agronomists turning to the study of these more complex communities need to be well aware of the ecological literature and particularly the co-ordination of responses to stress. The literature abounds with data on, and references to, competitive use of resources and, certainly, the potency of interspecific competition in determining the composition and distribution of natural communities is well represented.

Because of competition the distribution of plants is more restricted than is their physiological potential for growth, and the major ecological expression of a species, its ecological optimum, may be distinct from its physiological response (Ellenberg, 1952). This has important consequences for those who seek to interpret the physiological characteristics of a plant from observations of its ecological distribution and, likewise, for those who wish to predict the outcome of a plant in a mixture from observations of its behaviour, that is its physiological response, in sole culture. However, not all relationships within natural communities, by their existence successful, are competitive. There are examples of *complementary* use of resources in which access to the resource pools is partitioned in either space or time so that competition even under seemingly stressful

situations does not arise. Thus trees need not compete with annual herbs for water, given a relative distribution of the two root systems. Deciduous trees may allow the passage of a considerable annual integral of light to support the seasonal growth of an understorey.

Perhaps the most remarkable example of non-competitive adaptation to stress is seen in the behaviour of the sclerophyllous, evergreen shrublands studied by Mooney and Dunn (1970). In these widespread communities the basis for cohabitation of a diverse floristic group is the adoption by all of an identical, basically conservative, pattern of water use. Mooney has termed this phenomenon 'convergent evolution', and the co-ordinated response of all members gives the community the potential to rely upon the conserved water that would otherwise be available only to those rare monospecific, evergreen stands, for example, the semiarid shrubland *Acacia harpophylla* in S.E. Queensland, Australia (Downes and Connor, 1973; Tunstall and Connor, 1975).

LIGHT STRESS IN AGROFORESTRY ASSOCIATIONS

Plants respond to the quantity and to the quality of light. The number of quanta in the visible waveband is the energy available for photosynthesis (PAR) whilst the spectral distribution into the near infrared (NIR) combines with it to control various developmental aspects of plant growth. Within plant canopies the overall intensity of light decreases and the ratio of diffuse to direct radiation increases. The spectral composition also changes, becoming relatively richer in green and in the NIR (for example, Allen *et al.*, 1976; Ludlow, 1978). Both aspects potentially play important roles in the response of component species to the light stresses which are expected to arise within agroforestry associations.

Except in the early establishment phase, the tree or shrub component physically dominates the herbaceous substratum and hence its potential for growth. Since this, for any plant, is ultimately restricted by the energy available for photosynthesis. Stratified, mixed canopies are both easily studied and easily manipulated relative to those in which the cohabiting species are distributed throughout the same canopy volume. Depending upon the planting, the pattern of illumination on the understorey may be made more complicated (for example, Hadfield, 1974a, b). A simplification of horizontal homogeneity of light climate on the substratum, determined by a horizontally, homogeneous upper canopy, may or may not be appropriate in further analysis of photosynthetic response, but for any described canopy geometry the mathematical ability exists to define the illumination of either component of the canopy of a mixed community and hence its potential photosynthetic response (for example, Allen *et al.*, 1976, and see Jackson, this volume). Our ability to handle these complex geometrical problems should not, however, lead us to underestimate the value, given our ignorance about so much else of the system, of much simpler treatments (see Thornley, 1976; Trenbath, 1976).

Productivity under shade

The potential photosynthetic rate of closed canopies of C_4

plants is directly linear to the irradiance on the canopy up to full sunlight because these canopies are composed of foliage elements with a linear photosynthesis versus irradiance response (for example, Connor and Cartledge, 1970). In C_3 canopies the behaviour at high incident irradiance depends upon the degree of light saturation of the component foliage elements, which in turn depends upon their geometrical arrangement and the geometry of direct and diffuse radiation. The possibility exists that the canopies, like the leaves, will light saturate at high light levels and, consequently, some measure of shading may not lead to reduced growth, that is to light stress. The evidence on this comes from various experiments in which the CO_2 exchange of crops has been measured using field chambers. Most studies do show saturation of photosynthesis of C_3 communities at irradiance below the peak values of around 1000 Wm^{-2} (0-3 μm) that may be encountered, but of course the communities saturate in all cases at irradiance levels well above that at which the component leaves saturate. Saturation has been recorded for soybean and cotton crops around 900 Wm^{-2} (Jeffers and Shibles, 1969; Baker *et al.*, 1972), for wheat and tobacco crops around 700 Wm^{-2} (Connor and Cartledge, 1971; Puckridge and Ratowsky, 1971; Whitfield *et al.*, 1980), for sugar beet crops around 550 Wm^{-2} (Brown and Rosenberg, 1971), but for potato crops at only 400 Wm^{-2} (Sale, 1974). It is possible that the different efficiencies with which the direct and diffuse components of incident radiation may be utilized in canopy photosynthesis (Connor and Cartledge, 1971) may explain some of the differences recorded above, but it seems equally likely that some of the responses (for example, Sale, 1974) also include internal restrictions to photosynthetic productivity, that is sink limitation. However, if the responses, as outlined above, are persistent and characteristic of the crops concerned then they not only show at what levels light stresses will occur, but in all cases demonstrate an essentially linear response to irradiance within the nonsaturated range. It is evident from these data that the presence of trees in agroforestry associations need not necessarily seriously restrict the photosynthetic rate of some companion herbaceous plants but, perhaps more importantly, that there is considerable scope to select understorey species in which growth restriction is minimal.

Seasonal changes in light levels may cause a reduction in the reproductive yield of crops which is greater than the overall reduction of growth itself. This arises because in the sequential processes that determine reproductive yield there are stages which are particularly sensitive to stress, including stress arising from low light levels. Determinate crops like wheat (Fischer, 1975) or maize (Early *et al.*, 1967; Gerakis and Papakosta-Tasopoulou, 1980) have little opportunity to compensate for stresses which operate to reduce the grain set. Fischer (1975) demonstrated experimentally the severity of shade in an attempt to explain the possible role of dull weather in the year-to-year variability in the yield of irrigated wheat in Mexico. Indeterminate crops have the potential to compensate by further flowering but the possibility of an exaggerated decrease in yield remains. Root crops may have better inherent yield stability in conditions of transient stresses, as would pasture

species in which, except for the requirement of annuals to produce sufficient seed for year to year survival, the major interest is in biomass production only. Collins *et al.* (1978) studied the effect of shading from flowering onwards on the seed set by the annual pasture legume *Trifolium subterraneum*. A reduction of light intensity of 50 per cent caused a greater proportionate reduction in the number of seeds set. Since clover seed is an important part of the diet of grazing animals during the summer non-growth period seed dynamics and the year-to-year regeneration of the pastures have potentially complex interrelationships for sub-clover pastures under *Pinus radiata* (Anderson and Batini, 1979).

Photomorphogenic and photoperiodic responses determine plant form and reproductive performance. Etiolation is a commonly observed reaction of plants growing in low light intensities and has been reported for oats and lupins grown singly in an agroforestry association with *Pinus radiata* (Anderson and Batini, 1979). Yield reduction was associated with reduced seed set but in this the relative roles of photosynthetic productivity and developmental responses were not separated. Extreme effects of light stress may occur if the flowering response of understorey plants in agroforestry systems is affected by shifts in light quality. It does, however, seem unlikely that these effects would dominate the response of the plants to light stress, that is, cause serious developmental problems, at least at light levels which allow acceptable levels of productivity.

Selection of agroforestry associations and their management to minimise light stress

The selection of the tree component of agroforestry associations should concentrate on those species that have high efficiency of utilization of captured radiation, so that acceptable levels of productivity can be maintained at the lowest possible levels of light capture. In this way the potential productivity of the substratum can be maximized. The trees are practically certain to be C_3 species (see Tieszen, this volume) so that efficiency of utilization requires effective distribution of radiation over the foliage surfaces (Jackson, this volume). Trees with high leaf angles and high reflectivity will contribute to the construction of the most photosynthetically productive mixed canopy. Where trees are planted in rows east-west orientation will maximize the radiation reaching the herbaceous layer. If the trees are evergreen then they ought to be continuously productive, or replaced with deciduous trees probably at a closer spacing.

Continued productivity of the herbaceous stratum will require continued attention to the canopy of the tree layer so that by harvesting of individuals, coppicing or pruning, it is possible to adjust light penetration to minimize the effects of light stress on the yield of the herbaceous component. By attention to the timing of such manipulations it should be possible to minimize the effects of light stress on the growth, development and yield of the herbaceous layer.

In selecting the herbaceous component particular care should be directed towards ensuring that transient periods of more than usually extreme shade resulting, for example, from climate characteristics, or increases in tree leaf area, do not coincide

with sensitive stages in the development of yield. In some areas it might be advisable to avoid determinate crops and perhaps to choose the root or tuber crop alternative since they do appear to be less sensitive to transient severe stresses. Under deciduous trees it may be possible to devise a cropping programme in which there is no light limitation to the growth of the herbaceous component (for example, sorghum and millets associated with *Acacia albida*, El Houri Ahmed, 1980). Alternatively it may be necessary to start and/or finish the crop under shade. If there is a choice, then for determinate crops stress in the early stage is certain to have the least serious effect which, in many cases, may not be detectable in the final yield (for example, Earley *et al.*, 1967; Fischer, 1975).

WATER STRESS IN AGROFORESTRY ASSOCIATIONS

The water status, and hence metabolic activity, of the component organs of a plant - root, stem and leaves - through which water is drawn from soil to atmosphere, reflect not only the balance between the uptake by the roots, and the necessary loss from the canopy that must accompany an open pathway for the diffusion of CO_2 to the photosynthetic sites within the leaves. They reflect also the resistance - capacitance characteristics of the internal pathway itself. The evaporative demand is determined by the ambient microclimate and the extent of the canopy, whilst leaf diffusive characteristics and responses determine their ability to withstand it. The root density profile determines the capacity of the plant to extract water from the soil, and the capacitance of the plant relative to the diurnal fluxes determines its ability to buffer diurnal deficits. Within agroforestry associations the potential interactions governing the relative success of the components when soil water levels are below optimum are considerable.

Water use

Faced with a shortage of water plants may either seek to evade the consequences of desiccation, or they may seek to tolerate them. These are the two extreme strategies of what is most likely a continuum of adaptation which is becoming well documented in the ecological, and more recently in the agronomic literature (see Turner and Kramer, 1980). As was pointed out earlier, the appropriateness of any adaptation must depend not only upon the severity and frequency of droughts but also upon the behaviour of cohabiting species. Thus plants which continue to transpire as soil water levels fall depend for success, in the absence of additional rainfall, on either increasing their water supply by expanding their root zone and/or by lowering their root water potential, or by completing their life cycle or current growth phase before the water supply is exhausted. By contrast, plants which begin to modulate transpiration at relatively high levels of soil water by stomatal control to reduce water loss per unit foliage area, or by reducing net radiation load through leaf movement or a real reduction in leaf area, have the potential to survive at low levels of metabolic activity for comparatively long dry periods. These plants also have the opportunity to employ diurnal patterns of stomatal activity which allow the most

efficient use of transpired water.

Water stress will arise following periods when evapotranspiration exceeds rainfall but because of the nature of the association, the effect on either component may be unequal. Water stress will arise in agroforestry associations whenever there is insufficient water available to the root system of any plant component to meet the evaporative demand placed upon its canopy. Consider those features which lead to differential growth in agroforestry associations based upon either a depression of plant water status or action designed to avoid it.

Canopy. The evaporative demand per unit leaf area of the tree canopy must exceed that of the herbaceous layer because, due to its position and structure, it is subjected to a higher radiation load, greater ventilation and lower vapour pressure deficits. Each of these factors works to increase the transpirational load. To offset these disadvantages a tree canopy in a mixed agroforestry system needs, in turn, to exercise greater control of water loss by any anatomical and stomatal adaptations which can increase the partition of its net radiation load in favour of sensible heat and away from evaporation. The extent to which a tree canopy can affect this control, or the extent to which it can modify the disposition or extent of its leaf area to reduce it, will throw the balance of overall evaporative demand towards the herbaceous layer. However, provided there are surfaces in the tree canopy to intercept radiation, even if they are evaporatively inactive, the demand on the herbaceous layer will be diminished.

The fact that the herbaceous layer growing in association with trees enjoys a lowered evaporative demand, and hence a potential for an improved water status, is the basis of the well-documented effect of shelterbelts of which agroforestry can seek to take advantage (for example, Rosenberg, 1974; Sturrock, 1975; Russell and Grace, 1979). The challenge is to arrange the association such that water supply to the herbaceous layer allows it to take advantage of any improved water status condition, and to overcome the serious effects of shading that will operate over at least some of the protected area. At least for strip associations, the available studies of the microclimatic and yield response to shelterbelts must afford explanation and direction to the formulation and management of agroforestry associations.

Although there are probably trees with leaf water relationships comparable with those of herbaceous plants, on balance trees have more xeromorphic characteristics. From considerations of leaf reflectance (Sinclair and Thomas, 1972), photosynthetic capacity (Larcher, 1969), leaf diffusion characteristics (Körner *et al.*, 1979) and desiccation resistance (for example, Slatyer, 1960; Connor and Tunstall, 1968) tree leaves may show a greater ability to control water use, and hence to persist actively in low rainfall environments. The evergreens of drought prone environments of Australia (*Eucalyptus*, *Acacia*, and so on) certainly exhibit these characteristics.

Plant water status is not only under the control of cuticular and stomatal resistance but can also be effectively modulated by changes in the canopy display via leaf movements, or by reduction in the transpiring area itself. Whilst wilting has been

interpreted (Rawson, 1979) as a positive, adaptive mechanism rather than simply a structural result of excessive water use, there are other well-documented leaf movements, especially in the leguminosae, which can reduce radiation load and which are functionally linked to leaf water status (for example, Shackel and Hall, 1979; O'Toole and Cruz, 1980). Modification to canopy area is probably the most effective means of reducing transpiration and this can be achieved by either a reduction in the expansion of new leaf area, or in an increased rate of senescence. The interpretation of the value of alternative adaptations to the reduction of water use in response to stress must include a combined analysis of the efficiency of water use in producing new biomass, or in maintaining existing biomass which can remain productive for the future. In cassava, for example, water stress seriously restricts each aspect of leaf area development: apex division, leaf production per apex and leaf expansion itself. Although at the end of a stress period the crop had little leaf area, an increased rate of leaf senescence was not the cause (Connor and Cock, unpubl.). Since leaves of cassava maintain their photosynthetic capacity in excess of 100 days, this response can be seen as an effective use of the capital already invested in leaf area.

Stems. Trees are distinct from herbaceous plants by virtue of their greater investment in structural material which connects the photosynthesizing canopy to the absorbing roots. This material exists in substantial quantities both above and below ground and has important effects on their comparative water relationships (Hinkley *et al.*, 1978), and hence the differential response to stress of trees and herbaceous plants.

Since the pathway of water transport is longer in trees than in herbaceous plants the resistance to flow also tends to be greater. Tree canopies tend to be internally drier than herbaceous canopies under similar conditions of evaporation and water uptake by the roots. Except in very tall trees (Connor *et al.*, 1977) the static component of 0.1 bar m^{-1} is not likely to contribute excessively to this, but the flow related component, especially in trees in which vessel size is small, does become important (Hellkvist *et al.*, 1974). Higher internal stress and lower transpiration are the likely result of this increased resistance. This interplay between canopy height, water potential and consequent photosynthetic activity led Paltridge (1973) to an interesting theoretical analysis of the shape and productivity of trees.

To offset this disadvantage trees have a considerable internal water capacity, some of which may be released diurnally from the sapwood, or seasonally from the heartwood, to buffer the internal water deficits of metabolically active tissue, for example leaves and meristems. There are examples of trees in which the storage capacity is enormous, for example the Australian bottle tree (*Brachychiton* spp.), baobabs and eucalypts with lignotubers (the 'mallee' group); but water reserves are important in trees of a more conventional design also. There is some difference of opinion as to the quantity of internally available water but estimates as high as 27 mm have been made for a Douglas fir forest (Waring and Running, 1978). This aspect of

modulation of the differential stresses that trees and herbaceous plants might encounter in agroforestry associations needs to be assessed.

Root systems. Gross differences between the root penetration of trees and associated herbaceous plants, especially annuals, provide for significant interaction between the water relations of associated plants and for the development of differential stresses (Cohen, 1970). By virtue of their greater root depth (for example, Kimber, 1974) trees have access to soil water that is not available to the cohabiting herbaceous species. Whilst in the surface layer of the soil, to which the herbaceous component is morphologically restricted, both components may compete. The horizontal exploration by the roots of trees in the surface layers is a notable characteristic of trees, at least from water short environments (Story, 1967; Kummerow, 1980). Canopy interception and subsequent stem flow in trees can substantially redirect water to their relative advantage (for example, Pressland, 1976; and see Leyton, this volume). Whilst the water use characteristics of the herbaceous layer determine the penetration of non-intercepted rainfall into the subsoil from which trees have exclusive use. In many environments, trees clearly depend for their survival on water not available to the herbaceous stratum, for example woodlands of southern Australia during summer, and the significance of removing the herbaceous layer on the productivity of trees is well known in horticulture.

Models of plant water use adequate for soil water budgeting are now well enough developed to find a place in programming irrigation, optimizing sowing time of dryland crops (Baier, 1973; Fitzpatrick and Nix, 1979; Nix and Fitzpatrick, 1979) and in explaining the distribution of natural vegetation (Specht, 1972). An immediate challenge in agroforestry is to apply these techniques so as to be able to understand the response of soil water recharge to various structural and behavioural characteristics of a variety of plant combinations. It is probable that herein lies the possibility of limiting differential stresses and maximizing productivity in agroforestry in response to the most variable of the environmental resources determining plant productivity.

The problems of soil water recharge under silvopastoral systems are becoming well known in southern Australia, but here the current problem is the reverse of that alluded to above. During this century many of the grazed, natural woodlands carrying evergreen eucalypts over a seasonal herbaceous layer have either had tree populations reduced to encourage pasture growth, or trees removed completely as part of the development of cropping programmes. An effect of this practice has been the gradual increase in subsoil water because, on average, the winter-spring recharge is to depths below the root zone of the pasture. The problem has been aggravated because applied fertilizer (superphosphate) and grazing management have favoured the replacement of the summer growing, perennial native grasses (*Stipa*, *Danthonia*, *Themeda*) with annuals of winter-spring growth habit (*Lolium*, *Trifolium* and various weeds). Although rainfall in these areas is comparatively low (< 700 mm) and annual evaporation high (> 900 mm), the rainfall occurs when evaporation is low and, during the high evaporation of summer, transpiration in

the absence of trees is virtually suspended. The result of the gradual increase in subsoil water has been the mobilization of salt from depth in the soils and the deterioration of pastures initially in the lowest parts of the topography, death of remaining trees and high discharge of salt into rivers. A considerable research effort is currently directed to the measurement of the water use of trees (Greenwood and Beresford, 1979, Greenwood *et al.*, 1981) with the objective of finding species that tolerate the salt and transpire actively.

Long term changes in the soil water profile are a possible consequence of the implementation of agroforestry associations. Short-term runs of above or below average rainfall may obscure the real stability, or otherwise, of the association.

Water stress and yield

Although carbon gain and water loss by plant canopies are only loosely connected, it turns out that the ratio between them - water use efficiency (WUE), or its reciprocal transpiration ratio (TR) - is sufficiently identifiable for any vegetation type to allow estimates of dry matter production from the more easily calculable water use. This analysis is improved if a separation is made between the transpiration and soil evaporation components of evapotranspiration, since the ratios best relate water lost by transpiration alone (Fischer and Turner, 1978). This technique allows for the calculation of productivity, particularly in water stressed environments, and it will provide a useful means of estimating the growth of the components and likelihood of differential stresses in agroforestry associations. It also draws attention to the possibilities that exist to exploit the inherently different water use efficiencies of the C_3, C_4 and CAM photosynthetic pathways (Ludlow, 1976; Christie, 1978; and see Tieszen, this volume).

As with stress due to light, it is once again important to emphasize that the sequential processes which determine the reproductive yield of plants are also differentially susceptible to water stress. This applies at floral initiation and around flowering and it is particularly potent in reducing seed set and hence, the potential yield. Stresses early in fruit filling are more important than those near fruit maturity in disrupting the supply of assimilate to meet the demands of this sink. A single, comparatively short stress, may have devastating effects on the yield of determinate crops. And also upon the fruit yield of tree species in which floral initiation occurs over a well-defined period, often the year before the fruit is filled (Salter and Goode, 1967; Begg and Turner, 1976). Indeterminate annuals have the capacity to compensate for single stresses and perhaps, as was mentioned previously, root crops are best suited to withstand periodic stresses since their yield is apparently not determined by such a complex of processes and their storage organs persist to accept translocates when available.

Management of agroforestry associations to minimize stresses due to water shortage

In order to minimize the effects of water stress in agroforestry associations it is necessary to define, and then continue to pay

attention to the levels of the storage pool available to either component relative to their water use behaviour and the differential sensitivity of the physiological processes that determine their yield. The more unpredictable is the rainfall, then the more conservative must be the management to ensure continuity of the perennial, and hence of the association. Yield stability must take second priority to this.

The most effective means to reduce transpiration, and hence reduce stress and prolong survival, is to reduce the area of the transpiring surface (for example, Butcher, 1977). Reduction of the tree canopy will throw the evaporative balance of the community towards the herbaceous stratum which is generally dependent upon a smaller store of water which it shares with the trees. Temporarily removing the tree/bush canopy (by coppicing) may eliminate competitive needs for water between the plant associates where these are sharing the surface soil levels in some way. Pruning the roots of the trees also will allow the herbaceous stratum more complete control of its water resource. Reduction of the leaf area of the herbaceous stratum will not affect the immediate water balance of the trees but will favour a loss to the entire system by evaporation directly from the soil surface, and a preferential distribution of water to the trees by recharge to below the rooting depth of the herbaceous stratum. The losses to the system by soil evaporation can be considerable depending upon storm size distribution and ground cover, the latter including transpirationally inactive litter as well as transpiring leaf area. In an actively growing wheat crop in southern Australia, or in the Great Plains of the USA, as much as 50 per cent of the total water use can occur by soil evaporation (Fischer and Turner, 1978), principally during establishment and towards maturity. Particular attention needs to be paid to the control of soil evaporation in agroforestry associations in drought prone areas.

Improved yields of annual crops in water short environments have been largely achieved by shortening the overall growing season and by sowing phenologically adapted cultivars into moist fallows when the subsequent and predictable critical stages in the development of yield are least affected (see Huxley, this volume). There is little evidence that the substantial improvements in adaptation, that is in yield and yield stability, have yet included significant shifts in the physiological ability of the improved cultivars to tolerate stress. The same principles are likely to apply to the more constrained, competitive situation presented by agroforestry associations.

NUTRIENT STRESS IN AGROFORESTRY ASSOCIATIONS

One of the hopes of agroforestry is that it can capitalize upon the capacity of perennial plants to transfer nutrients from depth into the upper soil layers where they are accessible to the companion shallowly rooted herbaceous plants. In this way, on one site, the system of 'shifting agriculture' is replicated in space rather than in time.

As the association grows nutrients are fixed in the vegetation, especially in the perennial components. Nutrients are then removed from the site by harvesting. Whilst the pools of

available nutrients can be replenished by chemical conversions within the soil profile, and by accretion to the site, the nutrient content of the upper soil layer, to which the most intense root activity is restricted, will depend largely upon the external recycling system of the perennial component. From this description it can be concluded that a successful agroforestry association will have, by nature or management, the following characteristics.

- A perennial component with a root system effective in nutrient uptake at depths below the rooting zone of the herbaceous layer.
- A highly productive perennial component with high nutrient return to the upper soil layer.
- A herbaceous component that can either compete with the perennial for nutrient enrichment in the upper soil layer, or which is managed still to take advantage of this.

Productivity will be restricted at sites in which the uptake of nutrients is less than that required by the vegetation as a whole to meet the growth potential determined by its access to the other environmental resources, that is, nutrient stress will occur. Considering the number of plant nutrients, the intricacies of nutrient systems in vegetation and the anatomical and physiological differences between the perennial and herbaceous components of agroforestry associations it is unlikely that the same nutrient stress will be felt equally by either component. Selection of components of agroforestry associations and their management must account for these issues if nutrient flow and hence productivity are to be maximized and differential stresses between the components minimized. As was explained at the outset the characteristic feature of the nutrient resource at any site is its tendency to remain relatively constant, at least on a yearly time scale. Plants display a range of adaptations to such persistent nutrient shortages and, in this discussion, the interest lies in what combinations of them are compatible with the objectives of agroforestry.

Nutrient uptake

Plants require a continuing supply of nutrients to meet the demand of growing tissues. This supply can be aided by efficient transport of nutrients from the root system, by remobilization of nutrients already present in senescing tissue, that is by internal recycling, and the overall nutrient need can be minimized by genetic, environmental or management restrictions to the rate of growth (Gerloff, 1963). Generally, however, unrestricted growth requires some level of continuing uptake by the root system.

Uptake at the root surface establishes a concentration gradient from the root surface to the bulk soil down which further supply diffuses to the root. If water is also being adsorbed by the root then movement is aided by mass flow. Not all nutrients are equally mobile in soils and hence the rate at which they are replenished at the root surface differs. Of the major nutrients NO_3-N is highly mobile because it exists mainly in the solution phase, and the rate of supply is therefore critically affected by the soil water status. Phosphate-P, NH_4-N, and other cations

which are strongly associated with exchange surfaces have limited mobility (Bray, 1954) and rate of uptake is likely to be influenced by the time and extent of fine root extension.

Plants will compete for nutrients whenever the zones of depletion of their roots overlap and clearly this depends upon the nutrient in question, its concentration in the available pool, the rate at which this can be replenished, the soil water relationships and the nutrient uptake characteristics of the co-habiting species. Zones of depletion for mobile nutrients are wide and hence plant interaction can occur at relatively low rooting densities. By contrast for poorly mobile nutrients, with narrow zones of depletion, root systems of different plant associates may remain effectively independent to higher root densities. Whilst high root density is relatively unimportant for the effective uptake of mobile nutrients by monocultured species (Barley, 1970), this is not necessarily true for mixtures (Trenbath, 1976). In the mutual zone of depletion nutrients will move to either species in approximate proportion to their overall root surface activity. High root surface density by one species serves to minimize its proportion of interspecific contacts. Intraspecific contacts are not competitively disadvantageous. In addition to this static description of nutrient uptake, root growth and exploration of new soil volume are an important part of the search for nutrients. Clearly we need to know a great deal more about the situation in any particular agroforestry system before we can specifically suggest improvements in design or management.

In the ecological (Mosse, 1973; Bowen, 1980) and forestry (Harley, 1970) literature, and more recently in the agronomic literature also, (for example, Khan, 1975; Hale and Armstrong, 1977; Asimi *et al.*, 1980) the outstanding feature of nutrient uptake capacity is the range of symbiotic relationships with micro-organisms that plants have developed to improve nutrient uptake in nutrient-poor environments. Whilst rhizobial associations are restricted to the legumes, and these are the most important dinitrogen fixing systems, mycorrhizal associations of one type or another are almost universal in the roots of the components of natural vegetation and can be found in most agricultural crops and pastures. Mycorrhizal associations are known to increase the yield of the host plants under conditions of low fertility, and the nutrient most firmly implicated is P, although nutritional advantage with respect to N, Ca, Na, Mg, Fe, Mn, Cu, B and Al have also been recorded (Mosse, 1973). Since N and P are *the* important nutrients of the infertility syndrome it is important to explore the relevance of these symbiotic relationships to the development of successful agroforestry associations (Redhead, 1980).

The two types of symbiotic associations have important differences with respect to overall nutrient relationships. Rhizobial associations place at the disposal of the symbionts the enormous reserve of gaseous nitrogen which is unavailable directly to non-nodulated plants. Legumes are able to grow essentially independently of soil solution N, so that competition with non-legumes for this nutrient is not intensified by the symbiotic relationship. In fact the systems are generally quite 'leaky' so that associated non-legumes quickly benefit

from raised levels of N in the soil solution. By contrast, mycorrhizal associations do not allow access to previously unavailable reserves of nutrients. The available evidence suggests that the fungal hyphae which ramify extensively through the soil from infected roots absorb P from the same nutrient pool as uninfected roots. The major advantage appears to be the additional exploration potential of infected plants (Sanders and Tinker, 1973), although it is possible that uptake per unit active surface area is also more effective. In any event it is well known that per unit of plant root, depletion of soil solution P is greater in the presence of effectively infected roots.

Development of nutrient stress

In agroforestry associations the spatial and temporal distributions of the root systems of the two components are likely to dominate the development of nutrient stresses. The root system of the perennial component can be expected to penetrate to greater depths in the soil and, even though root density there may be low, the root can effectively exploit mobile nutrients and, with appropriate symbionts, less mobile nutrients also. By contrast the herbaceous component is often restricted to the upper soil layers, which it can expect to share with horizontally extensive roots of the perennial. Whereas the perennial will maintain a permanent root system *the herbaceous component is likely to have, seasonally, to re-establish a root system in a soil volume some part of which, at least, is already occupied by the roots of the perennial component.*

Although a common characteristic of vegetation of nutrient poor sites is its openness, it is important to realize that such vegetation may well be a closed stand *below ground*. Roots may represent the greater proportion of the total biomass in such a situation and the distribution of roots will match the capacity of the soil and biological systems to supply nutrients to the soil solution. Experiments involving trenching have demonstrated the potency of root competition and the need to reduce or eliminate it, if lower strata species are to thrive. Plants can only naturally invade such sites following catastrophic events, or if they have a significantly lower threshold concentration for nutrient uptake than the existing species.

The search for nutrient efficient plants must include consideration of the favourable, microbiological associations that exist widely in vegetation. However, regardless of the basis of superior nutrient uptake, physiological or symbiotic, the possibility of great differences between plants raises the question of the compatibility of nutrient uptake strategies. In the case where the strategy allows access to a separate and large pool of nutrient, for example, symbiotic dinitrogen fixation, the superior ability of one species need not lead to the development of nutrient stress with respect to the growth of the partner. It is possible that consequent shortages of other nutrients may ensue, as also might stresses due to water or light, but these are not inevitable and the major result is the continuing improvement of the nitrogen economy of the entire vegetation. In the case of mycorrhizal associations, however, the situation is different. Effective infection does not greatly increase the supply of the nutrient. The lowered phosphate concentration in

the zone of depletion does provide the possibility for a more rapid solubilization of unavailable P, but this depends upon the appropriate chemical equilibria. The ability of mycorrhizal plants to reduce the concentration of available soil phosphate suggests that interference between different plant associates for phosphate in the soil volume that they both explore can only be compatible if both have developed an *equally* efficient association. It is difficult to imagine that increased root density on the part of one partner, or improved activity or transport, can match the greatly expanded surface area for uptake upon which the success of the mycorrhizal association is apparently based. Plants which can extract nutrients to concentrations below that of companion species can exclude them from nutrient poor sites, where replenishment is slow, just as effectively as can be done by shading in dense vegetation. Thus for stable agroforestry associations on nutrient insufficient sites there can only be large differences in ability to absorb nutrients if the root system of one component is not completely overlapped, horizontally or vertically, by the other, or unless the growth of one component is significantly restrained by some management or other environmental factor.

The availability of nutrients may change slowly with time, not only because of the gradual removal by harvesting or loss by leaching, but also because of the developing soil - vegetation system. The accumulation of organic matter and the associated decrease in pH may also change the availability of macro- and micronutrients. Such changes have been recorded under long rotation forests and are currently assuming importance in southeast Australia following 30 to 50 years of improved annual pastures. In agroforestry associations the rotations are likely to be sufficiently long that nutrient availability will change. Under these conditions there are opportunities to match the herbaceous components to the changing conditions and, hopefully, not only in the sense of adjusting the plants to a continually declining pool of available nutrients. The perennial component should, however, be able to sustain its productivity during the rotation.

Selection of plant components and their management to minimize nutrient stress

The perennial plants in agroforestry associations must be adapted to the local nutrient environment. Which means that their potential growth rates are matched to their capacity to extract nutrients from the system. The most productive trees will be those that can extract nutrients at the highest rates, or which have the 'tightest' internal nutrient recycling system. In agroforestry associations an important balance must therefore be struck between the biomass, and hence nutrient accumulation by the tree layer, and its capacity to return nutrients to the upper soil by external recycling. That is, woody perennial species selection should favour plants with 'leaky' internal nutrient recycling systems. Without significant accretion of nutrients placed at the disposal of the more frequently harvested herbaceous layer, significant differential nutrient stresses are placed upon them.

Selection of plant components must take into consideration

the basis of adaptation to the local *nutrient* environment. Particular attention must be paid to the plant - micro-organism - nutrient interrelationships. Effective symbioses can so change the nutrition of a plant, and the relative value of a site for its growth, that physiologically based differences between species or genotypes may become irrelevantly small. Selection of genotypes must also recognize the importance of particular populations within the range of distribution of a species. Most examples of adaptation involve the differentiation into physiological ecotypes each adapted to a specific and generally narrow range of edaphic conditions (for example, Snaydon, 1962; Heslop-Harrison, 1964). However, there are other cases in which a wide adaptive range is achieved by broad physiological tolerance (for example, Parsons and Specht, 1967). Modern crop varieties are usually designed to be physiologically adapted to a broad range of environments but with significant amelioration of soil conditions; this will not be an option for low input agroforestry systems.

Management of the perennial component of agroforestry associations can be used to reproduce some of the theoretically advantageous features of associations adapted to nutrient poor conditions. Pruning the canopy can be used to improve the flow of nutrients to the upper soil layer. This procedure can be used to optimize the value of productive but nutrient efficient perennials to the association. Spatial redistribution of litter will offset the characteristically uneven natural recycling of all except very dense tree canopies.

If the herbaceous component is to capitalize upon the nutrients returned and added to the upper soil layer by the perennials, then its access to them must be ensured. Tight external nutrient cycles in vegetation rely upon effective foraging for nutrients in litter and surface soil. The most effective way to aid the herbaceous component is by removing or reducing root competition by the perennial. If the management of the herbaceous component involves cultivation then this may confer a sufficient advantage, but additional strategic root pruning remains a consideration. Because of the distinctly different nutrient relationships in agroforestry associations and monocultures it is possible that limited tillage systems will be less appropriate in this respect. Whilst contact herbicides are widely used in agriculture and horticulture, and have already found an important role in the establishment of the perennial component in agroforestry associations (Tustin *et al.*, 1979), their role in cropping the herbaceous component of agroforestry associations may be of limited value. This is because removal of the herbaceous layer without simultaneous modification to the root exploration of the perennial could allow it rapid access to available nutrients and seriously disadvantage the subsequent re-establishment of the herbaceous component.

SUMMARY

Plant growth requires a continuing and balanced supply of light, water and nutrients and a consequence of growth is the gradual depletion of the pool sizes of these environmental resources. Without replenishment, growth may reduce the levels of these

pools such that the subsequent growth of the plants is reduced. Reduced growth is the universal symptom of environmental stress, the actual internal strain on the plant may be minimal depending upon the way in which it responds to suboptimal levels of environmental resources.

The environmental resource pools have distinct characteristics with respect to the rate and predictability of their replenishment relative to the withdrawal rates for plant growth. Successful adaptations for handling suboptimal conditions depend upon the local characteristics of the resource pools, the relative ability of the cohabiting species to gain access to them and the kinds of interaction of use or conservation that they employ when faced with suboptimal levels.

When water and nutrients are in adequate supply, the interaction between the components of multispecies mixtures of plants operates via the light regime within the canopy. Photosynthesis, productivity, and hence success, depend upon the relative ability of the components to capture the diurnally predictable photosynthetic radiation and to use it photochemically. For productivity, the more important of these two steps is the efficient capture of radiation. This is governed principally by stature, that is the display of leaf surfaces above those of the associated species, but also by leaf angle and leaf dispersion. Agroforestry associations are characterized by great differences between the canopy distributions of the trees and herbaceous components. Because incident photosynthetically active radiation determines the potential productivity of vegetation there must always be competition for it in mixed associations in which water and nutrients are in adequate supply.

For the conditions of adequate supply of water and nutrients, arguably mainly restricted to high technology agriculture and horticulture, the management of associations of disparate species involves attention to the light supply of the desired components. This can be done by such temporal or spatial adjustments to the components of the canopy as are appropriate to ensure both a level and a distribution of photosynthetic carbon gain consistent with desired yield. The principles of community photosynthetic response are now well enough recognized for the situation to be managed optimally if other practical considerations allow.

The supply of water and nutrients is from storage pools located in the soil and subject to either intermittent and often massive replenishment in the case of water, or continuous but slow replenishment in the case of nutrients. Relative access to these pools by the component species of a mixture is determined by the extent of each root system. That is, its depth of penetration and, within this depth, its density. And by its relative ability per unit area of root surface to absorb from these pools. Differences in both of these characteristics are important in the competition between cohabiting species for water and nutrients. Demand for water depends upon canopy microclimate and canopy extent which are only loosely related to the current growth, and hence to the current absolute access to photosynthetically active radiation. Demand for nutrients depends upon current growth.

In response to these constraints plants have evolved a

range of adaptations to stresses of water and nutrients, that is to suboptimal levels of the storage pools. The analysis of these responses in mixed communities requires attention to:

- The definition of the resource pools available to the component species.
- Their relative ability to tap these pools.
- The temporal variation in the size of the pools with particular emphasis upon the predictability of replenishment.
- The extent to which the strategies of resource use of the cohabiting species are competitive or are complementary.

Plants may be physiologically capable of productive success when in sole control of nonoptimum resource pools of water or nutrients but unsuccessful when sharing them with competing plants with either a differential access or superior competitive capacity. When the supply of water or nutrients seriously limits growth the communities are more open and canopies less dense. Under these conditions the competition for available light diminishes but there exists a wide range in the availability of water and nutrients in which situations light stresses are generated and have important effects on the outcome of competition.

The selection of the components of agroforestry associations requires attention to the local characteristics of the resource pools and the inherent adaptations that potential components have evolved to handle suboptimal levels of them. The cohabitation of morphologically and physiologically distinct plants modifies the microenvironment in which each exists. The extent to which they may potentially grow will be modified by the way the canopies interact with respect to the capture of light. And the levels of the storage pools of water and nutrients, and hence their supply relative to the demand determined by the capture of energy, will also be modified. Management of mixed communities in stress prone environments requires continual attention to the spatial relationships of the components both above and below ground. The required productive balance must be struck between growth, and hence the use of water and nutrients when conditions are more nearly optimal, and the certain persistence of these resources for those components which need continuing access in order to survive to the next replenishment.

REFERENCES

Allen, L.H. Jr, Sinclair, T.R. and Lemon, E.R. (1976). Radiation and microclimate relationships in multiple cropping systems. *In* "Multiple Cropping" (R.I. Papendick *et al.*, eds), pp.171-200. ASA Special Publication 27, Madison, Wisconsin, USA.

Anderson, G.W. and Batini, F.E. (1979). Clover and crop production under 13- to 15-year-old *Pinus radiata*. *Aust. J. Exp. Agric. Anim. Husb.* 19, 362-368.

Asimi, S., Gianinazzi-Pearson, V. and Gianinazzi, S. (1980). Influence of increasing soil phosphorus levels on interactions between vesicular - abuscular mycorrhizae and *Rhizobium* in soybeans. *Can. J. Bot.* 58, 2200-2205.

Baier, W. (1973). Crop - weather analysis model. Review and model development. *J. appl. Met.* 12, 937-947.

Baker, D.N., Hesketh, J.D. and Duncan, W.G. (1972). Simulation of growth and yield in cotton. I. Gross photosynthesis, respiration and growth. *Crop Sci.* 12, 431-435.

Barley, K.P. (1970). The configuration of the root system in relation to nutrient uptake. *Adv. Agron.* 22, 159-201.

Begg, J.E. and Turner, N.C. (1976). Crop water deficits. *Adv. Agron.* 28, 161-217.

Bowen, G.D. (1980). Mycorrhizal roles in tropical plants and ecosystems. *In* "Tropical Mycorrhiza Research" (P. Mikola, ed.), pp.165-190. Oxford University Press, Melbourne.

Bray, R H. (1954). A nutrient mobility concept of soil - plant relationships. *Soil Sci.* 78, 9-22.

Brown, K.W. and Rosenberg, N.J. (1971). Energy and CO_2 balance of an irrigated sugar beet (*Beta vulgaris*) field in the Great Plains. *Agron. J.* 63, 207-213.

Butcher, T.B. (1977). Impact of moisture relationships on the management of *Pinus pinaster* Ait. plantations in Western Australia. *For. Ecol. Mngmt* 1, 97-107.

Christie, E.K. (1978). Ecosystem processes in semiarid grasslands. I. Primary production and water use of two communities possessing different photosynthetic pathways. *Aust. J. agric. Res.* 29, 273-287.

Christie, E.K. and Moorby, J. (1975). Physiological responses of semiarid grasses. I. The influence of phosphorus supply on growth and phosphorus absorption. *Aust. J. agric. Res.* 423-436.

Cohen, D. (1970). The expected efficiency of water utilization in plants under different competition and selection regimes. *Israel J. Bot.* 19, 50-54.

Collins, W.J., Rossiter, R.C. and Monreal, A.R. (1978). The influence of shading on seed yield in subterranean clover. *Aust. J. agric. Res.* 29, 1167-1175.

Connor, D.J. and Cartledge, O. (1970). Observed and calculated photosynthetic rates of *Chloris gayana* communities. *J. appl. Ecol.* 7, 353-362.

Connor, D.J. and Cartledge, O. (1971). Structure and photosynthesis of wheat communities. *J. appl. Ecol.* 8, 467-476.

Connor, D.J. and Turnstall, B.R. (1968). Tissue water relations for brigalow and mulga. *Aust. J. Bot.* 16, 487-490.

Connor, D.J., Legge, N.J. and Turner, N.C. (1977). Water relations of mountain ash (*Eucalyptus regnans* F. Muell.). *Aust. J. Plant Physiol.* 4, 753-762.

Downes, R.W. and Connor, D.J. (1973). Effect of growth environment on gas exchange characteristics of brigalow (*Acacia harpophylla* F. Muell.). *Photosynthetica* 7, 34-40.

Earley, E.B., McIlrath, W.O., Seif, R.D. and Hageman, R.H. (1967). Effects of shade applied at different stages of plant development on corn (*Zea mays* L.) production. *Crop Sci.* 7, 151-156.

El Houri Ahmed, A. (1980). Effects of land use on soil characteristics in the Sudan. *In* "Soils Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.1-14. ICRAF, Nairobi.

Ellenberg, H. (1952). Physiological and ecological behaviour of plants of the same species. *Ber. Deut. Bot. Gesell.* 65, 350-361.

Fischer, R.A. (1975). Yield potential in a dwarf spring wheat

and the effect of shading. *Crop Sci.* 15, 607-613.

Fischer, R.A. and Turner, N.C. (1978). Plant productivity in the arid and semiarid zones. *Ann. Rev. Plant Physiol.* 29, 277-317.

Fitzpatrick, E.A. and Nix, H.A. (1969). A model for simulating soil water regime in alternating fallow crop systems. *Agric. Meteorol.* 6, 303-319.

Gerakis, P.A. and Papakosta-Tasopoulou, D. (1980). Effects of dense planting and artificial shading on five maize hybrids. *Agric. Meteorol.* 21, 129-137.

Gerloff, G.C. (1963). Comparative mineral nutrition of plants. *Ann. Rev. Plant Physiol.* 14, 107-124.

Greenwood, E.A.N. and Beresford, J.D. (1979). Evaporation from vegetation in landscapes developing secondary salinity using the ventilated chamber technique. I. Comparative transpiration from juvenile *Eucalyptus* above saline groundwater seeps. *J. Hydrol.* 42, 369-382.

Greenwood, E.A.N., Beresford, J.D. and Bartle, J.R. (1980). Evaporation from vegetation in landscapes developing secondary salinity using the ventilated chamber technique. III. Evaporation from a *Pinus radiata* tree and the surrounding pasture in an agroforestry plantation. *J. Hydrol.* 50, 155-166.

Hadfield, W. (1974a). Shade in northeast Indian tea plantations. I. Shade pattern. *J. appl. Ecol.* 11, 151-178.

Hadfield, W. (1974b). Shade in northeast Indian tea plantations. II. Foliar illumination and canopy characteristics. *J. appl. Ecol.* 11, 179-199.

Hale, I.R. and Armstrong, P. (1979). Effect of vesicular - arbuscular mycorrhizas on growth of white clover, lotus and ryegrass in some eroded soils. *N.Z. J. Agric. Res.* 22, 479-484.

Harley, J.L. (1970). Mycorrhiza and nutrient uptake in forest trees. *In* "Physiology of Tree Crops" (L.C. Luckwill and Cutting, eds), pp.163-179. Academic Press, London.

Hellkvist, J., Richards, G.P. and Jarvis, P.G. (1974). Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with a pressure chamber. *J. appl. Ecol.* 11, 637-668.

Heslop-Harrison, J. (1964). Forty years of genecology. *Adv. Ecol. Res.* 2, 158-247.

Hinkley, T.M., Lassoie, J.P. and Running, S.W. (1978). Temporal and spatial variations in the water status of forest trees. *For. Sci.* , Monograph 20, 72 pp.

Huxley, P.A. (1979). Classification of plant aspects of agroforestry systems. ICRAF, Nairobi. 9 pp. (Mimeograph)

Jeffers, D.C. and Shibles, R.M. (1969). Some effects of leaf area, solar radiation, air temperature and variety on net photosynthesis in field-grown soybeans. *Crop Sci.* 9, 762-764.

Khan, A.G. (1975). The effect of vesicular - arbuscular mycorrhizal associations on growth of cereals. II. Effect on wheat growth. *Ann. appl. Biol.* 80, 27-36.

Kimber, P.C. (1974). The root system of jarrah (*Eucalyptus marginata* Sm). *For. Dept. W.A.*, Bull. 34. Perth, W. Australia.

Körner, C.H., Scheel, J.A. and Bauer, H. (1979). Maximum leaf diffusive conductance in vascular plants. *Photosynthetica* 13, 45-82.

Kummerow, J. (1980). Adaptation of roots in water-stressed mature vegetation. *In* "Adaptation of Plants to Water and High Temperature Stress" (N.C. Turner and P.J. Kramer, eds), pp. 57-73. John Wiley & Sons, New York, Chichester, Brisbane.

Larcher, W. (1969). The effect of environmental and physiological variables on the carbon dioxide gas exchange of trees. *Photosynthetica* 3, 167-198.

Levitt, J. (1978). Crop tolerance to suboptimal land conditions. A historical overview. *In* "Crop Tolerance to Suboptimal Land Conditions" (G.A. Jung, ed), pp.161-171. ASA Special Publication 32, Madison, Wisconsin, USA.

Ludlow, M.M. (1976). Ecophysiology of C_4 grasses. *In* "Ecological Studies, Analysis and Synthesis", Vol. 19 (O.L. Lange *et al.*, eds), pp.364-386. Springer-Verlag.

Ludlow, M.M. (1978). Light relations of pasture plants. *In* "Plant Relations in Pastures" (J.R. Wilson, ed.), pp.35-49. CSIRO, Melbourne.

Mooney, H.A. and Dunn, E.L. (1970). Convergent evolution of mediterranean climate evergreen shrubs. *Evolution* 24, 292-303.

Morrow, P.A. and Mooney, H.A. (1974). Drought adaptations in two Californian evergreen scherophylls. *Oecologia* (Berl.) 15, 205-222.

Mosse, B. (1973). Advances in the study of vesicular - arbuscular mycorrhiza. *Ann. Rev. Phytopath.* 11, 171-196.

Nix, H.A. and Fitzpatrick, E.A. (1969). An index of crop water stress related to wheat and grain sorghum yields. *Agric. Meteorol.* 6, 321-337.

O'Toole, J.C. and Cruz, R.T. (1980). Response of leaf water potential, stomatal resistance and leaf rolling to water stress. *Plant Physiol.* 65, 428-432.

Paltridge, G.W. (1973). On the shape of trees. *J. theor. Biol.* 38, 111-137.

Parsons, R.F. and Specht, R.L. (1967). Lime chlorosis and other factors affecting the distribution of *Eucalyptus* on coastal sands in southern Australia. *Aust. J. Bot.* 15, 95-105.

Pressland, A.J. (1976). Soil moisture redistribution as affected by throughfall and stem flow in an arid zone shrub community. *Aust. J. Bot.* 24, 641-649.

Puckridge, D.W. and Ratowsky, D.A. (1971). Photosynthesis of wheat under field conditions. IV. The influence of density and leaf area index on the response to radiation. *Aust. J. agric. Res.* 22, 11-20.

Rawson, H.M. (1979). Vertical wilting and photosynthesis, transpiration and water use efficiency of sunflower leaves. *Aust. J. Plant Physiol.* 6, 109-120.

Redhead, J.F. (1980). Soil mycorrhiza in relation to soil fertility and productivity. *In* "Soils Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.175-204. ICRAF, Nairobi.

Rosenberg, N.J. (1974). "Microclimate. The Biological Environment". John Wiley & Sons, New York, Chichester, Brisbane.

Russell, G. and Grace, J. (1979). The effect of shelter on the yield of grasses in southern Scotland. *J. appl. Ecol.* 16, 319-330.

Sale, P.J.M. (1974). Productivity of vegetable crops in a region of high solar input. III. Carbon balance of potato crops. *Aust. J. Plant Physiol.* 1, 283-296.

Salter, P.J. and Goode, J.E. (1967). Crop responses to water at different stages of growth. Res. Rev. No.2. Commonwealth Bureau Hort. Plant Crops, East Malling, UK.

Sanders, F.E. and Tinker, P.B. (1973). Phosphate flow into mycorrhizal roots. *Pestic. Sci.* 4, 385-395.

Shackel, K.A. and Hall, A.E. (1979). Reversible leaf movements in relation to drought adaptation of cowpeas, *Vigna unguiculata* (L.) Walp. *Aust. J. Plant Physiol.* 6, 265-276.

Sinclair, R. and Thomas, D.A. (1970). Optical properties of leaves of some species in arid South Australia. *Aust. J. Bot.* 18, 261-273.

Slatyer, R.O. (1960). Aspects of the tissue water relationships of an important arid zone species (*Acacia aneura* F. Muell.) in comparison with two mesophytes. *Bull. Res. Council Israel* 8D, 159-168.

Snaydon, R.W. (1962). The growth and competitive ability of contrasting natural populations of *Trifolium repens* on calcareous and acid soils. *J. Ecol.* 50, 439-447.

Specht, R.L. (1972). Water use by perennial evergreen plant communities in Australia and Papua New Guinea. *Aust. J. Bot.* 20, 273-299.

Story, R. (1967). Pasture patterns and associated soil water in partially cleared woodland. *Aust. J. Bot.* 15, 175-187.

Sturrock, J.W. (1975). Wind effects and their amelioration in crop production. *In* "Physiological Aspects of Dryland Farming" (U.S. Gupta, ed.), pp.283-313. Oxford and IBH Publ. Co., New Delhi.

Thornley, J.H.M. (1976). "Mathematical Models in Plant Physiology". Academic Press, London and New York.

Trenbath, B.R. (1976). Plant interactions in mixed crop communities. *In* "Multiple Cropping" (R.I. Papendick *et al.*, eds), pp.129-169. ASA Special Publication 27, Madison, Wisconsin.

Turner, N.C. and Kramer, P.J. (Eds) (1980). "Adaptation of Plants to Water and High Temperature Stress". John Wiley & Sons, New York, Chichester, Brisbane.

Turnstall, B.R. and Connor, D.J. (1975). The internal water balance of brigalow (*Acacia harpophylla* F. Muell.). *Aust. J. Plant Physiol.* 2, 489-499.

Tustin, J.R., Knowles, R.L. and Klomp, B.K. (1979). Forest farming: A multiple land use production system in New Zealand. *For. Ecol. Mngmt* 2, 169-189.

Waring, R.H. and Running, S.W. (1978). Sapwood water storage. Its contribution to transpiration and effect upon water conductance through stems of old growth Douglas fir. *Plant Cell Environ.* 1, 131-140.

Whitfield, D.M., Connor, D.J. and Sale, P.J.M. (1980). Carbon dioxide exchange of tobacco canopies in response to environment and defoliation. *Aust. J. Plant Physiol.* 7, 473-485.

DISCUSSION

KOZLOWSKI - Although adaptation to water stress involves a number of features, probably the most useful onces are those concerning structural characteristics. For example, in clones of poplar there is a strong relationship between ability to withstand drought and stomatal distribution and size.

CONNOR - Stomatal responses and leaf movements are clearly the first level reactions that plants have, but drought adaptation must often proceed beyond these reversible processes.

JACKSON - The concept of the resource pool which you applied is not generally applicable to stress factors. For example, stresses due to temperature could not be handled in this way.

CONNOR - I agree, and to apply it to light is to stretch the concept a little, but it is extremely valuable to deal with water and nutrients in this way.

LEYTON - Physiological knowledge should be used to identify critical periods in the development of plants so that management can be designed to avoid stresses that might affect the system. I feel that simple equipment, like evaporation pans, are more appropriate than more sophisticated equipment which is difficult to apply under actual management conditions.

CONNOR - It is important to distinguish between equipment for research and equipment for management. The development of simple tools often requires sophisticated instruments to measure plant status and function.

LOOMIS - There certainly can be a need for this so-called sophisticated equipment in order to understand the development and extent of stress.

TIESZEN - The Tea Research Foundation currently recommend cobalt chloride papers to measure stomatal condition, and hence water status, in tea. The technique is simple but its development required attention to many other details of the plant's condition which require complex measurements.

HUXLEY - Simple phenological observations can sometimes help in the study and management of stress.

STEPPLER - I agree that agroforestry research may require sophisticated research techniques but the objective should be to provide simple techniques for management.

OKIGBO - In my experience shading experiments with single species have not given results comparable to the responses that occur in the field in mixed communities.

CONNOR - The simplest answer is that other factors were probably operating in the field that were not included in the shading experiments.

TIESZEN - Agricultural and natural systems deal with stress in different ways. In agricultural systems we prevent extensive or excessive stress and manipulate resource pools to maximize yield. In ecological systems, however, most species avoid or minimize stress because survival is important, as well as productivity. Take for example water stress. This may lead to midday stomatal closure and, we may be tempted to conclude, to reduced productivity. The alternative would be the evolution of a lower minimum leaf resistance. Although this would conserve water it would

also reduce gas exchange at times of the day when evaporative demand is low. The daily CO_2 and water balance may be more favourable with just periods of transient stress and midday closure. An alternative response may be to allocate more biomass to root growth and soil exploration. This would improve the plant's capability for water uptake, but at the expense of top growth. Simulation modelling is one important technique to help sort out interactions of this type.

STEPPLER - Data on cassava have shown that, under some circumstances, yield of tubers can actually be increased following stress. This indicates that management need not only be directed towards maintaining constantly high levels of the resource pools.

RAINTREE - The examples presented in the paper dealt with single factors. Data of this type does not allow the prediction of interactions between factors which will be the typical situation under the type of low input systems that ICRAF is mostly concerned in developing.

CONNOR - The examples given were of single factors, but the thrust of the paper was the need to consider interactions. Clearly multiple factor experiments are needed in any situation as is the use of models to predict the outcome from whatever response data are available.

JACKSON - I do not agree that all agroforestry systems should be of the low input type. For example, those dealing with fruit crops may justify higher inputs.

COOMBS - I think that pests and diseases should be considered as one of the major limiting factors of equal importance as physiological stresses. (Agreed, but not covered by the meeting. Ed.)

THE INFLUENCE OF GENOTYPE AND ENVIRONMENT ON DRY MATTER DISTRIBUTION IN PLANTS

F.T. LEDIG
Institute of Forest Genetics, Pacific Southwest Forest and Range Experiment Station, Forest Service, US Department of Agriculture, Berkeley, USA.

ABSTRACT. Plants distribute growth among competing sinks in such a way as to retain a functional structure. When photosynthate is limiting it is used in the canopy and little, if any, is available to the roots. When water or nutrients are limited they are intercepted by the roots, growth of the canopy is restricted, and photosynthate is available for root growth.

Because most changes are adaptive, environmental effects are predictable. High levels of irradiance increase root growth relative to shoots, and low levels increase shoot growth relative to roots. Especially in temperate perennials short photoperiods signal a cessation of shoot growth, subsequently favouring root growth. Infertile soils and low water potential inhibit shoot growth proportionally more than root growth. The effect of temperature cannot be generalized as easily because it depends not only on the temperature regime to which the plant is adapted, but also on the climatic correlates of temperature.

Life form is intimately connected with the shoot - root balance and with reproductive allocation. The shoot:root ratio in annuals increases with time, and the reproductive allocation is a high proportion of total biomass. In woody perennials the shoot:root ratio generally declines with age, and reproductive allocations are usually less than those in annuals.

Within species the variation of growth distribution, and hence plant architecture, as a result of population adaptation to latitudinal, elevational, edaphic, and moisture gradients is well documented. Variation within populations is less well studied and estimates of heritability are rare.

INTRODUCTION

It is reasonable to assume that plants can adjust their architecture to fit their environment. Animals have behavioural modes to accomplish this. If they find themselves too warm, they seek the shade of a burrow; if too cold, they bask in the sun. Analogous responses in plants would be the differential allocation of growth to the stem in order to seek the sun when they find themselves in partial shade, or the allocation of growth to roots when the soil water status or nutrient environment become limiting to biological function. This is not a teleological argument. These responses have been fixed by natural selection: those individuals capable of adjusting their growth to seek a more favourable environment were better equipped to survive and reproduce than those that did not.

But the ability to respond to environmental stimuli entails a metabolic cost, and plants, with their limited capacity to sense stimuli, can err in their growth response when confronted with fluctuating environments. The bounds to environmental response, called phenotypic plasticity or individual adaptability, therefore, are not without limit. Plants have adapted to meet the demands of the environmental rigours that they most frequently encounter, and to respond to changes within limits around the mean.

The allocation of growth is a broad topic. It includes the division between reproductive and vegetative efforts and the distribution among vegetative organs: leaves, stem, and root system. Within organ systems there are also trade-offs: for example, long tap roots with few laterals versus fibrous, multi-branched root systems.

This paper is primarily a review of the patterns of distribution among vegetative organs, but also refers briefly to trade-offs within organ systems and to reproductive allocation.

MODELS FOR THE DISTRIBUTION OF GROWTH

Thornley (1972a, b, 1975, 1977a, b) and Hunt (1975, 1976, 1977) discussed models for the partition of photosynthate in which the balance between rate of nutrient and water uptake by the root and CO_2-fixation by the leaves determines the allocation of carbohydrate:

$$\text{root mass} \times \text{rate}_{(\text{absorption})} \propto \text{leaf mass} \times \text{rate}_{(\text{photosynthesis})}$$

If conditions limit photosynthesis (for example, low light) then most or all of the current photosynthate will be used near the source, and leaf and stem growth will exceed that of root growth until the canopy is capable of producing sufficient photosynthate to exceed its requirements. This agrees with most observations on translocation. For example, translocation of carbohydrates from the shoot is lowest when shoot growth is most active (Lister *et al.*, 1967). If nutrients limit growth, then photosynthate cannot be used in the canopy and it will be available for translocation to the roots. The limited nutrients that are absorbed will be used near the point of entry, the roots, so that root growth will exceed stem and leaf growth until the root is capable of exporting nutrients to the canopy. The model would

predict that periods of root growth should alternate with periods of shoot growth which, in fact, is the situation for many species even under constant conditions in growth chambers (Fig. 1 from Ledig *et al.*, 1976), or in tropical trees growing in an aseasonal climate (Borchert, 1973). And it has long been observed in the field (for example, Kienholz, 1934; Webb, 1977). Rhythmic growth patterns in pines are parallelled by rhythms in short-term translocation patterns as indicated by distribution of photosynthetically fixed ^{14}C (Shiroya *et al.*, 1966; Schier, 1970).

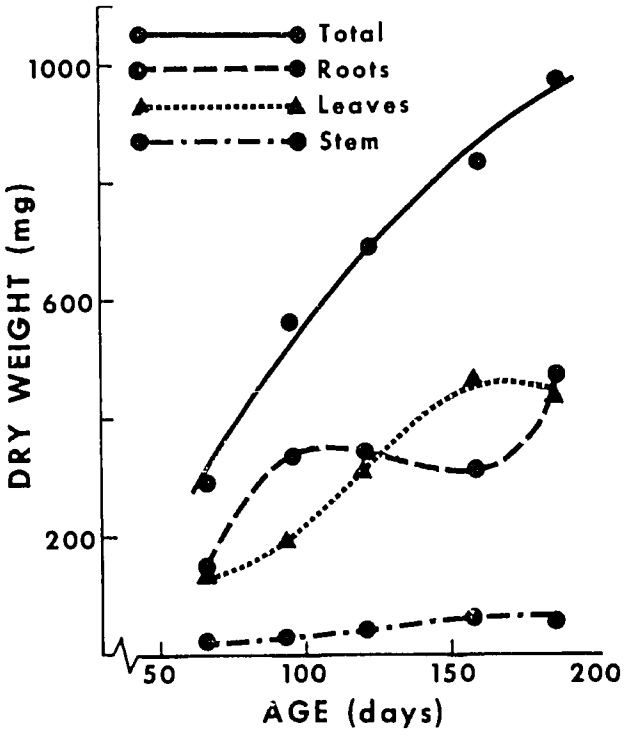


Fig. 1. Peaks of root growth activity alternate with peaks of shoot growth in seedlings of pitch pine (*Pinus rigida*) grown under constant conditions (Ledig *et al.*, 1976).

DEVELOPMENTAL PATTERNS

The shoot:root ratio increases with age in herbaceous plants and decreases in woody perennials, at least in seedlings (Figure 2). Rooted Monterey pine (*Pinus radiata* D. Don) cuttings from physiologically mature trees have lower shoot:root ratios than seedlings of the same size (Fielding, 1970). In general, the greater degree of perenniality (that is, the longer lived), the greater the root growth relative to shoot growth (Troughton, 1960). Because of developmental changes it is difficult to evaluate treatment effects by comparing proportions or ratios. It is better for many purposes to compare the parameters of the allometric equation (Ledig and Perry, 1966; Ledig *et al.*, 1970):

$$\ln Y = a + b \ln X.$$

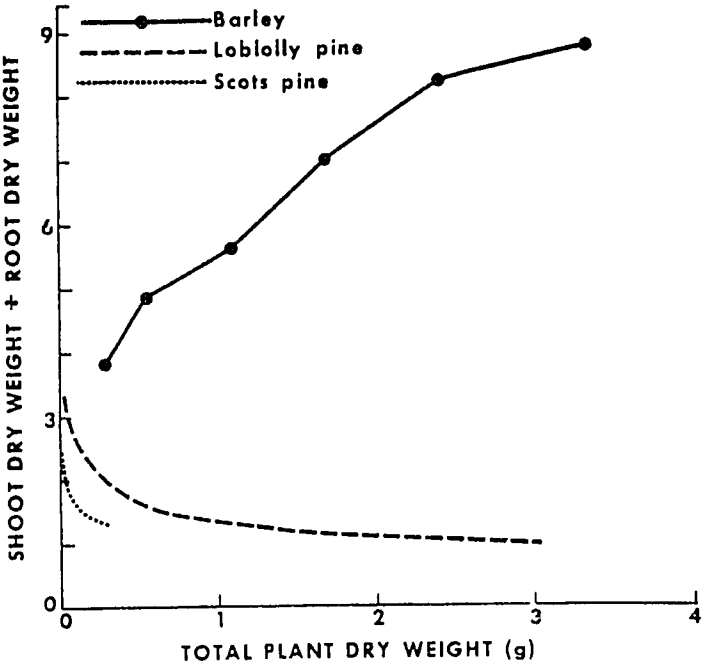


Fig. 2. Shoot:root ratio generally declines with age in woody species and increases in herbaceous species (Turner, 1922; Ledig *et al.*, 1970).

In the equation, lnY and lnX may be the natural logarithms of two organs, or one organ (lnY) and total dry weight (lnX). Allometric relationships among vegetative organs are constant until the onset of flowering, at least in grasses (Troughton, 1956, 1960). In tree species, the relationship seems to hold for at least three years, and perhaps much longer, for example, 15 years in peach (*Prunus persica* [L.] Stokes) (Chalmers and van den Ende, 1975) and 55 years in Scots pine (*Pinus sylvestris* L.) (Ledig *et al.*, 1970).

After perturbation, such as root pruning or shoot clipping, differential growth returns shoot and root to the relationship existing before disturbance (Brouwer, 1962). The relationship between shoot and root is obviously altered after leaf abscission in deciduous trees, but apparently returns in the following spring to levels that continue established trends (Figure 3). Photoperiodic responses in woody species cause alternating growth of shoots and roots, resulting in swings around the allometric relationship (Figure 4); nevertheless, over a sufficient period of time a consistent trend is obvious (Cannell and Willett, 1976).

Although environmental stimuli cue changes in the developmental pattern, controls on the distribution of growth are probably hormonal in nature. Certainly, the strength of reproductive organs as a sink for both nutrient elements and carbohydrates is the result of hormonal control rather than external limitations to growth of the leaves, stem, or roots. Changes in leaf or root activity change hormonal balance. And because subsequent growth

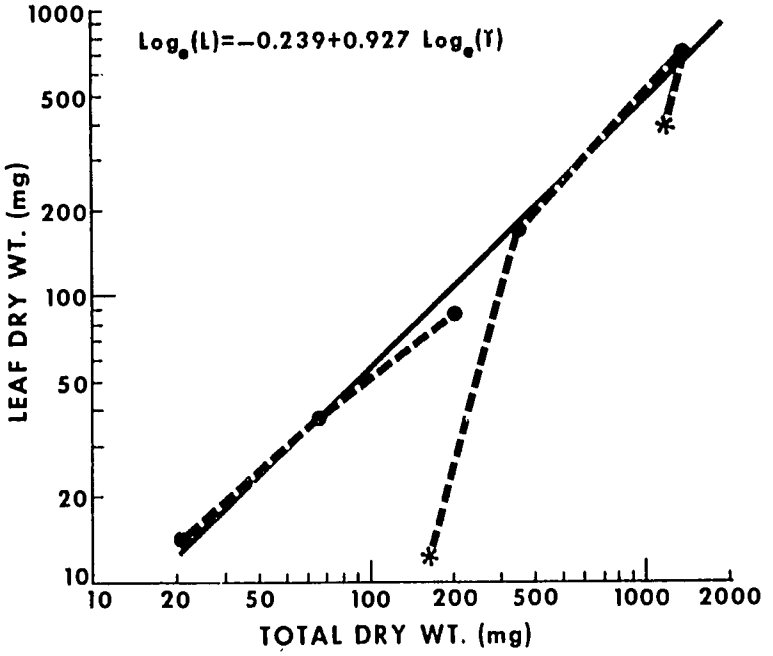


Fig. 3. After winter dormancy the relationship of leaf dry weight to total seedling dry weight tends to return to the patterns established in the first growing season in the deciduous European larch. Asterisks (*) indicate values during early spring when leaf growth was just beginning and in autumn after leaf fall had begun.

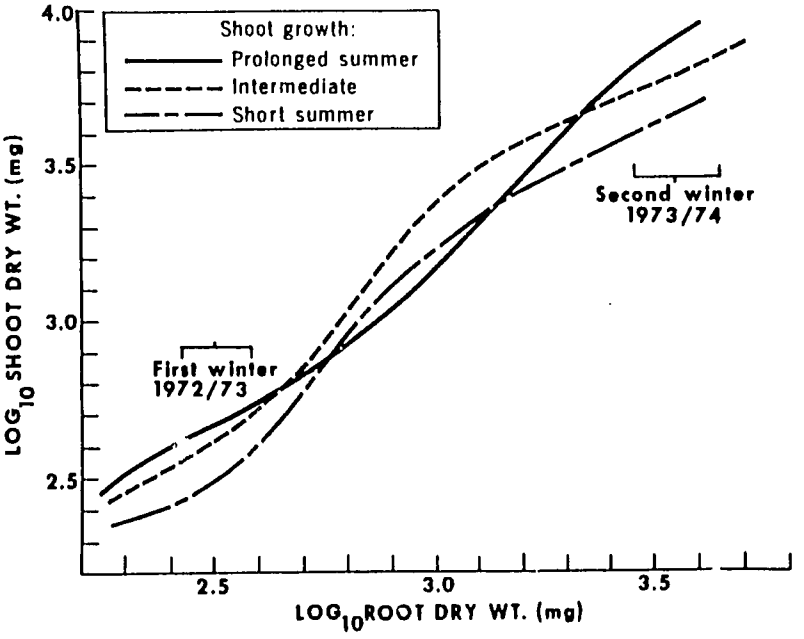


Fig. 4. Oscillation in the shoot:root relationship in lodgepole pine (*Pinus contorta*) provenances as affected by their duration of shoot growth (Cannell and Willett, 1976).

response to correct the imbalance is adaptive, hormonal control and control by limiting factors are indistinguishable in effect. Hormonal control is necessary to maintain growth along adaptive lines despite environmental noise.

ENVIRONMENTAL INFLUENCES

Physical environment

Light. If light has an effect on partitioning of photosynthate it is to increase root growth relative to shoot growth at higher levels of irradiance. Shading reduced the relative growth of roots in grass seedlings (Troughton, 1960), but had no effect on th relative growth of root to shoot in several tree species (Ledig *et al.*, 1970; Doley, 1978). Light *per se* had no effect on the allometric relationships in perennial ryegrass (*Lolium perenne* L.), but under a combination of shading and high levels of nitrogen fertilization, tops grew at a relatively greater rate than roots (Table 1 from Hunt, 1975). Based on the proportion of new growth accounted for by leaves, stem and root the allocation to leaves remained a constant proportion in chrysanthemum (*Chrysanthemum morifolium* Ramat.) irrespective of irradiance; and similar responses were cited for other species (Acock *et al.*, 1979). Under a combination of high light and high moisture Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) had relatively greater shoot growth than root growth compared with other combinations of light and moisture treatment (Ledig *et al.*, 1970).

Table 1. Effect of nitrogen and light on relative root to shoot growth in ryegrass (Hunt, 1975).

Treatment	Allometric constant
High nitrogen - high light	0.838
Low nitrogen - high light	0.953
High nitrogen - low light	0.694
Low nitrogen - low light	0.727

As expected, shoot:root ratios in several woody species were higher in shade than in full sun (Kozlowski, 1949; Huxley, 1967; Gordon, 1969; Carpenter, 1974; Patterson, 1980), but investigations based on the final proportion of dry matter in leaves or roots after extended periods of growth are difficult to interpret. Because shoot:root ratios change with ontogeny, developmental differences are confounded with treatment effects. In several studies of shoot:root ratios, the effect of irradiance may also be confounded with moisture stress (for example, Gordon, 1969; Carpenter, 1974).

Root growth response to illumination of the leaves resembles photosynthetic light response curves in some woody species (Richardson, 1953); that is, there is a light compensation point, a rapid increase in root growth with increasing irradiance, and finally an approach to an asymptote or saturation level. The response time was in the order of 12 to 24 hours in silver maple (*Acer saccharum* L.) seedlings, but substantially longer in red

oak (*Quercus rubra* L.) (Richardson, 1956). Studies on translocation of ^{14}C-labelled carbohydrates also indicate an increased export to roots with increasing irradiance. More labelled carbohydrates were translocated to roots after exposure at high irradiance than after low irradiance in Italian ryegrass (*Lolium temulentum* Lam.) and barley (*Hordeum vulgare* L.) (Ryle and Powell, 1976). The response is immediate, but not fully expressed until two or three days at high or low levels of irradiance. In some pines, and in sorghum (*Sorghum sudanense* [Piper] Stapf), translocation to the roots was greatest following several days of preconditioning under high irradiance (Shiroya *et al.*, 1962; Wardlaw, 1976).

The results agree with the hypothesis that requirements for shoot growth are satisfied first and, as the needs of the shoot are saturated, the carbohydrate gradient increases and the roots receive an increasing share of assimilates. If nutrients or water are limiting then carbohydrates cannot be utilized for shoot growth, and the root will receive a disproportionate share. Therefore, shoot growth should be saturated at a lower irradiance than root growth. In fact, for western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and Douglas fir, shoot dry weight was greatest when seedlings were grown at 50 to 75 per cent of full sunlight, but root growth was greatest when seedlings were grown without shade (Brix, 1970). For ryegrass and barley, the amount of ^{14}C-labelled products retained in the leaves was constant, so increased assimilation under high irradiance primarily favoured the roots (Ryle and Powell, 1976). Whether short-term change in translocation has an effect on developmental patterns is less certain. Short-term experiments do not always separate temporary storage products from structural growth.

Many species respond to levels of irradiance by changes in leaf and stem morphology without changes in the allocation of dry matter growth between tops and roots (Figure 5). Internodes are longer and/or leaves are broader and thinner when shaded, for both woody perennials and herbaceous species (for example, Jackson, 1967; Ledig *et al.*, 1970; Carpenter, 1974; Doley, 1978; Acock *et al.*, 1979).

Photoperiod. Without exception, the effect of lengthening photoperiod is to increase shoot growth relative to root growth in temperate perennials (Bourdeau, 1961; Giertych and Farrar, 1961; McNaughton, 1966; Read and Bagley, 1967; Eliasson, 1971; Heide, 1974; Anon., 1976; Immel *et al.*, 1978; Kinloch, 1980). Temperate plants respond to long photoperiods by extending their shoot growth period. Because growth is episodic roots elongate after shoot extension and leaf expansion slow down. Thus, extended periods of shoot growth result in an increase in shoot: root ratio. Tropical plants, not photoperiodically adapted, should show no response, or an erratic response, to variation in photoperiod.

Temperature. The effect of temperature on the allocation of growth is difficult to generalize about (for example, see literature reviewed in Acock *et al.*, 1979). Shoot:root ratios, or relative shoot growth to root growth, increase with temperature in some species (McNaughton, 1966; Cooper and Thornley, 1976;

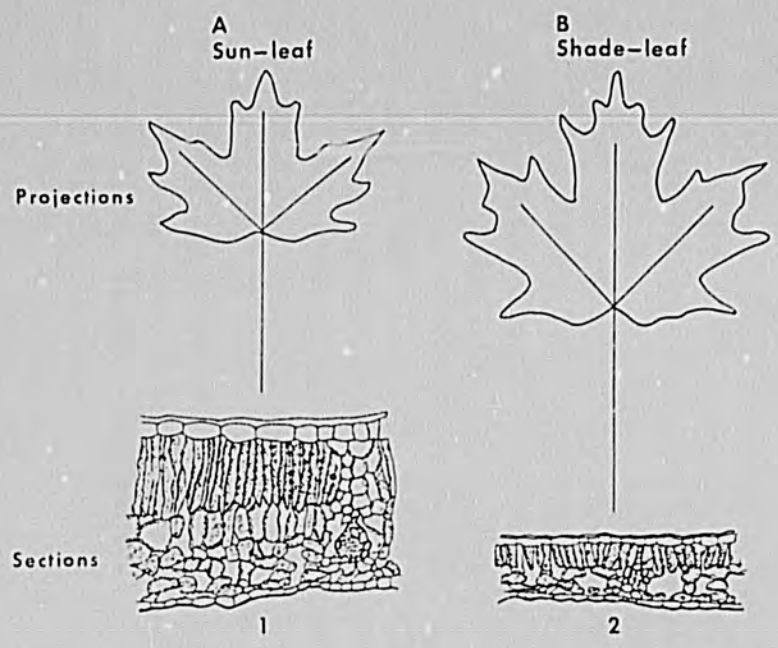


Fig. 5. Drawn for sugar maple (*Acer saccharum*). Shade leaves and sun leaves. Shade leaves are broader and produce higher concentrations of chlorophyll than sun leaves which are thicker and have higher levels of carboxylating enzymes.

Gur *et al.*, 1976; Hodgkinson and Quinn, 1976; Gowin *et al.*, 1980) and decrease in others (Troughton, 1961; Mahon *et al.*, 1976; Gottlieb, 1978; Acock *et al.*, 1979). Part of the problem may be the lack of temperature differential between shoots and roots in controlled environment experiments; an unusual situation in nature where variables such as light, photoperiod, soil water status and mineral nutrition impinge directly on one or the other of either the shoot or the root. However, temperature treatments in most controlled environments are usually applied to both simultaneously, and root and shoot responses and interactions are complex. For example, photosynthesis is partly a temperature insensitive photochemical reaction, while photorespiration increases with temperature as a result of the temperature dependence of leaf ribulose-1,5-diphosphate carboxylase/oxygenase activity. Therefore, as temperature increases, the rate of root absorption should increase more rapidly than the rate of net photosynthesis.

Thornley's model would, indeed, predict that shoot:root ratio will increase as root activity increases. However, this hypothesis was not borne out in several species of trees when root temperatures were varied from 19°C to 27°C and shoot temperature was held constant at 22°C (Heninger and White, 1974). Shoot:root ratios did tend to increase at 31°C, perhaps because of rapid rates of root respiration. Shoot:root ratio decreased with change in temperature from 19°C to 15°C in species with apparent growth optima of 19°C or above, which can be explained either by reduced root activity or by the observation that the optimum temperature for root growth is lower than that for shoot

growth (Nielsen and Humphries, 1966; Davidson, 1969a). The results suggest that the effect of temperature is directly on growth rate and not on relative activity.

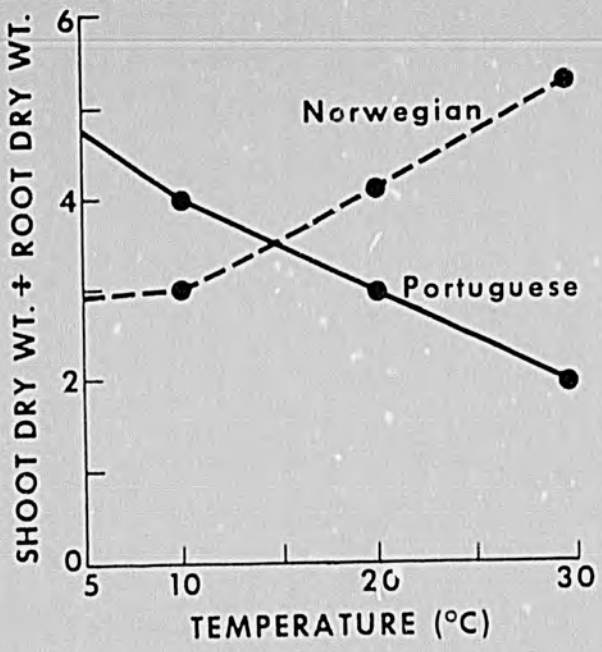


Fig. 6. Shoot:root ratio in a Norwegian race of orchard grass (*Dactylis glomerata*) increased with increasing temperature but decreased in a Portuguese race adapted to summer drought (Eagles, 1967).

Temperature responses may vary among species as a result of differences in climatic adaptation. For example, allometric root to total dry weight growth increased with increasing temperature in the subtropical species cassava (*Manihot esculenta* Crantz) (Mahon *et al.*, 1976), but decreased in several temperate species (McNaughton, 1966; Cooper and Thornley, 1976; Gur *et al.*, 1976). In orchard grass (*Dactylis glomerata* L.) relative shoot-to-root growth increased with increasing temperature in a race from a climate with a cool, moist growing season and decreased in a race from an area with summer drought (Figure 6 from Eagles, 1967).

If seasonal change is signalled by a difference in temperature its effects will also depend on the precipitation regime to which a plant is adapted.

Soil water status. Greater available soil water often reduces root growth relative to shoot growth (Figure 7 from Gales, 1979, and see Harris, 1914; Satoo, 1956; Troughton, 1960; Steinbrenner and Rediske, 1964; Zelawski *et al.*, 1969; Read and Bartlett, 1972; Barlow *et al.*, 1976; Timmis and Tanaka, 1976; Silvius *et al.*, 1977; Fisher and Turner, 1978; Blake *et al.*, 1979). Relatively few studies, however, have shown a change of the allometric coefficient in response to soil water status (Pearsall, 1927; Troughton, 1960; Ledig *et al.*, 1970).

In soybean (*Glycine max* [L.] Merrill) a condition of water

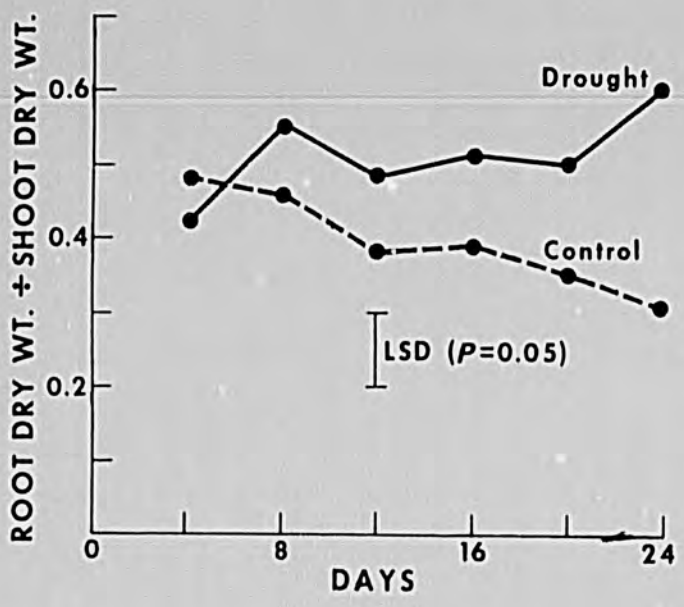


Fig. 7. Increase in root:shoot ratio as a result of drought treatment in ryegrass (*Lolium perenne*) (Gales, 1979).

stress as compared with adequate watering resulted in greater translocation of photosynthetic products to the roots, except during the period of pod-filling (Silvius *et al.*, 1977) because reproductive demands have priority of resources in annuals. Genotype can interact with drought treatment. For example, in cottonwood (*Populus deltoides* Bartr. ex Marsh.), or loblolly pine (*Pinus taeda* L.), clonal or family interactions with a water stress treatment were observed (Farmer, 1970; Cannell *et al.*, 1978). Even when effects of soil water on shoot:root dry weight balance appear to be lacking there are changes in root morphology (Penka, 1965).

Evans (1980) has suggested that the input of energy in the form of irrigation may permit the breeder to shift growth from the roots to the top to increase merchantable yield. Furthermore, this trend would reduce respiratory losses because roots can account for a high proportion of a plant's carbon loss through respiration. In addition, allocating a greater proportion of carbon resources to leaf growth would increase the growth rate (Ledig, 1976). Without irrigation the optimal shoot:root balance will necessarily be less than that where irrigation is practised. Furthermore, on dry sites, Cannell *et al.* (1978) have found a negative association between volume growth in loblolly pine families and high relative shoot-to-root growth.

Nutrient level and soil structure. The response of shoot and root growth to fertilization conforms to the expectations of Thornley's model. High levels of nutrients increase growth of shoot relative to root in both herbaceous and woody species (Figure 8 from Shamsi and Whitehead, 1977, and see Harris, 1914; Turner, 1922; Pearsall, 1927; Mitchell, 1934; White, 1937; Williams, 1948; Troughton, 1955, 1956, 1977; Vose, 1962;

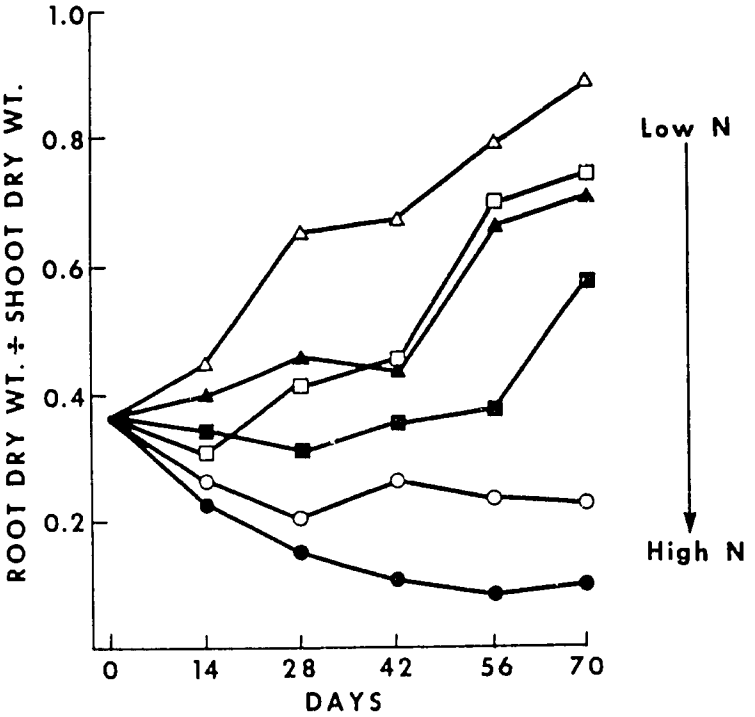


Fig. 8. Change in root:shoot ratio with various nitrogen concentrations in *Lythrum salicaria* (Shamshi and Whitehead, 1977).

Steinbrenner and Rediske, 1964; Davidson, 1969b; Blackmon, 1970; Giertych, 1970; Evans, 1972; Mathews, 1972; Drew *et al.*, 1973; Hunt, 1975; Haines and Dunn, 1976; Stribley and Read, 1976; Will, 1977; Joiner *et al.*, 1980; Maynard *et al.*, 1980). However, in some other examples nutrient level had no effect on the shoot:root balance (for example, Shamshi and Whitehead, 1977; Anderson and Ladiges, 1978; Joiner *et al.*, 1980). Perhaps because the range of fertilizer treatments was not broad enough to cause a measurable response. Potassium is less effective in altering the shoot:root balance than nitrogen or phosphorus (Vose, 1962; Shamshi and Whitehead, 1977; Bouma *et al.*, 1979; Joiner *et al.*, 1980).

Not all genotypes respond to changes in nutrient level to the same degree. For example, the relative shoot-to-root growth of various provenances of Norway spruce (*Picea abies* [L.] Karst.) was affected differently by changes in phosphorus level (Giertych, 1970). In European larch (*Larix decidua* Mill.) fertilization prolonged the shoot growth period (Pineau, 1968), a possible mechanism whereby nutrient level may influence shoot:root ratio in some tree species.

There is less information on the effect of soil structure on shoot:root balance. Root growth is retarded by compaction and lack of aeration, probably because of inhibition of root respiration. As a result shoot:root ratio may increase. In ryegrass and clover (*Trifolium repens* L.), shoot growth was favoured

against root growth in waterlogged soils (Davidson, 1969b). However, Ladiges and Kelso (1977) found no effect of waterlogging on shoot:root ratio in ribbon gum (*Eucalyptus viminalis* Labill.) or swamp gum (*E. ovata* Labill.).

Biotic competition

The effect of plant population is variable. A greater plant population may increase (Kamel, 1959), decrease (Troughton, 1955, 1956), or not affect the distribution of growth between shoot and root (Troughton, 1956; Rennie, 1974). This variability may result from differential effects of plant population on above- versus below-ground competition, depending on the species and levels of stocking used. Results that show an increase in shoot:root ratio in woody species with increasing nursery bed population, or under grass competition, are suspect because effects are confounded with developmental changes (Fober and Giertych, 1971; Wilson and Campbell, 1972). Changes under interspecific competition seem to be complementary. If shoot:root ratio is increased in one species it is decreased in the other (Troughton, 1955).

GENETIC VARIATION

Species patterns

Shoot:root ratios decrease from the annual to the herbaceous perennial habit, and to seedlings of woody perennials (Table 2 from Abrahamson, 1979, and see Monk, 1966). Tuber crops are exceptions having a high proportion of growth in below-ground organs (Bray 1963; Penka, 1965). Within the woody life form there is a trend for species of early seral stages to have greater shoot-to-root growth than those from later ones. Species like pin cherry (*Prunus pennsylvanica* L.), trembling aspen (*Populus tremuloides* Michx.) and red alder (*Alnus rubra* Bong.), which are geared to temporary occupancy of a site, distribute more growth to leaves and stems than to roots, and they enter the reproductive stage at an early age as contrasted with longer lived species such as beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) (Zavitkovski and Stevens, 1972; Marks, 1975).

Table 2. Per cent of biomass in vegetative and reproductive organs in herbaceous wildflower species from the eastern United States by life form (Abrahamson, 1979).

Life form	No. of species	Below-ground %	Stem %	Leaf %	Flowers %	Shoot: root
Field annuals	9	14	43	24	20	6.14
Field perennials	24	29	31	28	12	2.45

Habitat related gradients also are observed. Species specific shoot:root ratios increase along gradients from xeric to mesic habitats in both herbs and trees (Bray, 1963; Mooney *et al.*, 1978). Desert species have the lowest shoot:root ratios

(Mooney and Bartholomew, 1974; Evenari *et al.*, 1975). Apparently root morphology may vary as well. For example, from predominantly taprooted, in eucalypt species native to dryer habitats, to shallow fibrous-rooted, in species from mesic habitats (Zimmer and Grose, 1958). Shoot:root ratios may decrease from high values in species at low latitude and altitude to low values in species native to high latitudes and altitudes (Wiegolaski, 1975).

Intraspecific variation

Ecovariants. When the pattern of dry matter distribution varies among populations within a species the trends can generally be interpreted as adaptive. For example, two populations of ribbon gum and mugga (*Eucalyptus sideroxylon* [A. Cumm.] Benth.), native to areas with low rainfall, had lower shoot:root ratios (that is larger root systems for their size) than populations representative of high rainfall climates (Zimmer and Grose, 1958; Ladiges, 1974; Pederick, 1976). Seedlings with relatively larger root systems were less susceptible to wilting when water was withheld, and recovered from stress more rapdily than seedlings from populations characterized by high shoot:root ratios (Table 3 from Ladiges, 1974). Similar examples have been reported in a variety of species (Bey, 1974; Baldwin and Barney, 1976; Venator, 1976).

Table 3. Shoot:root ratios and drought damage for 3-month-old seedlings of ribbon gum (*Eucalyptus viminalis*) (Ladiges, 1974).

Population	Leaf material dead %	Plants killed %	Dry weight (mg)	Shoot:root ratio
Dry sites:				
Anakie granite	20.8	10	172	2.22
Anakie basalt	65.1	10	230	1.96
Mesic sites:				
Trentham	69.0	50	189	2.94
Mt Cole	73.0	40	230	2.56

Latitudinal trends in the distribution of growth are quite consistent in tree species. In uniform garden experiments provenances native to northern latitudes have relatively more root to shoot growth than provenances from southern latitudes (Kriebel, 1963; Gordon, 1966; Brown, 1969; Schultz and Gatherum, 1971; Brown and Cech, 1972; Farmer, 1975). Apparently, the proximal cause is photoperiodic. Growth is extended in provenances from areas south of the test location because photoperiods are longer than those to which they are adapted, and/or they are adapted to an inherently longer growing season. While the reverse is true for provenances from areas north of the test location. Shoot growth, therefore, continues longer in southern provenances. And by the time buds are set little time is available for root growth before temperatures become restrictive.

In northern provenances of lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Sitka spruce (*Picea sitchensis* [Bong.] Carr.), and black cottonwood (*Populus trichocarpa* Torr. et Gray), where

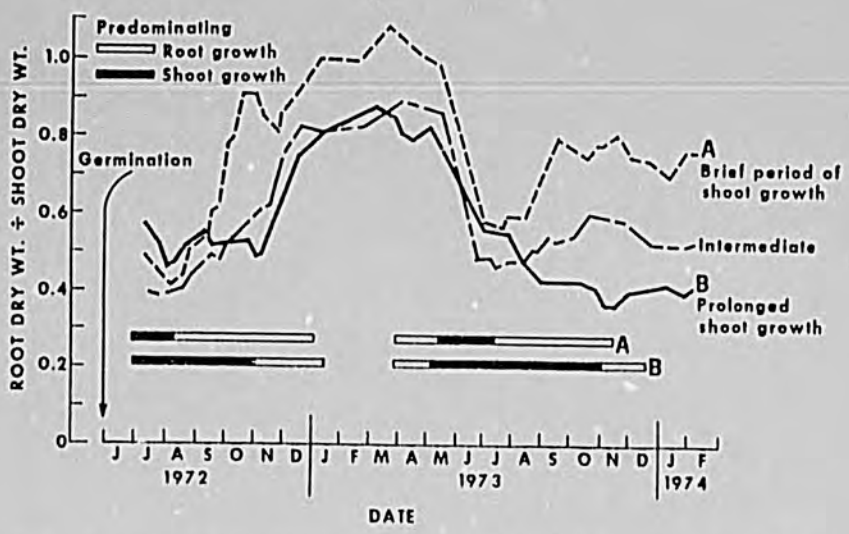


Fig. 9. Seasonal fluctuation in root:shoot ratio in lodgepole pine (*Pinus contorta*) provenances. The longer the period fo shoot growth, the less time for root growth and the lower the root:shoot ratio (Cannell and Willett, 1976).

terminal buds formed earlier, periods of root growth were longer and shoot:root ratios lower than in southern provenances (Cannell and Willett, 1976, and also Sweet and Wareing, 1968). However, more detailed analysis indicated that this compensation occurred in the spring. So for periods measured in years rather than months, the allometric relationships were similar for all provenances of Sitka spruce and black cottonwood (Cannell and Willett, 1976). The pattern of greater root growth relative to shoot growth was retained in lodgepole pine because shoot growth was not as strongly linked to photoperiod. In lodgepole pine current growth was fixed by the number of primordia laid down in the bud the previous year.

On the basis of trends for latitudinal races, and when grown in the same environment, provenances from high altitudes should have greater root growth relative to shoot growth than provenances from low altitudes. In fact, little information is available on relative shoot and root growth with relation to altitudinal transects, and it is conflicting. In lodgepole pine, shoot:root ratio was lower in montane provenances than in coastal provenances (Roberts and Wareing, 1975), but in Norway spruce shoot:root ratio increased with elevation (Holzer, 1966).

Not all differences among provenances are of the fixed or constitutive type. Different populations of the same species may differ in their environmental response, or even in the degree of their response, exhibiting phenotypic plasticity. As an example of differences in environmental response the shoot:root ratio of a Norwegian race of orchard grass increased with increasing temperature, but that of a Portuguese race decreased (Figure 6). For the Norwegian race, which evolved in a climate characterized by summer rainfall, higher temperatures favour water and mineral absorption by roots, so the shoot is free to grow. But for the Portuguese race, higher temperatures signal summer drought, and

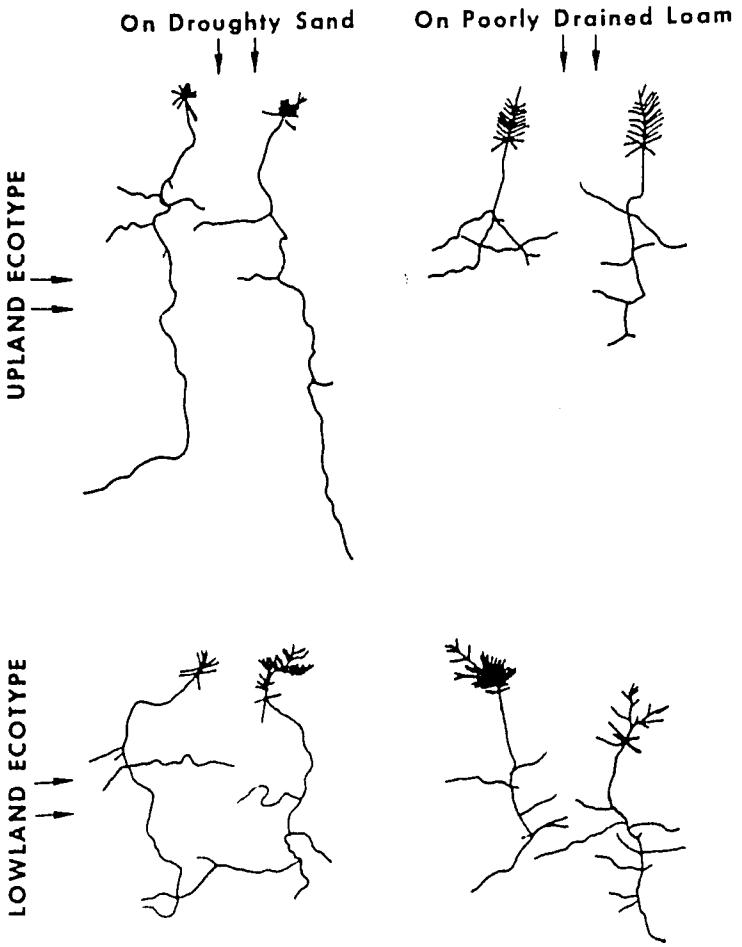


Fig. 10. The root system of seedlings from northern white cedar (*Thuja occidentalis*) growing on the uplands responded plastically to soil moisture conditions in an otherwise uniform environment. Seedlings from parents native to poorly drained lowlands lacked the ability to respond adaptively (Habeck, 1958).

survival depends on an extensive root system. The classic study of Habeck (1958) on upland and swamp ecotypes of northern white cedar (*Thuja occidentalis* L.) has demonstrated genetically determined differences in plasticity (Figure 10, from Habeck, 1958).

In addition to simple differences in the distribution of growth among organ systems, there may be differences among provenances in the way available carbohydrates are used within an organ system. For example, growth of roots may be dominated by formation of a taproot or by a much ramified and fibrous structure. Examples of variation in root morphology include provenances of Scots pine and black cherry (*Prunus serotina* Ehrh.) (Brown, 1969; Brown and Geck, 1972).

Intrapopulation variation. Much less is known about variation in growth allocation within populations. Ledig and Perry (1966)

and Cannell *et al.*, (1978) found differences among families in loblolly pine. In Cannell *et al.*'s (1978) sample, families having a high relative rate of root growth compared to shoot growth in the seedling stage produced the greatest wood volume at eight years when evaluated on a droughty site (r varied from -0.5 to -0.8), but not on a site with a high water table. Cottonwood clones vary in relative growth of shoot to root and in their interaction with moisture stress treatment (Farmer, 1970). Variation in shoot - root relations among varieties of ryegrass, orchard grass, and tall fescue (*Festuca arundinacea* Schreb.), was also related to differences in growth and yield (Troughton, 1963; MacColl and Cooper, 1967), but gains were predicted for selection of varieties with greater top growth (Troughton, 1977). The only report of heritability uncovered was 0.32 for shoot: root ratio in bread wheat (*Triticum aestivum* L.), and effects resulting from dominance variance were also significant (Kazemi *et al.*, 1978).

REPRODUCTIVE ALLOCATION

The induction of reproductive structures results in a decrease in allocation to vegetative organs (Leonard, 1962). In peach trees diameter increment, or dry weight growth of vegetative organs drops 80 per cent within four years after fruiting (Chalmers and van den Ende, 1975). Fielding (1960) estimated that 7-year-old Monterey pine allocated 16 per cent of current dry weight to sexual reproduction. Dwarf ecotypes of pitch pine (*Pinus rigida* Mill.) grow at almost the same rate as normal pitch pine for their first few years, and the distribution of growth between shoot and root is similar. But the dwarf forms are reproductively precocious and rapidly fall behind in stature after flowering begins (Good and Good, 1975; Ledig and Little, 1979). Dwarfing rootstocks are used to change allocation patterns in fruit trees to favour fruit at the expense of roots. Apparently phloem transport is checked in some graft combinations but, in others, swelling below the graft union suggests that there is an accumulation of carbohydrates in the roots (Sax, 1958). Therefore, more than one mechanism may be responsible for increased reproductive allocations. Rootstock - scion interactions are known (Tubbs, 1980).

In their wild state, annuals devote a greater proportion of photosynthate to reproduction than flowering perennials (Pitelka, 1977; Abrahamson, 1979). Annual allocation to fruit may be very high in domesticated perennials once they reach reproductive maturity; allocation to fruit can be greater than 60 per cent of annual increment in peach (Chalmers and van den Ende, 1975). However, the annual increment is only a fraction of the total accumulated dry weight in roots and stem, so fruit weight is a small proportion of total dry weight. Plants growing in more rigorous habitats and under limiting conditions allocate less to sexual reproduction than those more favoured, although the former may allocate more to vegetative reproduction through increased growth of below-ground parts, such as rhizomes. Thus, in a sample of native North American herbaceous species those indigenous to open habitats allocated 14.5 per cent to flower production and 24 per cent to below-ground organs, but figures for

Table 4. Per cent of biomass in vegetative and reproductive organs in herbaceous wildflower species from the eastern United States by habitat type (Abrahamson, 1979).

Habitat type	No. of species	Below-ground %	Stem %	Leaf %	Flowers %	Shoot:root
Fields	36	24	36	26	14	3.2
Woods	16	40	18	34	8	1.5

those from woodlands were 8.1 per cent to flower production and 40 per cent to below-ground organs (Table 4 from Abrahamson, 1979). Temperate plants growing under rigorous conditions at high elevation may depend on vegetative reproduction, allocating less to sexual reproduction but more to below-ground parts than those at low elevation (Jolls, 1980). However, for species relying primarily on sexual reproduction, reproductive allocation as a proportion of total growth may increase with elevation (Kawano and Masudo, 1980), because less time is available for vegetative growth in shorter growing seasons.

According to some authorities, natural selection may modify wild plants along an r- and K-selection gradient (Solbrig, 1971). For example, dandelions (*Taraxacum officinale* Weber) from frequently disturbed habitats enter the reproductive phase early, while those under severe competition in unmown fields devote considerable growth to leaf production before flowering (Solbrig, 1971); little bluestem (*Andropogon scoparius* Michx.) from older fields, fully stocked with competitors, devoted less to reproduction than those from recently abandoned fields (Roos and Quinn, 1977); and grazed colonies of raspberry (*Rubus hispidus* L.) put more growth into leaves and less into reproduction than ungrazed colonies (Abrahamson, 1975).

APPLICATION TO AGROFORESTRY

In many instances, the distribution of growth in temperate plants, particularly the partition between vegetative and reproductive growth, is regulated directly or indirectly by photoperiod. Photoperiod induces flowering and cues shoot growth cessation by inducing resting buds. Agriculturists and foresters in the tropics and subtropics use many introduced species from temperate zones. The lack of photoperiodic or climatic signals can disrupt their customary growth patterns. The short photoperiods typical of the equatorial regions induce precocious flowering in short-day plants and may prevent flowering entirely in long-day plants. However, these patterns are readily susceptible to modification by breeding. For tropical species, the signals for change from one growth phase to another are less well understood, and the subject is in need of a major research effort.

Responses to limiting factors, such as light, water, and nutrients are adaptive and enhance survival and growth. With intercropping, the patterns of dry weight distribution in understorey crops are likely to change in the direction of increased leaf and stem growth and reduced root growth as a response to

shading. However, root competition for water and nutrients could be compounded because of reduced transpiration under shading, and the net effect warrants study. Certainly, flowering and fruiting will be reduced by growth below an overstorey.

The effect of intercropping on the overstorey is less obvious. Root competition from pasture grasses may increase the distribution of growth to the roots in trees, but once past the seedling stage, competition between roots of annuals and perennials may be less important with respect to dry matter distribution. Species should be chosen that use different rooting zones. If we assume that trees intercropped with low plants will be grown at wide spacing, it seems likely that light will not be limiting to the overstorey and the relative distribution of growth to stem and roots will be greater than when they are grown in a closed canopy.

The types of studies needed to fill our information gap are empirical and practical in nature. In particular, we need more information on the effect of competition, especially comparisons of growth in pure culture versus performance in mixed crops of overstorey and understorey plants.

SUMMARY

The distribution of growth among vegetative parts can be modelled by reference to limiting factors: when photosynthate is limiting, it is used in the canopy and little or none is available for root growth; and when water or nutrients are limiting, they are used at their point of entry, the roots. The mechanism is adaptive because it corrects functional imbalances.

During the period of vegetative growth, relationships among leaves, roots, and stems can be described by the allometric equation, although oscillations around the relationship are observed in response to seasonal demands. The consequence of allometric growth is an ontogenetic change in the proportion of dry matter accumulated in different organs.

Because most changes are adaptive, environmental effects are predictable. High levels of irradiance increase root growth relative to shoot growth, and low levels increase shoot growth relative to root growth. In temperate perennials (and a few tropical ones) short photoperiods signal a cessation of shoot growth, subsequently favouring root growth. In annuals flowering is often keyed to photoperiod and will signal a switch from vegetative to reproductive growth. The effect of temperature cannot be so easily generalized because it depends not only on the temperature regime to which the plant is adapted, but also on the climatic correlates of temperature, such as the association between high temperature and drought in Mediterranean climates, versus high temperature and precipitation in climates with summer maxima. Infertile soils and low water potentials inhibit shoot growth proportionally more than root growth. In addition to changes in plant architecture there are also trade-offs within organ systems; for example, narrow, thick leaves versus broad, thin leaves, as in the sunleaf - shadeleaf dichotomy.

Life form is intimately connected with the shoot:root balance and with reproductive allocation. The shoot:root ratio

in annuals increases with time, and the reproductive allocation has highest priority. In perennials, the shoot:root ratio generally declines with age and reproductive allocations are less than those in annuals. Perennials adapted to a pioneering role are relatively short lived, and generally put less growth into root systems than perennials typical of late successional stages.

Variation in plant architecture within species is well documented. There are examples of population adaptation to latitudinal, elevational, edaphic, and moisture gradients. Variation within populations is less well studied, and estimates of heritability for the shoot:root balance are rare.

In agroforestry, the complex effects of species mixtures on light, water, and nutrients and, therefore, on plant proportions, will depend to a significant degree on the particular combination of species chosen and the number and kinds of plants per unit area. Choice of species will require careful research.

ACKNOWLEDGMENTS

I am grateful to Steve Strauss for his assistance in locating literature on the distribution of growth and for helpful discussions, especially about the effect of nutrients, soil water, and competition. However, any errors of interpretation are my own.

REFERENCES

Abrahamson, W.G. (1975). Reproductive strategies in dewberries. *Ecology* 56, 721-726.

Abrahamson, W.G. (1979). Patterns of resource allocation in wildflower populations of fields and woods. *Am. J. Bot.* 66, 71-79.

Acock, B., Charles-Edwards, D.A. and Sawyer, S. (1979). Growth response of a *Chrysanthemum* crop to the environment. III. Effects of radiation and temperature on dry matter partitioning and photosynthesis. *Ann. Bot.* 44, 289-300.

Anderson, C.A. and Ladiges, P.Y. (1978). A comparison of three populations of *Eucalyptus obliqua* L'Herit. growing on acid and calcareous soils in southern Victoria. *Aust. J. Bot.* 26, 93-109.

Anonymous (1976). Tree physiology. *Rep. Forest Res. Inst. for 1975*, pp.35-39. New Zealand Forest Serv., Wellington.

Baldwin, V.C. and Barney, C.W. (1976). Leaf water potential in planted ponderosa and lodgepole pines. *Forest Sci.* 22, 344-350.

Barlow, E.W.R., Boersma, L. and Young, J.L. (1976). Root temperature and soil moisture potential effect on growth and soluble carbohydrate concentration of corn seedlings. *Crop Sci.* 16, 59-62.

Bey, C.F. (1974). Drought hardiness tests of black walnut seedlings as related to field performance. *Proc. Ninth Central States Forest Tree Improv. Conf.*, pp.138-144. Ames, Iowa, USA.

Blackmon, B.G. (1970). Response of loblolly pine (*Pinus taeda* L.) seedlings to various levels and combinations of nitrogen and phosphorus. *Diss. Abstr. Int., B*, 30(III): 4862-B.

Blake, J., Zaerr, J. and Hee, S. (1979). Controlled moisture

stress to improve cold-hardiness and morphology of Douglas fir (*Pseudotsuga menziesii*) seedlings. *Forest Sci.* 25, 576-582.

Borchert, R. (1973). Simulation of rhythmic tree growth under constant conditions. *Physiol. Plant.*29, 173-180.

Bouma, D., Dowling, E.J. and Wahjoedi, H. (1979). Some effects of potassium and magnesium on the growth of subterreanean clover (*Trifolium subterraneum*). *Ann. Bot.* 43, 529-538.

Bourdeau, P.F. (1961). Vegetative growth and photosynthesis of *Pinus elliottii* seedlings in relation to photoperiod. *IX Int. Bot. Congr. Proc.* 2, 42. (Abstract)

Bray, J.R. (1963). Root production and the estimation of net productivity. *Can. J. Bot.* 41, 65-72.

Brix, H. (1970). Effect of light intensity on growth of western hemlock and Douglas fir seedlings. *Can. For. Serv., Dept Fisheries and For. Bimonthly Res. Notes* 26, 34-35.

Brouwer, R. (1962). Distribution of dry matter in the plant. *Neth. J. Agric. Sci.* 10, 361-376.

Brown, J.H. (1969). Variation in roots of greenhouse grown seedlings of different Scotch pine provenances. *Silvae Genet.* 18, 111-117.

Brown, J.H. and Cech, F.C. (1972). Top and root characteristics of greenhouse grown seedlings of different black cherry provenances. *Silvae Genet.* 21, 130-133.

Cannell, M.G.R. and Willett, S.C. (1976). Shoot growth phenology, dry matter distribution and root:shoot ratios of provenances of *Populus trichocarpa*, *Picea sitchensis* and *Pinus contorta* growing in Scotland. *Silvae Genet.* 25, 49-57.

Cannell, M.G.R., Bridgwater, F.E. and Greenwood, M.S. (1978). Seedling growth rates, water stress responses and root - shoot relationships related to eight-year volumes among families of *Pinus taeda* L. *Silvae Genet.* 27, 237-248.

Carpenter, S.B. (1974). Black walnut in central Kentucky: growth and development of half-sib families under artificial shade. *Proc. Ninth Central States Forest Tree Improv. Conf.*, pp.120-129. Ames, Iowa, USA.

Chalmers, D.J. and van den Ende, B. (1975). Productivity of peach trees: factors affecting dry-weight distribution during tree growth. *Ann. Bot.* 39, 423-432.

Cooper, A.J. and Thornley, J.H.M. (1976). Response of dry matter partitioning, growth and carbon and nitrogen levels in the tomato plant to changes in root temperature: experiment and theory. *Ann. Bot.* 40, 1139-1152.

Davidson, R.L. (1969a). Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover. *Ann. Bot.* 33, 561-569.

Davidson, R.L. (1969b). Effects of soil nutrients and moisture on root/shoot ratios in *Lolium perenne* L. and *Trifolium repens* L. *Ann. Bot.* 33, 571-577.

Doley, D. (1978). Effects of shade on gas exchange and growth in seedlings of *Eucalyptus grandis* Hill ex Maiden. *Aust. J. Plant Physiol.* 5, 723-738.

Drew, M.C., Saker, L.R. and Ashley, T.W. (1973). Nutrient supply and the growth of the seminal root system in barley. I. The effect of nitrate concentration on the growth of axes and laterals. *J. exp. Bot.* 24, 1189-1202.

Eagles, C.F. (1967). The effect of temperature on vegetative growth in climatic races of *Dactylis glomerata* in controlled environments. *Ann. Bot.* 31, 31-39.

Eliasson, L. (1971). Adverse effect of shoot growth on root growth in rooted cuttings of aspen. *Physiol. Plant.* 25, 268-272.

Evans, G.C. (1972). "The Quantitative Analysis of Plant Growth." California Press, Berkeley and Los Angeles, USA.

Evans, L.T. (1980). The natural history of crop yield. *Am. Sci.* 68, 388-397.

Evenari, M., Bamberg, S., Schultze, E.-D., Kappen, L., Lange, O.L. and Buschbom, U. (1975). The biomass production of some higher plants in Near-Eastern and American deserts. *In* "Photosynthesis and Productivity in Different Environments" (J.P. Cooper, ed.), pp.121-127. Cambridge Univ. Press, Cambridge, London, New York, Melbourne.

Farmer, R.E. Jr (1970). Variation and inheritance of eastern cottonwood growth and wood properties under two soil moisture regimes. *Silvae Genet.* 19, 5-8.

Farmer, R.E. Jr (1975). Growth and assimilation rate of juvenile northern red oak: effects of light and temperature. *Forest Sci.* 21, 373-381.

Fielding, J.M. (1960). Branching and flowering characteristics of Monterey pine. *Aust. Forestry and Timber Bur.* Bull. No.37. 59 pp.

Fielding, J.M. (1970). Trees grown from cuttings compared with trees grown from seed (*Pinus radiata* D. Don). *Silvae Genet.* 19, 54-63.

Fisher, R.A. and Turner, N.C. (1978). Plant productivity in arid and semiarid zones. *Ann. Rev. Plant Physiol.* 29, 277-317.

Fober, H. and Giertych, M. (1971). Effect of grass competition on the growth and mineral nutrition of spruce *Picea abies* Karst. *Arboretum Kornicke* 16, 81-106.

Gales, K. (1979). Effects of water supply on partitioning of dry matter between roots and shoots in *Lolium perenne*. *J. appl. Ecol.* 16, 863-877.

Giertych, M.M. (1970). Growth as related to nutrition and competition. *In* "Second World Consult. on Forest Tree Breeding", Vol.1, pp.37-59. United Nations Food and Agriculture Organization, Rome.

Giertych, M.M. and Farrar, J.L. (1961). The effect of photoperiod and nitrogen on the growth and development of seedlings of jack pine. *Can. J. Bot.* 39, 1247-1254.

Good, R.E. and Good, N.F. (1975). Growth characteristics of two populations of *Pinus rigida* from the Pine Barrens of New Jersey. *Ecology* 56, 1215-1220.

Gordon, J.C. (1966). "Photosynthesis, respiration and growth of Scotch pine seedlings". PhD Thesis. Iowa State Univ., Ames, Iowa, USA.

Gordon, J.C. (1969). Effect of shade on photosynthesis and dry weight distribution in yellow birch (*Betula alleghaniensis* Britton) seedlings. *Ecology* 50, 924-927.

Gottlieb, L.D. (1978). Allocation, growth rates and gas exchange in seedlings of *Stephanomeria exigua* ssp. *coronaria* and its recent derivative *S. malheurensis*. *Am. J. Bot.* 65, 970-977.

Gowin, T., Lourtioux, A. and Mousseau, M. (1980). Influence of

constant growth temperature upon the productivity and gas exchange of seedlings of Scots pine and European larch. *Forest Sci.* 26, 301-309.

Gur, A., Bravdo, B. and Hepner, J. (1976). The influence of root temperature on apple trees. III. The effect on photosynthesis and water balance. *J. Hort. Sci.* 51, 203-210.

Habeck, J.R. (1958). White cedar ecotypes in Wisconsin. *Ecology* 39, 457-463.

Haines, B.L. and Dunn, E.L. (1976). Growth and resource allocation responses of *Spartina alterniflora* Loisel. to three levels of NH_4-N, Fe, and NaCl in solution culture. *Bot. Gaz.* 137, 224-230.

Harris, F.S. (1914). The effect of soil moisture, plant food, and age on the ratio of tops to roots in plants. *J. Am. Soc. Agron.* 6, 65-75.

Heide, O.M. (1974). Growth and dormancy in Norway spruce ecotypes (*Picea abies*). I. Interaction of photoperiod and temperature. *Physiol. Plant.* 30, 1-12.

Heninger, R.L. and White, D.P. (1974). Tree seedling growth at different soil temperatures. *Forest Sci.* 20, 363-367.

Hodgkinson, K.C. and Quinn, J.A. (1976). Adaptive variability in the growth of *Danthonia caespitosa* Gund. populations at different temperatures. *Aust. J. Bot.* 24, 381-396.

Holzer, K. (1966). Die Vererbung von physiologischen und morphologischen Eigenschaften der Fichte. I. Samplingsuntersuchungen. [The heritability of physiological and morphological characteristics of spruce. I. Results.] *Forstlichen Bundesversuchsanstalt Mitteilungen* No.71. Mariabrunn. (English summary.)

Hunt, R. (1975). Further observations on root - shoot equilibria in perennial ryegrass (*Lolium perenne* L.). *Ann. Bot.* 39, 745-755.

Hunt, R. (1976). Significant relationships in the analysis of root - shoot equilibria. *Ann. Bot.* 40, 895-897.

Hunt, R. (1977). Significant relationships in the analysis of root - shoot equilibria: a further explanation. *Ann. Bot.* 41, 657-659.

Huxley, P.A. (1967). The effects of artificial shading on some growth characteristics of Arabica and Robusta coffee seedlings. I. The effects of shading on dry weight, leaf area and derived growth data. *J. appl. Ecol.* 4, 291-308.

Immel, M.J., Rumsey, R.L. and Carpenter, S.B. (1978). Comparative growth responses of northern red oak and chestnut oak seedlings to varying photoperiods. *Forest Sci.* 24, 554-560.

Jackson, L.W.R. (1967). Effect of shade on leaf structure of deciduous tree species. *Ecology* 48, 498-499.

Joiner, J.N., Johnson, C.R. and Krantz, J.K. (1980). Effect of light and nitrogen and potassium levels on growth and light compensation point of *Ficus benjamina* L. *J. Am. Soc. Hort. Sci.* 105, 170-173.

Jolls, C.L. (1980). Phenotypic patterns of variation in biomass allocation in *Sedum lanceolatum* Torr. at four elevational sites in the Front Range, Rocky Mountains, Colorado. *Bull. Torrey Bot. Club* 107, 65-70.

Kamel, M.S. (1959). A physiological study of shading and density effects on the growth and the efficiency of solar energy

conversion in some field crops. *Mededelingen Landbouwhogeschool Wageningen* 59(5), 1-101.

Kawano, S. and Masudo, J. (1980). The productive and reproductive biology of flowering plants. VIII. Resource allocation and reproductive capacity in wild populations of *Heloniopsis orientalis* (Thunb.) C. Tanaka (Liliaceae). *Oecologia* 45, 307-317.

Kazemi, H., Chapman, S.R. and McNeal, F.H. (1978). Components of genetic variance for root/shoot ratio in spring wheat. *Proc. 5th Int. Wheat Genetic Symp.*, pp.597-605. New Delhi, India.

Kienholz, R. (1934). Leader, needle, cambial and root growth of certain conifers and their interrelations. *Bot. Gaz.* 96, 73-92.

Kinloch, B.B. (1980). Effect of photoperiod and container size on sugar pine seedling growth and infection by white pine blister rust. *US Forest Serv. Res. Note* PSW-343. 4 pp.

Kozlowski, T.T. (1949). Light and water in relation to growth and competition of Piedmont forest species. *Ecol. Monogr.*19, 207-231.

Kriebel, H.B. (1963). Selection for drought resistance in sugar maple. *Proc. World Consult. Forest Genet. and Tree Improv.* Vol.1, Paper 3/9. Stockholm, Sweden.

Ladiges, P.Y. (1974). Variation in drought tolerance in *Eucalyptus viminalis* Labill. *Aust. J. Bot.* 22, 489-500.

Ladiges, P.Y. and Kelso, A. (1977). The comparative effects of waterlogging on two populations of *Eucalyptus viminalis* Labill. and one population of *E. ovata* Labill. *Aust. J. Bot.* 25, 159-169.

Ledig, F.T. (1976). Physiological genetics, photosynthesis and growth models. *In* "Tree Physiology and Yield Improvement" (M.G.R. Cannell and F.T. Last, eds), pp.21-54. Academic Press, London, New York, San Francisco.

Ledig, F.T. and Little, S. (1979). Pitch pine (*Pinus rigida* Mill.): ecology, physiology and genetics. *In* "Pine Barrens: Ecosystem and Landscape" (R.T.T. Forman, ed.), pp.347-371. Academic Press, New York, London, San Francisco.

Ledig, F.T. and Perry, T.O. (1966). Physiological genetics of the shoot - root ratio. *Proc. Soc. Am. Foresters*, 1965, pp.30-43. Detroit, Michigan, USA.

Ledig, F.T., Bormann, F.H. and Wenger, K.F. (1970). The distribution of dry matter growth between shoot and roots in loblolly pine. *Bot. Gaz.*131, 349-359.

Ledig, F.T., Drew, A.P. and Clark, J.G. (1976). Maintenance and constructive respiration, photosynthesis, and net assimilation rate in seedlings of pitch pine (*Pinus rigida* Mill.). *Ann. Bot.* 40, 289-300.

Leonard, E.R. (1962). Interrelations of vegetative and reproductive growth, with special reference to indeterminate plants. *Bot. Rev.* 28, 353-410.

Lister, G.R., Slankis, V., Krotkov, G. and Nelson, C.D. (1967). Physiology of *Pinus strobus* L. seedlings grown under high or low soil moisture conditions. *Ann. Bot.* 31, 121-132.

MacColl, D. and Cooper, J.P. (1967). Climatic variation in forage grasses. III. Seasonal changes in growth and assimilation in climatic races of *Lolium*, *Dactylis* and *Festuca*.

J. appl. Ecol. 4, 113-127.

McNaughton, S.J. (1966). Ecotype function in the *Typha* community type. *Ecol. Monogr.* 36, 297-325.

Mahon, J.D., Lowe, S.B. and Hunt, L.A. (1976). Photosynthesis and assimilate distribution in relation to yield of cassava grown in controlled environments. *Can. J. Bot.* 54, 1322-1331.

Marks, P.L. (1975). On the relation between extension growth and successional status of deciduous trees of the northeastern United States. *Bull. Torrey Bot. Club* 102, 172-177.

Mathews, R.G. (1972). A look at shoots'n roots in the nursery. *In* "Proc. Workshop on Container Planting in Canada" (R.M. Waldron, ed.), pp.72-76. Dept of the Environment, Canadian Forestry Service, Report DPC-X-2, Ottawa, Canada.

Maynard, D.N., Lorenz, O.A. and Magnifico, V. (1980). Growth and potassium partitioning in tomato. *J. Am. Hort. Soc.* 105, 79-82.

Mitchell, H.L. (1934). Pot culture tests of forest soil fertility. *Black Rock Forest Bull.* No.5. 138 pp.

Monk, C. (1966). Ecological importance of root/shoot ratios. *Bull. Torrey Bot. Club* 93, 402-406.

Mooney, H.A. and Bartholomew, B. (1974). Comparative carbon balance and reproductive modes of two Californian *Aesculus* species. *Bot. Gaz.* 135, 306-313.

Mooney, H.A., Ferrar, P.J. and Slatyer, R.O. (1978). Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia* 36, 103-111.

Nielsen, K.F. and Humphries, E.C. (1966). Effects of root temperature on plant growth. *Soils and Fertilizers* 29, 1-7.

Patterson, D.T. (1980). Shading effects on growth and partitioning of plant biomass in cogongrass (*Imperata cylindrica*) from shaded and exposed habitats. *J. Weed Sci.* 28, 735-740.

Pearsall, W.H. (1927). Growth studies. VI. On the relative sizes of growing plant organs. *Ann. Bot.* 41, 549-556.

Pederick, L.A. (1976). The genetic resources of the Victorian eucalypts. *Forests Comm., Victoria, Bull.* No.22. Melbourne, Australia. 31 pp.

Penka, M. (1965). Root-shoot ratio in irrigated plants. *Biol. Plant.* 7, 129-135.

Pineau, M. (1968). Observations phénologiques et morphologiques sur le comportement de quelques essences forestières soumises à l'action des engrais N, P et K. [Phenological and morphological observations on the behaviour of some forest tree species given N, P and K fertilizers.] Thesis no.3936. L'Ecole Polytechnique Fédérale A, Zürich. Buhler Buchdruck, Zürich, Switzerland. 142 pp. (English summary.)

Pitelka, L.F. (1977). Energy allocation in annual and perennial lupines (*Lupines*: leguminosae). *Ecology* 58, 1055-1065.

Read, D.J. and Bartlett, E.M. (1972). The physiology of drought resistance in the soybean plant (*Glycine max*). I. The relationship between drought resistance and growth. *J. appl. Ecol.* 9, 487-499.

Read, R.A. and Bagley, W.T. (1967). Response of tree seedlings to extended photoperiods. *US Forest Serv. Res. Paper* RM-30. 16 pp.

Rennie, J.C. (1974). Some effects of competition and density of plants on dry weight produced. *Ann. Bot.* 38, 1003-1012.

Richardson, S.D. (1953). Studies of root growth in *Acer saccharum* L. I. The relation between root growth and photosynthesis. *Proc. Kon. Ned. Acad. Wetenschappen*, Ser. C56, 185-193.

Richardson, S.D. (1956). Photosynthesis and root growth in tree seedlings. *Landbouwk. Tijdsch.* 68, 775-782.

Roberts, J. and Wareing, P.F. (1975). A study of the growth of four provenances of *Pinus contorta* Dougl. *Ann. Bot.* 39, 93-99.

Roos, F.H. and Quinn, J.A. (1977). Phenology and reproductive allocation in *Andropogon scoparius* (Gramineae) populations in communities of different successional stages. *Am. J. Bot.* 64, 535-540.

Ryle, G.J.A. and Powell, G.E. (1976). Effect of rate of photosynthesis on the pattern of assimilate distribution in the Graminaceous plant. *J. exp. Bot.* 27, 189-199.

Satoo, T. (1956). Drought resistance of some conifers in the first summer after their emergence. *Bull. Tokyo Univ. Forests* 51, 1-108.

Sax, K. (1958). Experimental control of tree growth and reproduction. *In* "The Physiology of Forest Trees" (K.V. Thimann, W.B. Critchfield and M.H. Zimmerman, eds), pp.601-610. Ronald Press, New York.

Schier, G. (1970). Seasonal pathways of ^{14}C-photosynthate in red pine labelled in May, July and October. *Forest Sci.* 16, 1-13.

Schultz, R.C. and Gatherum, G.E. (1971). Photosynthesis and distribution of assimilate of Scotch pine seedlings in relation to soil moisture and provenance. *Bot. Gaz.* 132, 91-96.

Shamsi, S.R.A. and Whitehead, F.H. (1977). Comparative ecophysiology of *Epilobium hirsutum* L. and *Lythrum salicaria* L. III. Mineral nutrition. *J. Ecol.* 65, 55-70.

Shiroya, T., Lister, G.R., Slankis, V., Krotkov, G. and Nelson, C.D. (1962). Translocation of the products of photosynthesis to roots of pine seedlings. *Can. J. Bot.* 40, 1125-1135.

Shiroya, T., Lister, G.R., Slankis, V., Krotkov, G. and Nelson, C.D. (1966). Seasonal changes in respiration, photosynthesis, and translocation of the ^{14}C-labelled products of photosynthesis in young *Pinus strobus* L. plants. *Ann. Bot.* 30, 81-91.

Silvius, J.E., Johnson, R.R. and Peters, D.B. (1977). Effect of water stress on carbon assimilation and distribution in soybean plants at different stages of development. *Crop. Sci.* 17, 713-716.

Solbrig, O.T. (1971). The population biology of dandelions. *Am. Sci.* 59, 686-694.

Steinbrenner, E.C. and Rediske, J.H. (1964). Growth of ponderosa pine and Douglas-fir in a controlled environment. *Weyerhaeuser Forestry Paper* No.1. Weyerhaeuser Co., Forestry Res. Center, Centralia, Washington, USA. 31 pp.

Stribley, D.P. and Read, D.J. (1976). The biology of mycorrhiza in the Ericaceae. VI. The effects of mycorrhizal infection and concentration of ammonium nitrogen on growth of cranberry (*Vaccinium macrocarpon* Ait.) in sand culture. *New Phytol.* 77, 63-72.

Sweet, G.B. and Wareing, P.F. (1968). A comparison of the rates of growth and photosynthesis in first-year seedlings of four provenances of *Pinus contorta* Dougl. *Ann. Bot.* 32, 735-751.

Thornley, J.H.M. (1972a). A model to describe the partitioning of photosynthate during vegetative plant growth. *Ann. Bot.* 36, 419-430.

Thornley, J.H.M. (1972b). A balanced quantitative model for root:shoot ratios in vegetative plants. *Ann. Bot.* 36, 431-441.

Thornley, J.H.M. (1975). Comment on a recent paper by Hunt on shoot:root ratios. *Ann. Bot.* 39, 1149-1150.

Thornley, J.H.M. (1977a). Interpretation of shoot-root relationships. *Ann. Bot.* 41, 461-464.

Thornley, J.H.M. (1977b). Root:shoot interactions. *In* "Integration of Activity in the Higher Plant" (D.H. Jennings, ed.), pp.367-389. Soc. Exp. Biol. Symp. No.31, Cambridge University Press, London, New York.

Timmis, R. and Tanaka, Y. (1976). Effects of container density and plant water stress on growth and cold-hardiness of Douglas fir seedlings. *Forest Sci.* 22, 167-172.

Troughton, A. (1955). The application of the allometric formula to the study of the relationship between the roots and shoots of young grass plants. *Agric. Progress* 30, 197-206.

Troughton, A. (1956). Studies on the growth of young grass plants with special reference to the relationship between the shoot and root systems. *J. Brit. Grassland Soc.* 11, 56-65.

Troughton, A. (1960). Further studies on the relationship between shoot and root systems of grasses. *J. Brit. Grassland Soc.* 15, 41-47.

Troughton, A. (1961). The effect of photoperiod and temperature on the relationship between the root and shoot systems of *Lolium perenne*. *J. Brit. Grassland Soc.* 16, 291-295.

Troughton, A. (1963). A comparison of five varieties of *Lolium perenne* with special reference to the relationship between the root and shoot systems. *Euphytica* 12, 49-56.

Troughton, A. (1977). The rate of growth and partitioning of assimilates in young grass plants: a mathematical model. *Ann. Bot.* 41, 553-565.

Tubbs, F.R. (1980). Growth relations of rootstock and scion in apples. *J. hort. Sci.* 55, 181-189.

Turner, T.W. (1922). Studies of the mechanism of the physiological effects of certain mineral salts in altering the ratio of top growth to root growth in seed plants. *Am. J. Bot.* 9, 415-445.

Venator, C.R. (1976). Natural selection for drought resistance in *Pinus caribaea* Morelet. *Turrialba* 26, 381-387.

Vose, P.B. (1962). Nutritional response and snoot/root ratio as factors in the composition and yield of genotypes of perennial ryegrass, *Lolium perenne* L. *Ann. Bot.* 26, 425-437.

Wardlaw, I.F. (1976). Assimilate movement in *Lolium* and *Sorghum* leaves. I. Irradiance effects on photosynthesis, export and the distribution of assimilates. *Aust. J. Plant Physiol.* 3, 377-387.

Webb, W.L. (1977). Seasonal allocation of photoassimilated carbon in Douglas fir seedlings. *Plant Physiol.* 60, 320-322.

White, H.L. (1937). The interaction of factors in the growth of *Lemna*. XII. The intereaction of light intensity in relation to root length. *Ann. Bot.* 1, 649-654.

Wielgolaski, F.E. (1975). Primary production of tundra. *In*

"Photosynthesis and Productivity in Different Environments" (J.P. Cooper, ed.), pp.75-106. Cambridge University Press, Cambridge, London, New York, Melbourne.

Will, G.M. (1977). The influence of nitrogen supply on the growth form of *Pinus radiata* seedlings. *Forest Sci.* 23, 64-68.

Williams, R.F. (1948). The effects of phosphorus supply on the rates of intake of phosphorus and nitrogen and upon certain aspects of phosphorus metabolism in gramineous plants. *Aust. J. Sci. Res., B, Biol. Sci.* 1, 333-361.

Wilson, B.C. and Campbell, R.K. (1972). Seedbed density influences height, diameter, and dry weight of 3-0 Douglas fir. *Tree Planters' Notes* 23(2), 1-4.

Zavitkovski, J. and Stevens, R.D. (1972). Primary productivity of red alder ecosystems. *Ecology* 53, 235-242.

Zelawski, W., Kucharska, J. and Lotocki, A. (1969). Productivity of photosynthesis in Scots pine (*Pinus sylvestris* L.) seedlings grown under various soil moisture conditions. *Acta Soc. Bot. Pol.* 38, 143-155.

Zimmer, W.J. and Grose, R.J. (1958). Root systems and root/shoot ratios of seedlings of some Victorian eucalypts. *Aust. Forestry* 22, 13-18.

DISCUSSION

LEYTON - How many of your examples of root:shoot ratios were obtained indoors and how many under outdoor conditions? Also, has your equation taken into account presence versus absence of mycorrhizas, since infection by these can lead to a substantial reduction in root:shoot ratio because improved uptake of phosphorus and water means that the plant can survive with a smaller root system?

LEDIG - In all my own experiments the seedlings had mycorrhizas.

CANNELL - It is difficult to achieve absence of mycorrhizas even in pot-grown plants, and all field plants would have had mycorrhizas.

OLDEMAN - *Hevea* shows rhythmic growth in the upper parts while underground growth is continuous. I suggest a model relating photosynthesis and cambial activity which gives a more complete picture than the model you presented.

LOOMIS - Thornley's model shows a balance depending on a variable resistance, which is difficult to think about. Brouwer's model shows that under conditions of water stress shoots cannot grow but roots can, whereas under carbohydrate stress shoots can grow but roots cannot.

LEDIG - I am not wedded to Thornley's model. It does break down in certain conditions.

HUXLEY - What about complementary changes in root:shoot ratios in mixtures of crops? Do the ratios for both components become higher, since there is often deeper rooting of both components in mixtures?

LEDIG - No. Root:shoot ratio seems to increase in one component and decrease in the other, but the data are fragmentary.

KIRA - There are some dangers in the interpretation of some of the data you have presented. First, it is dangerous to base generalizations on work with young seedlings, since over a period of 20 to 50 years the root:shoot ratio decreases. Second, density of stand is important as, for example, dry matter partition to reproductive organs greatly decreases under overcrowded conditions. Isolated plants should therefore not be compared with plants in dense stands. Third, it is dangerous to depend too heavily on allometric relationships, since even when there is no flowering the log-log linear relationship is not always maintained over long periods of time.

LEDIG - There are many problems with the allometric constant, but it does hold for long periods of time. For example, for 15 years in peach and 55 years in Scots pine. However, you are right that the root:shoot ratio seems to decrease in older trees, although this may be due to our inability to reach the entire root system in older trees.

LOOMIS - Kira raises an important point, in that functions must be balanced (mass of roots · water uptake must equal mass of leaves · water loss) and we should consider the activity of the balance, that is not root mass but root surface, water uptake, and so on.

The ordinary allometric equation deals with the change in the ratio between two different dimensions of an organism with time. However, the changes caused by such growth factors as light, nutrients and water can also be formulated by the same equation. In terms of differential equations, the former is given as

$$\frac{1}{S} \cdot \frac{dS}{dt} \alpha \frac{1}{R} \cdot \frac{dR}{dt}$$

where S and R are shoot and root weight, while the latter is

$$\frac{1}{S} \cdot \frac{\partial S}{\partial f} \alpha \frac{1}{R} \cdot \frac{\partial R}{\partial f}$$

where f is the level of a certain growth factor. The allometry in the latter sense is much more stable and highly useful.

455

PLANT MANAGEMENT IN AGROFORESTRY: MANIPULATION OF TREES, POPULATION DENSITIES AND MIXTURES OF TREES AND HERBACEOUS CROPS

M.G.R. CANNELL
Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian, Scotland.

ABSTRACT. A review is given of some plant management practices that alter dry matter production and distribution, and hence the yield, of trees and herbaceous crops. The topics covered are: (a) the manipulation of individual trees for vegetative and reproductive yield; some principles and methods of tree pruning, and some problems and techniques of fruit tree culture; (b) effects of increasing plant population densities; some general principles involved, and some implications for agroforestry, and (c) the likely effects of manipulating tree/herbaceous crop mixtures; the principles of resource sharing, and some speculations on the management, in agroforestry, of trees grown for different purposes.

INTRODUCTION

This contribution draws together information relevant to tropical agroforestry on some of the ways in which the production and distribution of dry matter in trees and herbaceous crops can be altered by management practices. Practices involving the time of planting and seasonal phenology are described by Huxley (this volume), and the whole subject of soil management (tillage, fertilization, mulching, use of N_2 fixers, etc.) was dealt with at a previous ICRAF meeting (Mongi and Huxley, 1979). Consequently the scope of this contribution will be limited to (a) tree pruning and tree fruit culture, (b) effects of altering the population density (plants per hectare), and (c) the likely effect of growing various types of trees and herbaceous crops together in mixtures. The emphasis is on spatial rather than temporal aspects of plant management.

The objective is to summarize the main principles involved in the different forms of management, and then to consider some of the options relevant to tropical agroforestry. The merits of the different options will be judged, in this paper, by their

effects on yield per plant and per hectare. This is not to say that it will always be possible, or desirable, to maximize yields per hectare. One of the main objectives of agroforestry is to maintain soil fertility, usually with low inputs, and tropical farming systems need to be designed to meet socio-economic needs, to reduce risks of crop failure, to prevent soil degradation, and so on, all of which may limit the ability to maximize yields per hectare. Nevertheless, it is important to know what the options are for increasing yields.

This paper is divided into three sections. The first deals with the management of individual plants, and concerns exclusively the management of trees for leaves, wood, fruits and nuts. The trees in agroforestry systems are almost bound to demand, or benefit from, individual management, because of their persistence, size and dominance, because they may become too large or unfruitful if unpruned, and because various products may be harvested from them over many years. The second section deals with relevant aspects of the effects of plant population density on crop performance and should be read in conjunction with the second paper (Cannell, this volume) on the responses of different types of tree and herbaceous crops to density stress in monocultures. For many crops this is the best information available on their responses to density stress and so it has to form part of the foundation for speculation on the likely responses of different crops to resource deprivation in the various mixtures contemplated in agroforestry. Also, there may often be some practical and yield advantages in growing particular crops as monocultures, in 'zones', or groves, as part of agroforestry farming systems. The third section considers the principles of manipulating crop plants in mixtures, and presents some speculations on how trees and herbaceous crops may be grown together in different arrangements to influence the yield per unit area of fuel, fodder and food.

MANIPULATING INDIVIDUAL TREES

Horticultural herbaceous vegetable and flower crops can, in some cases, be profitably manipulated as individuals; for example, tomatoes, cucurbits and chrysanthemums. Experiments have shown also that defoliation, shoot thinning and tipping of cotton, cowpeas and cassava, can divert assimilates to the yield portion (as occurs in tomatoes and cucurbits), but for most field crops the increased yield is small per unit of labour (e.g. Ezedinma, 1973). Trees on the other hand, often need to be managed individually. The principles and practices involved obviously depend on whether the product is a vegetative part (wood, leaves, resin etc.) or a reproductive part (fruits, nuts, etc.).

Vegetative yield

Pruning of any sort can alter (a) tree shape, (b) total dry matter production per tree and (c) dry matter distribution within the tree, all according to a general set of principles which need to be understood before judging the outcome and merits of different pruning practices.

Principles regarding tree shape (Fig. 1a). Many woody perennials

can be trained and pruned to a variety of shapes and sizes quite unlike those they assume in nature. The author's experience with temperate-zone broadleaved trees, fruit trees, and crops such as tea and coffee, would suggest that the morphological responses of many angiospermous trees conform to a general set of principles. However, these principles will need to be tested on any new species used in agroforestry, with due regard to each species' 'architectural model' as defined by Hallé *et al.* (1978).

(i) Pruning stimulates the outgrowth of dormant buds that are often present at old nodes over the whole shoot system.
(ii) Distal buds, near the cut ends, are stimulated to grow more than basal buds ('acrotony') and more shoots grow than would normally do so (sometimes producing more fruiting points).
(iii) The length to which the new shoots grow depends on their position: pruning near ground level produces longer shoots than pruning higher up ('topophysis', Molisch, 1916; demonstrated on apple, Maggs, 1964; *Eucalyptus*, Maggs and Alexander, 1967; explained by Mullins and Rogers, 1971 and Wareing, 1977). Notching the bark on old woody stems stimulates bud outgrowth in the same way as pruning.
(iv) In a sense, pruning reverses tree ageing: the new shoots are 'vigorous', less periodic in growth, have fewer short shoots and greater apical dominance, all possibly resulting from increased supplies of root cytokinins and nutrients per shoot (e.g. peach, Chalmers and Van den Ende, 1975).
(v) There is a tendency for new shoots, derived from resting buds, to grow orthotropically, that is vertically, where branches in that position would normally grow plagiotropically. This is not the case, however, on a few species, such as coffee, where the buds on branches are irreversibly plagiotropic ('propriété fixée', Champagnat, 1954), and cuttings rooted from such branches produce horizontally spreading trees.
(vi) The highest upwardly directed orthotropic shoots attain dominance, especially in nutrient deficient conditions (Wareing, 1968), and left alone these shoots will reconstitute the tree in its juvenile form ('réitération, Hallé *et al.*, 1978).
(vii) Bending shoots horizontally checks their elongation and stimulates buds to grow on their upper sides, especially those buds at the highest point on the arched shoots nearest the root systems ('gravimorphism', Wareing and Nasr, 1961; 'epitrophy', Hallé *et al.* 1978).

Principles regarding dry matter production (Fig. 1b). Pruning usually decreases total dry matter production per tree because leaves are removed, and root pruning has the same effect because new foliage development is checked. However, the decrease in productivity may be less than expected because there can be an increase in net photosynthesis by the remaining leaves, possibly owing to increased sink/source ratios, and because the leaves become better illuminated and receive a greater share of root-originated metabolites (e.g. *Betula*, Sweet, 1966; *Liriodendron*, Madgwick, 1975). Indeed, if only old, shaded foliage is pruned, there may be no decrease in dry matter production at all: basal branch pruning in closed forest stands has little effect on

volume increment (Zavitkovski *et al.*, 1974), 75 per cent of the leaves of young *Populus* can be removed in early summer without any effect on height growth (Bassman and Myers, 1979) and tea yields can actually be promoted by removing the older leaves (Magambo, pers. comm.). Thus, whenever foliage is to be removed from trees for fodder or mulch, there is an advantage in removing only old shoots, especially from closed stands.

Principles regarding dry matter distribution (Fig. 1c). There are three relevant points that should be made with regard to the effect of pruning practices on dry matter distribution within trees.

First, the proportion of dry matter devoted to bole wood as opposed to leafy shoots depends on the size of the bole cambial sink relative to other sinks. If the trees are kept small, and branching is encouraged, a relatively small proportion of the total dry matter increment will be used to produce bole wood, whereas if the trees are allowed to grow tall, and branching is discouraged (by pruning or competition) a larger proportion of the total dry matter increment will be used to produce bole wood. Accordingly, the proportion of current dry matter increment going to stems in forest trees increases during stand closure (see below); the proportion of dry matter going to thick woody stems is decreased in tea by pruning and plucking (Magambo and Cannell, 1981), and *Prosopis cineraria* (syn. *spicigera*) yields more fodder and less wood when completely lopped than when only partly lopped (Tejwani, 1979). Thus, by manipulating the height and branchiness of trees, one can alter the proportion of dry matter devoted to leafy shoots as opposed to large diametered fuelwood or timber.

Second, it should be realized that the relative growth rates of the stems of trees are proportional to the relative growth rates of both the roots and crowns; that is, there are strong stem - leaf and stem - root allometric relationships, just as there are strong shoot - root allometric relationships. The cambium is an integral part of the total vegetative structure. This fact has been discovered and rediscovered many times: Maggs (1962) suggested that radial growth was proportional to extension growth in apple; Dawkins (1963) and many others in forestry have related bole diameters to various crown dimensions; trunk sapwood cross-sectional areas are positively related to total leaf areas per tree (e.g. Grier and Wareing, 1974); the summed cross-sectional areas of branches at one level can be linearly related to the leaf area above (distal to) that position (the 'pipe model

Fig. 1 (*Opposite*) Diagrammatic representation of some responses of trees to pruning.

(*a*) 1 and 2 illustrate topophysis and acrotony; 3 réitération; 4 dominance and the effect of notching; 5 epitrophy and gravimorphism.

(*b*) This illustrates the partial recovery of open-grown trees from pruning (see text).

(*c*) (i), (ii), and (iii) illustrate relationships between crown size and stem diameter; (iv) allometric relationships with diameter (D) and height (H); (v) effects of root and shoot pruning, and (vi) effects of lopping on height - diameter relationships.

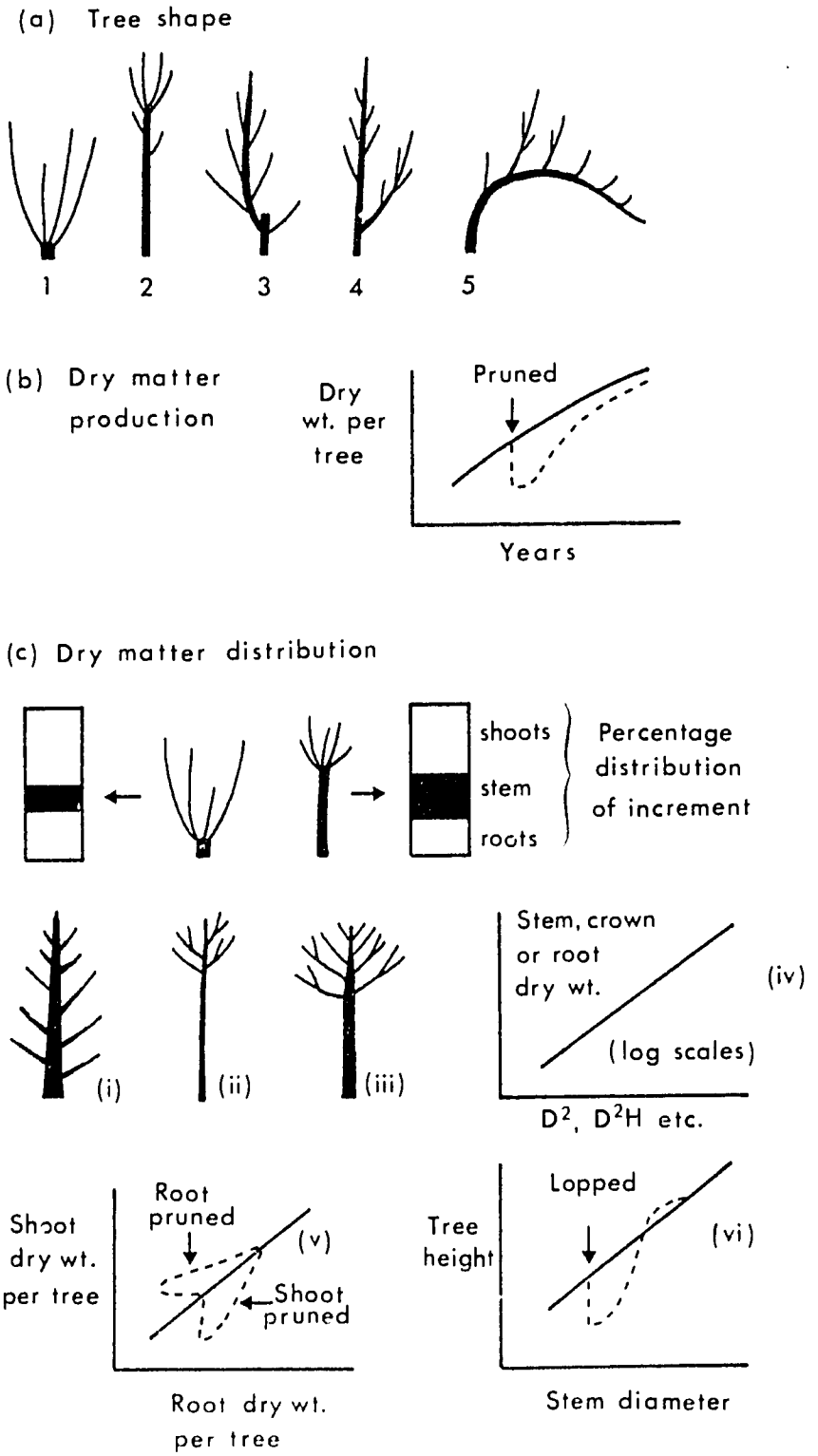

(a) Tree shape
1
2
3
4
5
(b) Dry matter production
Dry wt. per tree
Pruned
Years
(c) Dry matter distribution
shoots
stem
roots
Percentage distribution of increment
(i)
(ii)
(iii)
Stem, crown or root dry wt.
(log scales)
(iv)
D², D²H etc.
Shoot dry wt. per tree
Root pruned
(v)
Shoot pruned
Root dry wt. per tree
Tree height
Lopped
(vi)
Stem diameter

Figure 1.

theory' of Shinozaki *et al.*, 1964); and many workers have related root, crown or total tree biomass to some function of stem diameter (notably diameter squared times height, Ogawa and Kira, 1977). In short, this means that (a) it is not possible to permanently change the growth rate of one part of the vegetative structure without simultaneously changing the growth rates of all other vegetative parts, and (b) the diameter increment and taper of the stems will depend on the size and disposition of the crowns (Figure 2c).

Third, and following from the above, neither shoot nor root pruning can permanently alter shoot - cambial - root *allometric* relationships. Shoot pruning temporarily checks root growth, and root pruning temporarily checks shoot growth, in both cases in proportion to the amount of shoot or root removed and for as long as it takes the original shoot - root allometry to be restored (apple, Maggs, 1965; orange, Alexander and Maggs, 1971; peach, Richards and Rowe, 1977). Root pruning never diverts assimilates to the shoots, it diverts them to the roots. Severe lopping increases the *proportion* of dry matter taken by new leafy shoots (Maggs, 1960), it does not alter the allometric relationships between roots, cambium and leaves.

Pruning practices. For convenience, pruning practices can be divided into four types, three of which are illustrated in Figure 2: (a) operations which spread the trees laterally, namely, bending and coppicing, or multiple-heading, (b) operations which lop off the main stem and encourage branching, (c) operations which limit branching but leave the main stem intact, and (d) root pruning. Of course, there can be many combinations of these four operations.

Two *tree spreading operations* are shown in Figure 2a. Both bending and coppicing increase the ground cover per tree so that fewer need to be planted, or greater use can be made of those already growing - an advantage if planting stock is in short supply. Also, the vertical shoots can be repeatedly harvested, they are rapidly replaced by new shoots, there is less need to weed than when replanting, and one has all the other advantages of ratoon cropping (Plucknett *et al.*, 1970). Regular coppicing will also keep the leafy shoots accessible for harvesting or browsing, and by restricting the development of the boles and woody frames, coppicing will increase the proportion of dry matter going to new leafy shoots.

However, there is often some difficulty with coppicing systems in promoting the growth of new orthotropic shoots or suckers, because the existing shoots shade the suckers and exercise apical dominance over them. One solution can be to bend the existing shoots horizontally, or to notch them, but if this does not work they will need to be cut off altogether. This means that new growth has to rely entirely on root reserves, which is successful only when the individual stumps and root systems are large, implying a minimum tree size and spacing, combined with timely coppicing and a minimum coppice cycle. There are no rules about this: many willows in Europe can be coppiced annually at very close spacings; tea in the tropics can be coppiced every 4 to 6 years, while sweet chestnut and aspen in temperate regions yield most on coppice rotations of 10 to 25 years (e.g. Berry and

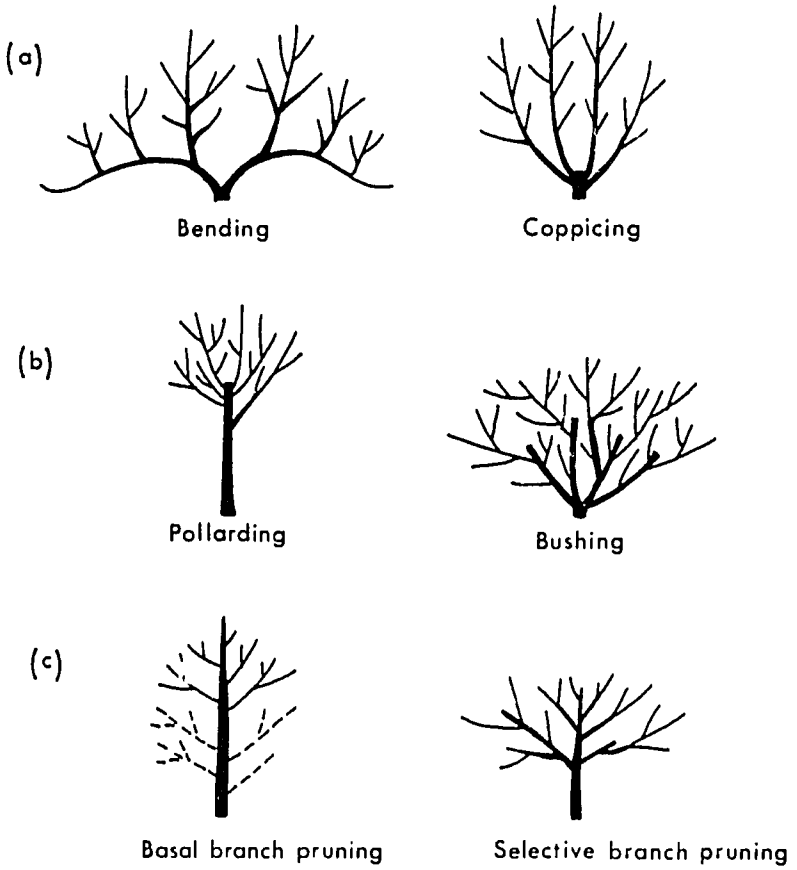


Fig. 2. Diagrammatic representation of trees, illustrating the effects of (*a*) pruning operations which spread the tree canopies, (*b*) lopping, and (*d*) selective pruning of branches.

Steill, 1978). By analogy with grasslands, the optimum cutting frequency may be shorter with increased mineral nutrition. Each species brought into an agroforestry system for fodder or mulch production will need to be tested.

Two basic *lopping operations* are shown in Figure 2b. Pollarding is no more than elevated coppicing: high pollarding will produce trees with a greater potential for wood production and the development of large individual root systems, while low level pollarding and lopping will produce spreading bushes with a greater potential for fodder production. The regrowth of new shoots will be less vigorous with increased distance from the roots. As with coppicing, the optimum cutting frequency to ensure survival and rapid recovery will depend on the species, environment and amount of foliage left. *Prosopis cineraria* growing in dry areas of India can be killed if lopped for fodder more often than every three years (Bhimaya *et al.*, 1964). Bearing in mind that pollarded trees have more reserve capacity left after cutting than coppiced ones, trees which recover poorly after coppicing may recover better after pollarding. However, pollarding itself may be preferred, for instance, to keep the new

foliage out of the reach of animals, and to allow some timber and thick fuelwood production.

Branch pruning (Figure 2c) may involve simply the removal of lower branches, as in intensive forestry (for example, poplars for matchwood or *Pinus radiata* for high quality sawlogs in New Zealand), thereby lessening stem taper and decreasing the number of knots in the bolewood without greatly decreasing bole volume increment. This is a highly desirable operation in forests grown for high-value timber, and yields some small diameter brash and firewood. Alternatively, branch pruning may be highly selective, as in tree fruit culture, restricting height growth, encouraging the development of spreading, shallow, well-illuminated canopies, enhancing fruit bud production (see below) and allowing some light to reach herbaceous crops beneath.

Although *root pruning* checks shoot growth, apparently in direct proportion to the amount of roots removed (Richards and Rowe, 1977), it can have two beneficial effects: (a) enhanced flower bud production, apparently as a direct result of checked shoot growth, and (b) the regrowth of a more fibrous root system, with greater access to immobile soil nutrients, and occasionally, in P deficient soils, temporarily enhanced tree growth. In the case of nursery seedlings, the more fibrous root system produced by undercutting or wrenching helps them to survive after transplanting.

Fruit and nut yield

In general, woody perennials present many more problems than herbaceous crops when grown for fruits or seeds, rather than for some vegetative product; a feature related to their life strategy and evolutionary history. On the one hand woody perennials may need to be intensively managed to encourage them to bear fruits. For example, it may be necessary to overcome prolonged vegetative juvenile periods, poor floral initiation, poor pollination, poor fruit set and fruit shedding. These are all mechanisms evolved to ensure that the potentially very powerful reproductive sinks do not usurp all assimilates and threaten the survival of the perennial vegetative structure. On the other hand, management is needed to limit the fruit load so as to maintain a satisfactory balance between fruit and vegetative growth, and to safeguard future yield.

Consequently wherever trees are grown specifically for fruits or nuts they will generally benefit from intensive care. An enormous amount has been learned about fruit tree culture which could be applied to fruit trees in tropical agroforestry. All that can be attempted here is a summary of the main problems, their causes and possible cures, all of which are elaborated in the following volumes: Ferwerda and Wit, 1969; Williams, 1975; Alvim and Kozlowski, 1977; Tomlinson and Zimmermann, 1978; Brooks *et al.*, 1965; Luckwill and Cutting, 1970; Pereira, 1975; Landsberg and Cutting, 1977.

Juvenile vegetative period. Small, juvenile trees do not flower. For instance, few flowers are produced for 1 to 2 years in open-grown coffee, 5 to 8 years in citrus, and 30 to 40 years in many forest conifers, depending on the cultivar. Recommendations to shorten the juvenile period may include any combination of the

following three general management techniques: (i) to promote early growth by growing the trees on the most fertile patch of soil, applying fertilizers, mulch and irrigation, and removing competition; (ii) to graft on to flower-promoting rootstocks, as done routinely in apple, mango, orange, walnut and many other fruit trees; and (iii) if all else fails, or the trees have been neglected, to partially girdle, root prune, or bend the stems horizontally; all measures that could be used on old trees before they are destroyed for fuel.

Floral initiation. This is inhibited as much by shading in trees as it is in cereals and legumes (Jackson and Palmer, 1977). But, whereas herbaceous crops need to be well illuminated at critical stages of development, many tropical perennials need to be well illuminated all the time, because they initiate flowers over most of the year. The numbers of floral initials produced within the canopies of apple, citrus, cashew, grape vine, oil palm and coconut have all been related to some measure of solar radiation receipt and, in oil palm, shading reduces the proportion of female to male flowers. High insolation must occur during the periods of potential floral initiation and at the points in the trees where the initials form. Some species and cultivars are more light-demanding than others: coconut is particularly shade intolerant, whereas coffee, naturally an understorey shrub, produces some flower buds in deep shade. In fact, for fruit trees like coffe, some shade may be desirable on infertile sites, in order to keep the fruiting load in balance with limited nutrient supplies (Willey, 1975). Also, trees which fruit on young shoots, that is, on the outside of the canopy, like mango, may need less intensive pruning than trees which fruit on old wood. However, for most fruit trees overstorey or mutual shading depresses yield.

Consequently trees grown for fruits or seeds are traditionally grown in the open, widely and preferably evenly spaced, often trained when young to produce a well-distributed 'scaffold' and regularly pruned and 'handled' to maintain low, accessible, shallow canopies with limited within-tree mutual shading. However, precocious fruiting species can also be tried in closely spaced, short-duration systems which are renewed either by cutting down or replanting before the canopy becomes too dense.

The details of pruning for maximum fruit bud production (and adequate fruit size and ripening) differ for different species, but my impression is that many trees used in agroforestry naturally grow either too tall, too upright (with vigorous vegetative orthotropic shoots), or too densely branched, for efficient fruit production. The contrast between an unmanaged and a managed cherry tree is illustrated in Figure 3.

Pollination. With exceptions such as clove and coffee, most tropical fruit trees are at least partially self-incompatible or self-unfruitful. Poor cross-pollination can be a major cause of poor fruit set, for three reasons: (i) the flowers may be poorly developed or 'effectively' receptive for only a very short period (the 'effective pollination period', Williams, 1970), for instance 3 to 4 days in oil palm and mango, 2 days in cashew, 1 day in avocado; (ii) there may be insufficient pollen,

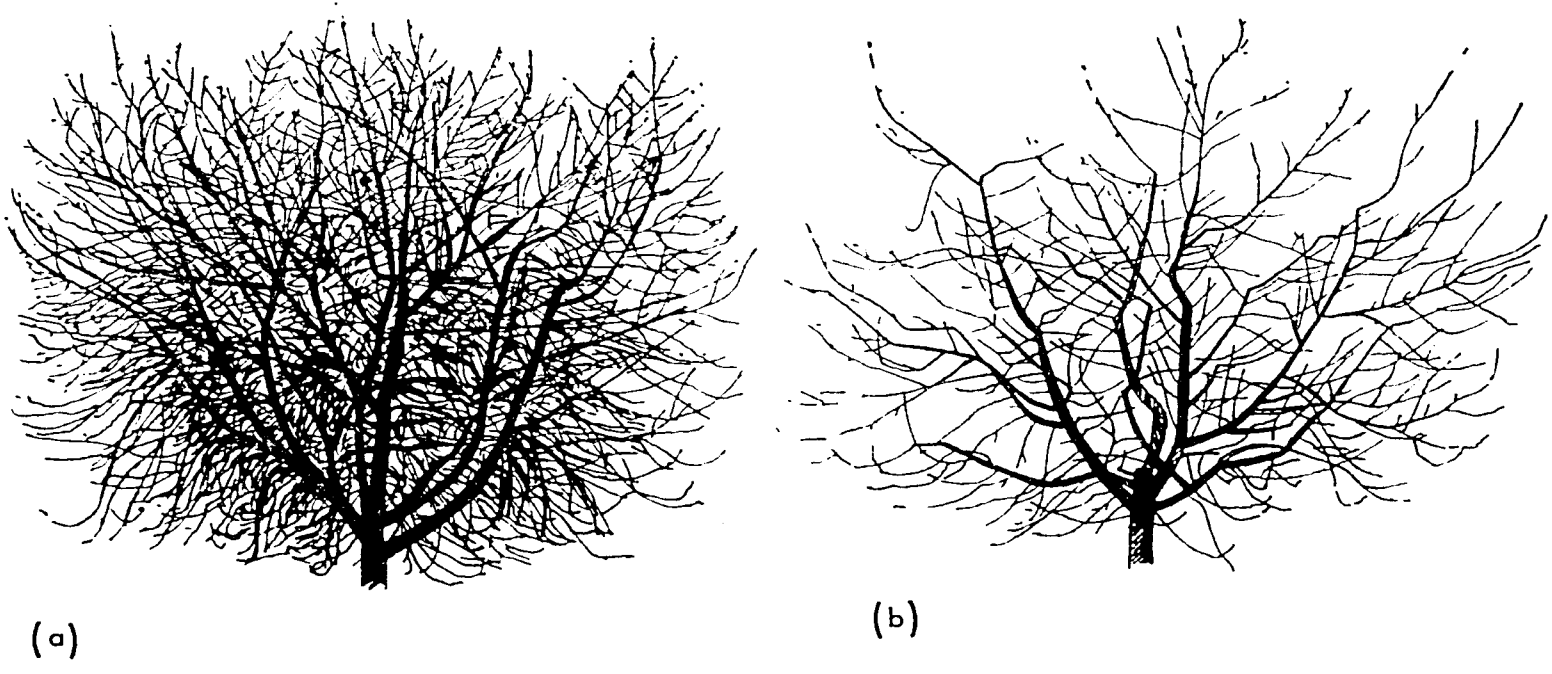


Fig. 5. Ten-year-old cultivated European cherry trees (cv. Morello) (*a*) completely unpruned, and (*b*) pruned to develop a spreading, open crown favouring fruit production. Taken from Hilkenbäumer (1976)

sometimes due to an imbalance between male and female flowers; or (iii) there may be too few general or specific pollen vectors (e.g. midges for cocoa) or hostile weather conditions for pollen transfer, especially heavy rainfall. The obvious answer to these problems is to select self-fertile or parthenocarpic cultivars, but even these may benefit from measures which enhance cross-pollination. These measures include: growing the trees reasonably close together, interspersing with pollinator trees, withholding insecticides, keeping bees, timely and selective pruning to phase flowering with favourable weather conditions and, in the last resort, supplementary hand pollination.

Fruit shedding. Having obtained a good fruit set, a large percentage (up to 80 per cent, or more) of the fruits can be shed before they mature. June drop of apples in Europe has counterparts in cherelle wilt of cacao, abortion of button coconuts, citrus and coffee fruit drop 2 to 4 months after anthesis, grape drop 2 to 3 weeks after anthesis and mango drop throughout the period of fruit development. At one stage or more, young tree-fruits seem to be weak sinks for nutrients and carbohydrates compared with the shoot tips, especially when there are synchronous leaf flushes or environmental stresses, especially droughts. The preventative measures are to alleviate water stress and/or internal competition for nutrients and carbohydrates by irrigating, applying fertilizers, removing shade, synchronizing the sensitive stages of fruit growth with favourable climatic conditions, usually by selective pruning, and by removing shoot tips at critical stages when fruit shedding is anticipated (for example, grape, citrus, apple, Coombe, 1962; Quinlan and Preston, 1971).

Irregular bearing. Biennial or irregular bearing is a feature of many woody perennial plants, especially as they get older. It is a serious problem in some cultivars of apple, citrus and mango and is a characteristic of nut tree crops such as pecan, hazelnut, walnut and almond. It is especially common in trees with prolonged periods of fruit development, where fruiting overlaps with both vegetative growth and floral initiation for the next season's crop. Cashews, with only a three-month period of nut and receptacle development, usually bear regularly. In nature, irregular bearing may have subtle adaptive advantages, for instance in combating seed predators, and so it should not be regarded as simply a mechanism to balance fruit and vegetative growth. And in seeking explanations for irregular bearing we have to look further than the well-established fact that the fruits utilize reserves and divert assimilates from vegetative parts, particularly the roots (Maggs, 1963; Rogers and Booth, 1964; Cannell, 1971; Chalmers and Van den Ende, 1975; Heim *et al.*, 1979). In many instances it seems that the fruits directly inhibit floral initiation, perhaps by producing growth regulators (apple, Luckwill, 1970; orange, Moss, 1971). One obvious preventative measure is to partially deblossom or thin the fruitlets, but this assumes that one knows how many fruits will be shed, anyway, or lost to pests and pathogens. The best solution is to select regularly bearing cultivars. If that is not possible, selective pruning can be done to obtain a balance of 'on' and

'off' trees, or a balance of 'on' and 'off' branches, for instance on mango (Scarrone, 1969). Heavily bearing 'on' trees may, in fact, use environmental resources efficiently: net photosynthetic rates, and possibly root activity, will be enhanced by the large sink capacities (see Avery, 1975; Richards *et al.*, 1979), the fruits will meet some of their own assimilate demands, and some assimilates will be off-loaded into seeds, which have lower maintenance respiratory rates than new shoots and roots. The ideal may, in fact, be a half 'on' tree, half 'off' tree system, where fruits are able to draw assimilates from leaves on the other side of the tree (at least one metre away in apple, Hansen, 1977) but are too far away to inhibit floral initiation - a technique developed on some cultivars of apple (Parry, 1974)

Other problems. To complete this list, mention should be made of (i) replant problems possessed, for instance, by peach and citrus, (ii) the need to produce virus-free stock, (iii) the problems of fruit ripening and storage, as well as (iv) nutritional, pest and disease problems.

Concluding remarks. Many of the management techniques developed for fruit trees and palms for plantation culture could be transferred directly and *immediately* to fruit trees growing on tropical smallholdings, with no need for further research. This is important because the fruit trees often occupy the best land; also if there were sufficient improvements in yield and quality, many fruits could become cash rather than subsistence crops, given adequate marketing and processing facilities. Some of the 1000 or more 'new', potential agroforestry fruit and nut trees (Weaver, 1980) may have immediate appeal but there is need for caution: fruit trees are expensive to grow, tend to be labour-intensive, and are clearly problem-prone. A lot needs to be learned about each species before it can be introduced to greatest effect with minimum risk of failure.

MANIPULATING SOLE CROP POPULATIONS

So far we have considered the management of trees as individuals, essentially by altering the relationships between assimilate sinks within the plant. Another way to alter the shape and yield of crop plants is to alter the plant population, by altering the degree of density stress (or environment resource deprivation) experienced by each individual. Again, there is a vast literature on this subject, and my aim is to select only those concepts and examples that are relevant to tropical agroforestry. The accompanying paper (Cannell, this volume) provides a background on the main effects of plant population density on the performance of individuals and communities of different crop types. From that paper, and from the literature on population density effects, I shall, first elaborate some relevant general principles and second, draw some specific implications for agroforestry.

General principles

Asymptotic and parabolic yield-density relationships (Fig. 4a). In general, total dry matter production per hectare, and 'vegetative yield' such as storage roots, wood or leaves, increases with increase in planting density to a plateau, which remains constant regardless of further increase in plant population, barring lodging, disease, drought stress, or in the case of trees, arrested development following severe inter-tree competition early in life (see Cannell, this volume, his Figures 1 and 3). By contrast, 'reproductive yields' such as grains or fruits tend to be greatest at specific plant populations, above which yields decrease and then level off (see Cannell, this volume, his Figures 2 and 4).

Reciprocal yield relationships (Fig. 4b). Once there is inter-plant competition mean individual plant weight decreases (relative to open-grown plants) and becomes inversely related to plant population, often conforming to the reciprocal equation

$$y/\text{wt per plant} = \{a + b\ (\text{plants per hectare})\}$$

where a and b are constants, and y is either 1 for plateau-type relationships and less than 1 for parabolic-type relationships. In both cases y is approximately the slope of a line relating total plant weight to the weight of the yielded part (that is, the allometric relationship, Willey and Heath, 1969; Harper, 1977). This relationship applies to trees as well as herbaceous plants (Cannell, 1980) and, as long as it holds, then the mean weights of individual plants, or vegetative parts such as storage roots and woody stems, can be manipulated simply by changing the plant population, without decreasing total dry matter production per hectare. Also, the relationship between individual plant weight and planting density, and hence between yield per hectare and planting density, can be found using only two or three spacings, with substantial savings in research costs.

Economic optima (Fig. 4c). The most profitable planting density is not necessarily that giving the greatest yield. Indeed it is almost always less than the optimum for yield when either, the planting material is expensive, as with grafted fruit trees, yam setts (as opposed to yam vine cuttings) and pulse seeds (see Cannell, this volume, his Figure 4), or there is a premium on large sized products, such as graded potatoes, pineapples for canning, and timber for sawlogs (see Cannell, this volume, his Figure 1).

Size-frequency distributions (Fig. 4d). The weights of individual plants within populations are not uniform: plant weight-frequency distributions become positively skewed with increase in density stress, giving a preponderance of small individuals. Tree diameter-frequency distributions are less skewed and can become bimodal when two-tiered canopies develop (Ford, 1975), while height-frequency distributions often remain or become normal in both tree and herbaceous crop stands (Harper, 1977; Mohler *et al.*, 1978).

Self thinning (Fig. 4e). When competition becomes intense, the

smallest individuals or ramets die, often following the relationship between mean individual plant weight and plant population shown in Figure 4e. Although this so-called -3/2 power law of self-thinning may not hold the value of exactly -3/2 in all environments, for plant parts, or for ramets of clonal perennial herbs (Westoby, 1977; Mohler *et al.*, 1978; Hutchings, 1979) it is of some practical value. It defines the maximum number of plants that can possibly exist of a given mean size, so it can be used as a point of reference to determine the degree of stocking and the stocking density at which plants are likely to die because of competitive stress rather than other causes (Drew and Flewelling, 1977; the concepts of limiting tree basal area, Dawkins, 1959; and stand density index, Reineke, 1933).

Rectangularity (Fig. 4f). Per hectare yields can be substantially greater, and occur at higher plant populations, with uniform square or hexagonal planting rather than with rectangular, row or 'hill' planting (Berry, 1967; Willey and Heath, 1969) (see Figure 4f). Competition is a spatial process and will of itself tend to give rise to an even dispersion of large and small plants (Ford, 1975). However, the depressive effect of spatially uneven planting may be small in crops which can spread by profuse tillering or branching, especially in wet, fertile conditions (for example, potatoes and vining legumes). And in many crops, like potatoes, groundnuts and cereals, row planting offers considerable advantages for ease of planting, fertilizer placement, weeding and harvesting, although these advantages will be less with hand cultivation on tropical smallholdings. Finally, where rows are used there can be a benefit in north-south orientation, even in the tropics (Donald, 1963).

Plant environment and habit (Fig. 4g). The optimum plant population is often lower in conditions of nutrient or water shortage than in wet, fertile conditions, and the optimum is lower and less critical for spreading and profusely tillering genotypes as opposed to single stem, determinate or erect genotypes. There can, for instance, be 100-fold differences in the optimum densities for different legume cultivars (for example, cowpea, Erskine and Khan, 1976), and marked genotype-environment interactions, which call for large numbers of local spacing trials.

Plasticity of plant characters (Fig. 4h). Not all plant characters are affected equally by competitive stress, and some effects tend to be species and environment specific. However, some general points can be made, illustrated by Cannell (this volume) as effects on yield components.

Fig. 4 (*Opposite*) Some principles regarding the effects of planting density on the growth and yields of crop plants. (*a*) to (*e*) 0, a, b and c are constants; ρ is population density in numbers of plants per hectare; (*f*) apple data are for years 5 to 8 after planting in western Australia, from Cripps *et al.* (1975), where 1 = square planting; 2 = spaced x by 2x; and 3 = x by 3x. Pea data are for dried peas in England, from Willey and Heath (1969) where 8, 16, and 24 refer to row widths in inches.

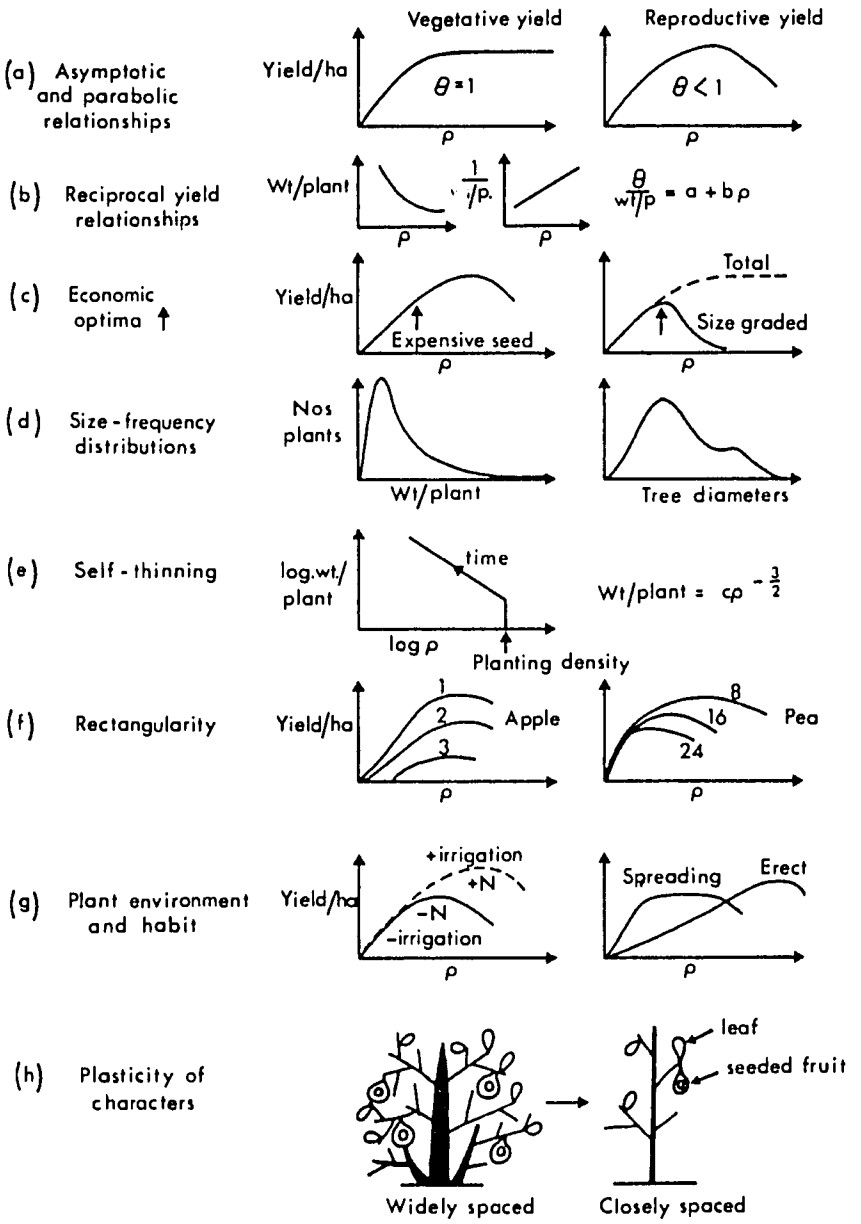

(a) Asymptotic and parabolic relationships
Vegetative yield
Reproductive yield
Yield/ha
θ=1
θ<1
ρ
(b) Reciprocal yield relationships
Wt/plant
1/ρ
θ/wt/ρ = a + bρ
(c) Economic optima
Yield/ha
Expensive seed
Total
Size graded
(d) Size-frequency distributions
Nos plants
Wt/plant
Tree diameters
(e) Self-thinning
log.wt/plant
time
log ρ
Wt/plant = cρ^-3/2
Planting density
(f) Rectangularity
Yield/ha
1
2
3
Apple
8
16
24
Pea
(g) Plant environment and habit
Yield/ha
+irrigation
+N
-N
-irrigation
Spreading
Erect
(h) Plasticity of characters
leaf
seeded fruit
Widely spaced
Closely spaced

Figure 4.

(i) Lateral spread by branching and/or tillering (suckering, sprouting, etc.) is always suppressed by density stress, be it in cereals, potatoes, legumes, bananas or trees. Consequently, all the components of yield associated with lateral spread such as numbers of branch nodes per plant, ears per plant and branch-borne fruits or pods per plant, are all decreased (see Cannell, this volume). But conversely, a greater proportion of the total dry matter is devoted to stalks and stems, and as discussed above, in trees there is an increase in the proportion of the total increment devoted to bolewood.

(ii) Mutual shading further decreases the number of fruits which form on the stems and branches which do develop. The degree to which fruiting points are shaded depends on where the fruits are borne: it is obviously less on wheat than on maize, and less on palms than citrus. Also, the fruiting points most likely to be shaded are those which develop in the axils of old nodes during the later stages of plant development, for instance on indeterminate legumes, or trees which fruit only on 'old' wood.

(iii) Density stress has relatively little effect on the heights of trees and herbaceous crops - they may increase or decrease - but it always greatly decreases the diameter growth of trees (in accordance with the above-mentioned decrease in branching, crown size and allometric relationships).

(iv) The weights of individual fruits, fleshy roots or tubers are decreased by density stress (Cannell, this volume, his Figures 2 and 3) but individual seed weights (for example, nuts, grains and pulses) are characteristically relatively little affected (Cannell, this volume his Figures 2, 3 and 4; Salisbury, 1942; Harper *et al.*, 1970), although exceptions can be found, notably sunflower (Clements *et al.*, 1929).

(v) There is some evidence that the root systems of closely-planted forest and fruit trees tend to be denser per unit volume of soil and grow deeper than those of widely-planted trees (Adams, 1928; Atkinson, 1973). However, shoot/root biomass ratios may change relatively little (Rennie, 1974).

Implications for agroforestry

Sole or mixed cropping? It should be stated explicitly that, for most crops, the greatest yield per hectare is obtained when each individual is under some critical level of 'density stress', that is, deprived of some light, water or nutrients by its neighbours. In agroforestry, where crops will be planted at different times in complex mixtures, it will be almost impossible to ensure that each individual of each crop species experiences its optimum level of density stress throughout its development. For some crops the sacrifice in yield may be small, or may be compensated by other considerations, such as soil protection and weed control, but for other crops this may not be the case, and these crops might be better grown as sole crops at their optimum densities. I would speculate that this could be so for (*a*) trees grown for wood and (*b*) some herbaceous crops grown for reproductive yield.

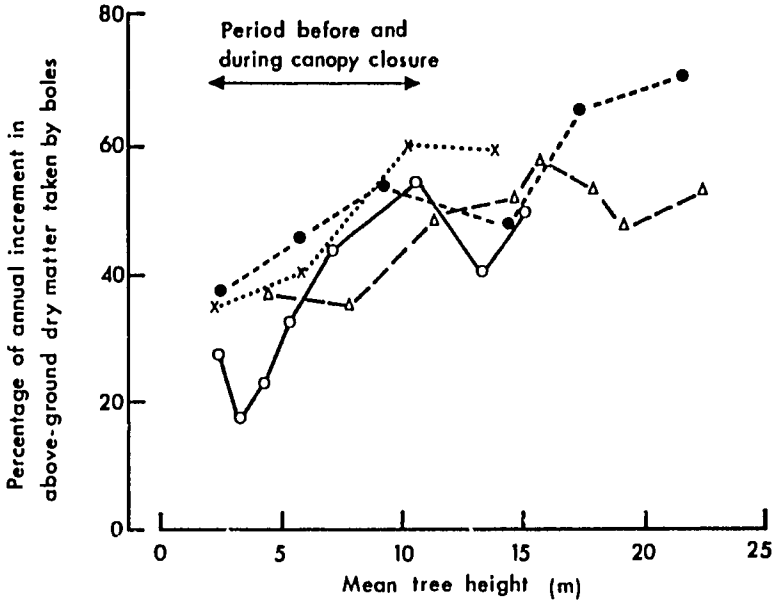


Fig. 5. Increase in the proportion of the annual dry matter increment taken by the stems in temperate forest plantations during canopy closure.
O - *Pinus sylvestris* in England (from Ovington, 1957);
Δ - *Cryptomeria japonica* in Japan (Ando *et al.*, 1968);
● and X - *Pinus radiata* in New Zealand and Australia (Madgwick *et al.*, 1977; Forrest and Ovington, 1970, respectively).

(*a*) Most trees produce more stemwood, and possibly more total wood (stems plus branches; Adams, 1928) per unit leaf area, and per unit of intercepted light, when 'density stressed', that is in forests or groves, rather than when grown as widely-spaced individuals. The proportion of the total annual dry matter increment per hectare taken by the main stems of trees increases from about 30 per cent to 60 per cent during the periods of stand closure (Fig. 5). This is partly because the trees get taller, partly because branching is suppressed, and in some instances because mutual shading suppresses fruiting: as a result the size of the stem cambial sinks is increased relative to the size of the other sinks (shoot apices, fruits and roots). Consequently, if the objective is to produce wood, especially large-diametered wood for slow burning (because the ignition time of wood varies inversely with its surface-to-volume ratio), or for building materials, stakes, tools, etc., then the most efficient way to produce it is to plant the trees in groves or plantations.

It should be added that where the objective is to produce large-diametered sawlogs, the trees need to be widely spaced and regularly thinned, thereby losing some of the benefits of density stress (increased stemwood production per unit leaf area, branch suppression, weed suppression and reduced knot size). 'Taungya' systems of agroforestry offer some obvious advantages here, because many of the above benefits can be provided by the farmer if he cultivates the land between the trees and prunes the lower

branches for fuel and improved light penetration. Obviously these systems have thrived because both the forester and farmer have benefitted.

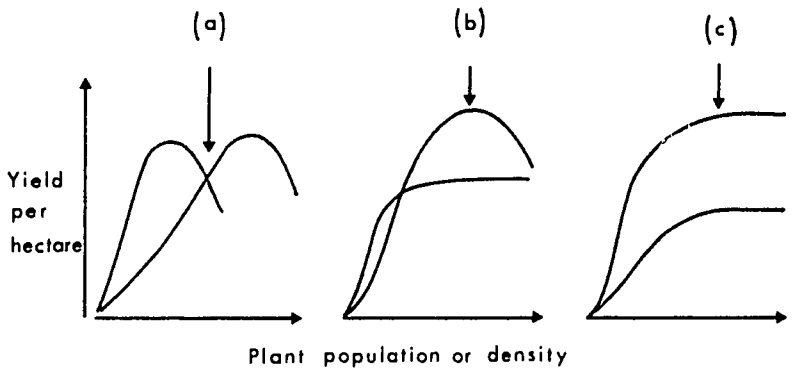


Fig. 6. The optimum plant population (or degree of density stress) for mixtures of (*a*) two crops with reproductive yield having parabolic yield - density relationships; (*c*) two crops with vegetative yield having asymptotic yield - density relationships and (*b*) a mixture of the two. The downward pointing arrows mark the optimum population for each mixture.

(*b*) The problem of obtaining the critical level of density stress needed for maximum yield efficiency is likely to be greatest when growing two or more crops together, each of which has a very different specific optimum population density as a sole crop. This is most likely to occur (i) when growing mixtures of herbaceous crops with reproductive yield, such as grain legumes and maize, (ii) when the crops are planted and harvested at the same time, (iii) when the crops differ in stature and habit, and (iv) when one or more of the crops has a compact habit, and so is unable to spread by tillering or branching, perhaps because it has been selected for high density, sole cropping (for example, some maize and sorghum cultivars). In such cases, it may be impossible to manipulate the total plant population, and the proportions of each crop, so that the overall yield of the mixture on a given land area is as great as the sum of the yields of pure stands of each component, each at its optimum spacing (Fig. 6; Donald 1963; Willey and Osiru, 1972). In such cases it might be better to grow each component crop in monoculture, if yield were the only objective, as was suggested by Huxley and Maingu (1978) for maize and cowpea in Tanzania.

The problems of maximizing yield will be less for mixtures which include crops with vegetative yield, such as storage root crops, and perhaps also for some cultivars of cereals and legumes which can spread by tillering and branching. This is because these crops have less critical optimum population densities. Indeed, as mentioned above, storage root crops will require only some minimal level of density stress for maximum yield per ground area (Fig. 6). Consequently, there may be less yield penalty in growing, for instance, maize and sweet potatoes together rather than maize and grain legumes.

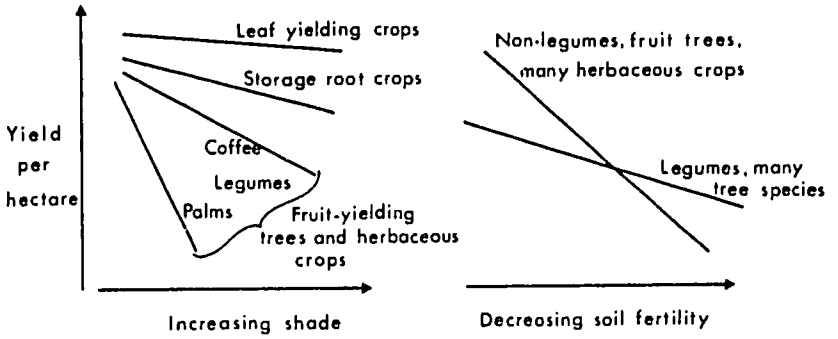


Fig. 7. Diagrammatic representation of general crop differences in response to shading and soil fertility.

Different crop responses to resource deprivation (Fig. 7). The responses of different crop types to density stress give some idea about how they may respond to interference from neighbours in mixtures; although their exact responses will be different, depending on the timing and kind of interference that occurs. For instance, wheat and rice are tolerant of density stress as sole crops, but they are very intolerant of shading during the periods of ear initiation and grain filling. Nevertheless, the following inferences may be drawn from the literature on sole crop population density effects.

First, most fruit-yielding trees and palms are very shade intolerant (for fruit yield). The pruning and management of fruit trees will often be made more complicated by close spacing and, as mentioned above, dense shade will markedly decrease the number of fruits, decrease the size of the fleshy parts, hamper ripening, and probably exacerbate pest and disease problems. Also, anything that hampers individual tree growth will delay the onset of fruiting. This is also the case for bananas under coconuts (Tai, 1977) and density stressed oil palms. Like many plants, oil palms produce fruits only when their vegetative structures have reached a minimum size (Cannell, this volume, his Figure 2), and any form of interference, including pruning, that decreases individual palm growth tends to occur at the expense of fruit production rather than of vegetative growth.

Second, it should be restated that fruit and seed yielding herbaceous crops are also shade intolerant and should, where possible, occupy open spaces, or be able to grow to the top of the canopy in a mixture. Tall or climbing legumes might be better in mixtures than prostrate ones; the ancestors of peas (*Pisum sativum*) were climbers, quite unlike the short statured cultivars selected for monoculture.

Third, the crops that will suffer least from competitive interference, or shading beneath trees, will be those that yield some vegetative parts. The most shade tolerant crops will probably be those yielding leaves, including trees grown for fodder or mulch, and crops like tea, tobacco, forage grasses and legumes. Shading will decrease total dry matter production but this will be partially compensated by an increase in leaf area ratio and shoot - root ratio, ignoring for the moment the soils aspects and other effects of shading (Willey, 1975). Silvo-

pastoral systems are evidently successful in many parts of the world (Tejwani, 1979). It is also worth noting that most trees, especially late successional ones, are very shade tolerant during their juvenile stages and will make efficient use of low intensity radiation (Jarvis *et al.*, 1976) and so will grow satisfactorily beneath tall herbaceous crops such as maize. Coffee seedlings grow better in shade than in full sunlight (Huxley, 1967). Storage root crops are also reasonably tolerant of mutual shading at high population densities and the shading of taller plants. The bulking rates and yields of sweet potatoes, cassava and cocoyams, like those of European potatoes, are regulated principally by the size of the storage sinks, and yields can be unaffected by up to 50 per cent shade in the tropics, provided the conditions during storage root initiation are satisfactory (that is, there are short or cool days, and N fertilizers are withheld; sweet potato, Hahn, 1977; cassava, Wholey and Cock, 1975). Consequently, there may be little yield penalty in growing climbing cocoyams under trees, and sweet potatoes and cassava among fruit or multipurpose trees.

Fourth, crops differ in their responses to poor nutrition, and the harmful effect of competition for light and water may be either diminished or amplified by a shortage of mineral nutrients. As mentioned above, the optimum degree of density stress may be lower under low nutrient conditions. On the other hand, crops which already yield little because of poor mineral nutrition may not suffer much loss in yield as a result of overstorey shade (for example, coffee and cacao, Willey, 1975). And obviously, legumes and other crops that form dinitrogen-fixing symbiotic associations, tend to be more tolerant of N-deficient soils than non-N-fixing crops provided there is adequate P and K, although their capacity to fix nitrogen may be seriously impaired by light deprivation.

MANIPULATING CROP MIXTURES

So far we have considered some of the ways in which trees can be managed as individuals; how different crop types respond to competitive stress; and how competitive stress can be exploited to maximize the yield per unit area of ground. In practice, however, a subsistence farmer may be better able to maximize yields by *avoiding* competitive stress rather than by exploiting it. To do that he needs to alter the relationships between crops in the horizontal, vertical and temporal dimensions so that the different crops share environmental resources of light, water and nutrients (that is, there is annidation, Trenbath, 1976) in a way that minimizes mutual interference and maximizes resource sharing (commensalism, Bunting, 1976). In this section, I shall consider some of the principles governing this form of crop management, that is, the management of crop mixtures, followed by some speculations on ways in which tree crops might be mixed with herbaceous crops to meet some of the objectives of agroforestry.

General principles

De Wit (1960), Donald (1963) and others (see Harper, 1977) developed models to evaluate two-species herbaceous crop mixtures

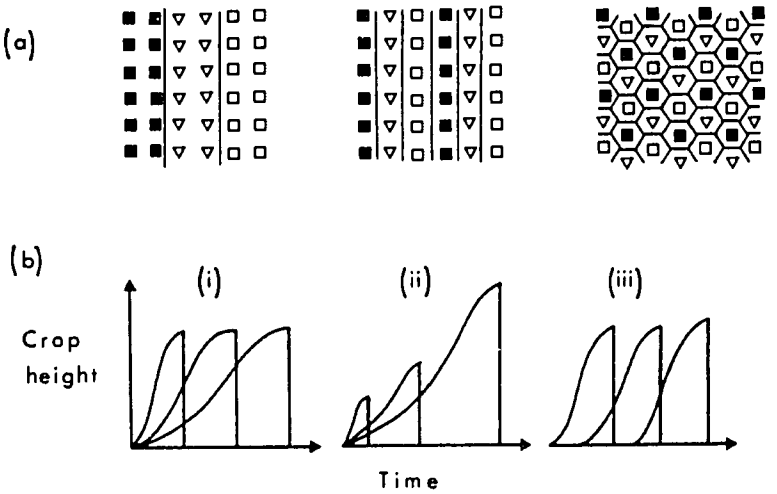


Fig. 8 Differences in spatial and vertical arrangements of three crops. (*a*) Three spatial arrangements with a 5-fold difference in area of interface between different crops (marked with lines). (*b*) Three ways of managing mixtures so that each matures at the top of the canopy (i, ii, and iii as described in the text).

which describe the effects of changing the proportions and populations of the two components. In these models, indices such as 'relative yield totals' or 'land equivalent ratios' that are greater than one indicate that mixtures yield more than their components would as sole crops on the same area of land. These concepts have been helpful in discussions on mixed cropping restricted to two species of herbaceous crops, but only Donald's model copes with the problem of differential optimum populations discussed above (Huxley and Maingu, 1978), and none of the models cope with the complex three-dimensional situation in agroforestry. Consequently, this discussion will be limited to the general concepts and principles of resource sharing in three dimensions, without going into details on inappropriate two-species models.

Resource sharing in the horizontal dimension (Fig. 8a). Environmental resources of light, water and nutrients can be shared in the horizontal dimension by altering the spatial dispersion of different crops in a mixture and by altering the proportions of each crop. Having decided what crops are to be grown in an agroforest, and where they are to be grown (depending on soil fertility, slope, objectives, etc.) one needs to focus on the areas of land occupied by each type of herbaceous crop - tree *boundary* or *interface* and to determine how the yield of each component is altered along each interface (Trenbath, 1976; Huxley, 1981). Appropriate steps could then be taken to maximize the desired yield of the different components by altering their spatial dispersions and proportions as much as possible in such a way as to maximize the area of profitable crop - tree interfaces and minimize the unprofitable ones. Let us consider this further.

The minimum areas of interface between herbaceous and tree

crops will occur when each is grown in monoculture in 'zones' and when fewest different types of crop are grown (Huxley, 1980). The maximum area of interface will occur when there are many crops and each is evenly dispersed in a hexagonal arrangement. Between these two extremes there will be clumped, multiple row, random, single row, rectangular and square planting arrangements giving progressively smaller areas of interface. In this way the area of herbaceous crop - tree interfaces could be changed 3- to 5-fold (Figure 8a; Trenbath, 1976).

The changes in yield of the trees, and of the herbaceous crops growing beneath them, need to be explored, perhaps using the designs suggested by Huxley (1979). Not only will some crops be more shade tolerant than others, but some may benefit more than others from the nutrients in tree litter, any changes in soil pH, water relations, shelter from wind and rain, and so on. In some instances there may be no effects on either herbaceous or tree crop yields, for instance where forage legumes are grown beneath trees on fertile soils. In other instances, herbaceous crop yields may be depressed by allelopathic toxins produced by the trees, or tree yields may be depressed by competition for nutrients, poor mycorrhizal development, or because the trees along the interface are not subjected to competition by other trees. In each study one would need to determine the yield of the herbaceous and tree crops along the interface compared with their yield within similar areas of monoculture (within the stable agroforest system) preferably with some auxillary information so that one could explain the results in terms of annidation, allelopathy or mutual interference for given environmental resources.

Then, by altering the area of each type of herbaceous crop - tree interface it will be possible to alter not only the total yield, but also the balance of yield obtained from the two components. The greater the area of interface, the more opportunity there will be for the dominant component to benefit and the weaker component to be suppressed. Consequently, the proportions of yield taken from the different components will diverge more and more from the proportions 'expected' on the basis of the land area allocated to it (Huxley and Maingu, 1978). Thus, with increase in interface area, more land has to be devoted to the weaker component in order to obtain the proportions of herbaceous and tree crop yield expected.

This approach could, of course, be applied to tree - tree and crop - crop mixtures, but for the latter it is usually too difficult to quantify interface and non-interface areas, and de Wit - type models still serve some purpose if the crops share the same land over the same time period. Also, the optimum design of herbaceous crop mixtures is difficult to predict because the relative dominance of the component species is often itself dependent on the plant populations and proportions in the mixture (Osiru and Willey, 1972; Harper, 1977).

Lastly, I should repeat that the spatial configuration of trees and crops in agroforests will be influenced by many factors other than those considered here. Very likely the soil will be heterogeneous, some trees and crops may thrive only in certain areas, some may need to be near homesteads or boundaries, and so on.

Resource sharing in the vertical dimension (Fig. 8b). If light is the main limiting environmental resource, then leaves become organs of aggression, and the dominant crop will be that which is tallest. One of the most potent ways of resource sharing is to plant crops so that they each become tallest in turn. Five ways of doing this spring to mind (Figure 8b): (i) by planting crops together which attain similar heights but with different life cycles, (ii) by planting crops together which attain different heights such that the shorter ones mature before the taller ones; (iii) by planting crops at different times; (iv) by planting crops which can climb up the stalks of crops that mature before them, and (v) by minimizing the shade cast by the tall crops, by using erect-leaved crops (for example, maize), by pruning trees or by planting deciduous trees. Baker (1979) describes examples in the tropics where cereals have been mixed so that each spends the latter part of its life at the top of the canopy, and in most instances there is a substantial increase in total yield. By contrast, when cereals with similar stature have been planted and harvested simultaneously, the yields in the majority of studies have been no greater than the yield of the highest yielding cereal in monoculture (Trenbath, 1974).

If we regard the soil as part of the vertical dimension, then we can include here the sharing of soil nutrients and water by planting deep-rooted 'nutrient pumping' trees like some *Acacia* with relatively shallowly rooted crops like millet, sorghum and sesame. And to complete the list we should include the mixing of legumes with non-legumes as a means of sharing atmospheric and soil nitrogen (see Mongi and Huxley, 1979).

Resource sharing in time. If no one crop fully utilizes environmental resources available throughout the year, then yields will be increased by skilfully phasing the growth cycles of different crops. The skill is required in (i) chosing the species and cultivars according to their phenology, stature, habit, product, etc., and (ii) staggering planting or sowing, relay planting, etc., so that soil water resources are fully utilized, the soil is protected from rain, weeds are suppressed, erosion is prevented, crops with reproductive yield are not overshadowed after the onset of floral initiation, and so on (Andrews, 1972, 1974; Baker, 1978, 1979; Fisher, 1977, 1979). Subsistence farmers are apparently very skilled in this way, and much could probably be learned from them (Bunting, 1980; Okigbo, 1980). No more needs to be added here because this subject is treated elsewhere in this volume (see Huxley, p.503).

Tree-herbaceous crop mixtures

Before speculating on some ways in which trees and herbaceous crops might be managed to advantage in agroforestry systems, it is important to recall the many possible objectives of agroforestry beside that of maximizing yield. First, in order to conserve the soil and its fertility it may be imperative to have a minimum number of trees, perhaps deeply rooted ones or dinitrogen fixing ones, and a continuous ground cover. Second, to spread risks it may be necessary to grow low-yielding hardy crops (for example, sorghum instead of maize, or drought-deciduous trees) and also to reorder one's ideal priorities on how much land is

devoted to food, fuel, fodder and cash crops. Third, to control weeds it may be desirable to grow crops which establish large leaf areas quickly, such as cucurbits and pioneer tree species. Fourth, to further ease the workload, it may be important to stagger planting and harvesting, to grow low yielding but problem free fruit trees, or root crops (which have a high yield per unit of labour), to minimize transport distances and the use of ladders, and to provide shade for animals or to make field work agreeable. Fifth, to control pests and diseases it may be preferable to plant crop mixtures, even if sole crops yielded more, to mix crops with differing heights, smell, colour and susceptibility, and to provide shade (for example, to lessen banana leaf spot or cacao capsid damage). And to these rational objectives may be added the 'irrational' ones of tradition, culture, religion, division of labour within families and so on. Clearly, with so many factors to consider, it would be foolish to offer general management prescriptions. As I have said above, all that can be usefully done here is to consider some of the options with respect to yield per unit area.

Let us suppose that trees were grown in agroforestry systems as multipurpose trees, or for timber, fodder, as planted fallows, for fuel, fruit or shelter. For each of these purposes, how could the trees be managed to advantage, and what herbaceous crops might be grown with them, bearing in mind the foregoing discussion on tree pruning, effects of spacing and resource sharing in mixtures?

Multipurpose trees (Fig. 9a). Multipurpose trees, and all the other kinds listed below, should be established by underplanting beneath herbaceous crops such as beans and maize. As the trees grow taller and cast more shade the best companion crops might be 'vegetative' crops such as cassava and forage crops, climbers such as yams, or tall 'reproductive' crops such as bananas. Where possible all tree and herbaceous crops that have 'reproductive' yield should be relatively unshaded or at the top of the agroforest canopy.

Multipurpose trees could be grown as widely spaced individuals, in small groups or rows, but should not be in closed stands if they are required to yield fruits and browse as well as wood. 'Multipurpose' might mean 'multimanagement'; some trees might be pruned for fruits, others lopped for browse, others allowed to grow tall for shade and ground cover; trees for different purposes might be planted on different patches of soil; fruit trees might become 'multipurpose' if poorly managed; some trees might be culled for fuel and continuously replaced; and old trees might be girdled to obtain a last crop of fruits before felling. The management options are legion.

Timber trees (Fig. 9b). As discussed earlier, the forestry enterprise most compatible with tropical subsistence farming is high value sawlog production. Wide spacings and the pruning of basal branches benefit the forester by improving the timber quality and shortening the time to maximum mean annual increment (see Cannell, this volume), and provide the farmer with fuel or mulch and open ground for agriculture. Obviously a wide range of crops can be grown in the early years including cereals and

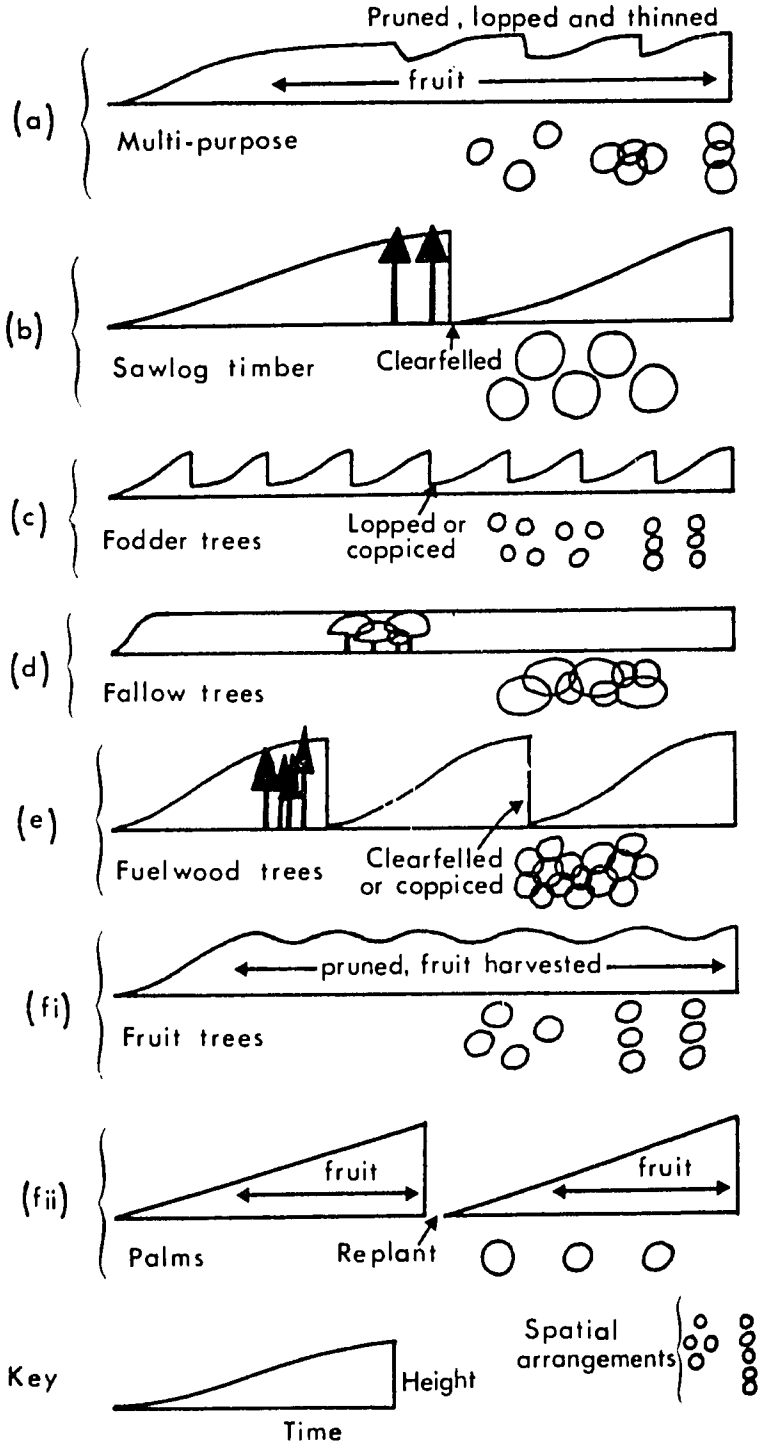


Fig. 9. Diagrammatic representation of the suggested management of trees grown for different purposes in agroforestry. For each tree type a diagram is given of the change in height of the trees with time, and their spatial dispersion at maturity (see text).

legumes, provided the growth of the trees is not severely checked and their leaders are not damaged. In temperate regions, where wheat and barley have been grown among widely spaced poplars, and soybeans among walnuts, tree growth has been checked where crops were grown within about one metre of the trees after the first year. But shallow-rooted crops may be less harmful to the trees than deeply rooted ones; for instance, *Poa* spp. check apple tree growth less than *Lolium* spp. The tree canopy can be kept open by thinning, or by growing seasonally deciduous species, but in most cases the choices open to the farmers will become restricted to vegetative crops and eventually to the grazing of animals.

Fodder trees (Fig. 9c). Trees grown for browse, fodder or mulch should be coppiced, or if animals are grazed beneath them, pollarded. They will recover from coppicing best, and yield most, if widely spaced or in rows or small groups, possibly alongside paths or roads, so that the fodder can be accessed, or the mulch easily carried to nearby fields. Coppicing and lopping could be phased to coincide with the interplanting of field crops such as maize and cassava, in the same way that ratooned sugar cane can be intercropped (Pillay and Mamet, 1978). Short-statured coppice might be grown permanently with bananas or small shrubs and, being a vegetative crop, coppice could be grown with overstorey shade from fruit or multipurpose trees.

Planted fallow trees (Fig. 9d). The species suitable for short forest fallows in shifting agriculture should obviously be highly competitive pioneers, able to grow in nutrient deficient soils, be dinitrogen fixers and soil improvers which will quickly cover the ground and oust weeds such as *Imperata* grass. They should ideally have low spreading canopies, low density wood, large leaves and continuous aperiodic shoot growth, such as the natural pioneers *Macaranga* spp. in West Africa and *Macaranga* spp. in south-east Asia. They should also produce large quantities of seeds and be easy to germinate or propagate. Apart from their role as restorers of soil fertility, they could be sources of fodder and mulch, and of edible seeds, but their low density wood would not be ideal for fuel.

Fuelwood trees (Fig. 9e). Arguments were presented above for growing fuelwood trees as sole crops, in groves or large clumps, where the trees would be allowed to grow tall and there would be inter-tree competition. There would be little opportunity to grow anything other than herbage crops with them, except during the early years, so evergreen fuelwood species could be used, and the groves could occupy the poorer land with limited animal grazing. The wood should have a high specific gravity, and the trees should be spaced to produce stems and branches of the desired diameters in the shortest time. The outer edges of the groves might be planted with fodder-producing trees, or coppices, which would yield satisfactorily in the shade of the taller fuelwood trees and would also provide some competition for the outer fuelwood trees. This would be better than planting the groves alongside paths or fields or herbaceous crops, or using the edge fuelwood trees themselves for browse.

Fruit trees and palms (Fig. 9f i and ii). As mentioned above, fruit trees should be widely spaced, yet be within reach of pollinators. Palms, which are circular, benefit from lateral illumination on all sides, whereas angiospermous fruit trees could be grown in rows. The trees should occupy the most fertile land, perhaps near homestead refuse or a source of animal manure, and should be subjected to little competition of any sort. The trees need to be regularly visited for pruning (except palms), harvesting and probably pest and disease control, so there needs to be access, which might be given by planting alongside paths, within animal pastures, homestead gardens or field boundaries. The fruit trees should be small, without overstorey shade (except perhaps unfertilized coffee, cacao and a few shade tolerant species) and should have open canopies, enabling legumes, cereals and bananas to be grown close to them and perhaps climbing plants to be grown on them. Other points regarding fruit tree management were covered above.

Shelterbelts. Where there are strong winds or there is strong advection or wind erosion, shelterbelts increase crop yield, especially of vegetables and legumes. Work on strip intercropping, summarized by Radke and Hagstrom (1976), has shown that the shelterbelts should be perpendicular to the prevailing wind, spaced at intervals 10 to 15 times their heights and should be wind porous. Crops sheltered in this way often grow taller than they otherwise would, produce more dry matter and larger fruit and vegetative yields, mostly because of improved water relations.

REFERENCES

Adams, W.R. (1928). Studies in tolerance of New England forest trees. VIII. Effect of spacing in a jack pine plantation. *Vermont Agr. Exp. Stn Bull.* 282, 49 pp.

Alexander, D.McE. and Miggs, D.H. (1971). Growth responses of sweet orange seedlings to shoot and root pruning. *Ann. Bot.* 35, 109-115.

Alvim, P. de T. and Kozlowski, T.T. (1977). "Ecophysiology of Tropical Crops". Academic Press, New York and London.

Ando, T., Hatija, K., Dio, K., Kataoka, H., Kato, Y. and Sakaguchi, K. (1968). Studies on the system of density control of sugi (*Cryptomeria japonica*) stand. *Bull. Govt For. Expt Stn Tokyo* 209, 1-76.

Andrews, D.J. (1972). Intercropping with sorghum in Nigeria. *Expl Agric.* 8, 139-150.

Andrews, D.J. (1974). Responses of sorghum varieties to intercropping. *Expl Agric.* 10, 57-63.

Atkinson, D. (1973). *Ann. Rep. E. Malling Res. Stn for 1972*, pp.58-59.

Avery, D.J. (1975). Effects of fruits on photosynthetic efficiency. *In* "Climate and the Orchard" (H.C. Pereira, ed.) pp. 110-112. CAB Research Review No.5. East Malling, Kent, UK.

Baker, E.F.I. (1978). Mixed cropping in Northern Nigeria. I. Cereals and groundnuts. *Expl Agric.* 14, 293-298.

Baker, E.F.I. (1979). Mixed cropping in Northern Nigeria. II. Cereals and cotton. III. Mixtures of cereals. *Expl Agric.* 15, 33-40, 41-48.

Bassman, J.H. and Myers, W.L. (1979). Growth response of three *Populus* clones subjected to simulated insect defoliation. *In* Proc. Fifth North Am. For. Biol. Workshop (C.C. Hollis and A.E. Squillace, eds), p.413. Univ. Florida, Gainesville, USA.

Berry, A.B. and Steill, W.M. (1978). Effect of rotation length on productivity of aspen sucker stands. *For. Chron.* 56, 265-267.

Berry, G. (1967). A mathematical model relating plant yield with arrangement for regularly spaced crops. *Biometrics* 23, 505-515.

Bhimaya, C.P., Kaul, R.N. and Ganguti, B.N. (1964). Studies on lopping intensities of *Procopis spicigera*. *Indian Forester* 90, 19-23.

Brooks, H.J., Fogle, H.W. and McKay, J.W. (1965). Progress and problems in tree fruit and nut production. *Adv. Agron.* 17, 283-326.

Bunting, A.H. (1976). Maximizing the product, or how to have it both ways. *In* "Tree Physiology and Yield Improvement" (M.G.R. Cannell and F.T. Last, eds), pp.1-20. Academic Press, London and New York.

Bunting, A.H. (1980). The future of research on mixed cropping in tropical agriculture. *In* "Opportunities for Increasing Crop Yields" (R.G. Hurd, P.V. Biscoe and C. Dennis, eds), pp.247-252. Pitman, Boston, London and Melbourne.

Cannell, M.G.R. (1971). Production and distribution of dry matter in trees of *Coffea arabica* L. in Kenya as affected by seasonal climatic differences and the presence of fruits. *Ann. appl. Biol.* 67, 99-120.

Cannell, M.G.R. (1980). Productivity of mini-rotation, closely-spaced poplars on agricultural land in Britain. *Forestry* 53, 1-21.

Chalmers, D.J. and Van den Ende, B. (1975). Productivity of peach trees: factors affecting dry weight distribution during tree growth. *Ann. Bot.* 39, 423-432.

Champagnat, P. (1954). Les corrélations sur le rameau d'un an des végétaux ligneux. [Correlations on one-year-old branches of woody plants.] *Phyton* 4, 1-104.

Clements, F.E., Weaver, J.E. and Hanson, H.C. (1929). Competition in cultivated crop plants. *Carnegie Inst. Wash. Publ.* 398, 202-233.

Coombe, B.G. (1962). The effect of removing leaves, flowers and shoot tips on fruit set in *Vitis vinifera*. *J. hort. Sci.* 37, 1-15.

Cripps, J.E.L., Melville, F. and Nicol, H.I. (1975). The relationship of Granny Smith apple tree growth and early cropping to planting density and rectangularity. *J. hort. Sci.* 50, 291-299.

Dawkins, H.C. (1959). The volume increment of natural tropical high forest and limitations on its improvement. *Empire For. Rev.* 38, 175-180.

Dawkins, H.C. (1963). Crown diameters; their relation to bole diameters in tropical forest trees. *Commonw. For. Rev.* 42, 318-333.

Donald, C.M. (1963). Competition among crop and pasture plants. *Adv. Agron.* 15, 1-118.

Drew, T.J. and Flewelling, J.W. (1977). Some recent Japanese

theories of yield - density relationships and their application to Monterey pine plantations. *For. Sci.* 23, 517-534.

Erskine, W. and Khan, T.N. (1976). Effects of spacing on cowpea genotypes in Papua New Guinea. *Expl Agric.* 12, 401-410.

Ezedinma, F.O.C. (1973). Effects of defoliation and topping on semi-upright cowpeas (*Vigna unguiculata* L. Walp.) in a humid tropical environment. *Expl Agric.* 9, 203-207.

Ferwerda, F.P. and Wit, F. (1969). Outlines of perennial crop breeding in the tropics. *Landbouwhogeschool, Wageningen, Netherlands, Misc. Papers* 4, 511 pp.

Fisher, N.M. (1977). Studies in mixed cropping. II. Population pressures in maize - bean mixtures. *Expl Agric.* 13, 185-191.

Fisher, N.M. (1979). Studies in mixed cropping. III. Further results with maize - bean mixtures. *Expl Agric.* 15, 49-58.

Ford, E.D. (1975). Competition and stand structure in some even-aged plant monocultures. *J. Ecol.* 63, 311-333.

Forrest, W.G. and Ovington, J.D. (1970). Organic matter changes in an age series of *Pinus radiata* plantations. *J. appl. Ecol.* 7, 177-186.

Grier, C.C. and Wareing, R.H. (1974). Conifer foliage mass related to sapwood area. *For. Sci.* 20, 205-206.

Hahn, S.K. (1977). Sweet potato. *In* "Ecophysiology of Tropical Crops" (P de T. Alvim and T.T. Kozlowski, eds), pp.237-248. Academic Press, New York, San Francisco and London.

Hallé, F., Oldman, R.A.A. and Tomlinson, P.B. (1978). "Tropical Trees and Forests, an Architectural Analysis". Springer-Verlag, Berlin, Heidelberg and New York.

Hansen, P. (1977). The relative importance of fruits and leaves for cultivar-specific growth rate of apple fruits. *J. hort. Sci.* 52, 501-508.

Harper, J.L. (1977). "Population Biology of Plants". Academic Press, London, New York and San Francisco.

Harper, J.L. , Lovell, P.H. and Moore, K.G. (1970). The shapes and sizes of seeds. *Ann. Rev. of Ecol. Systematics* 1, 327-356.

Heim, G., Landsberg, J.J., Watson, R.L. and Brain, P. (1979). Ecophysiology of apple trees: dry matter production and partitioning by young Golden Delicious trees in France and England. *J. appl. Ecol.* 16, 179-194.

Hilkenbäumer, F. (1976). "Pruning in the Fruit Garden". Blandford Press, Poole, Dorset, UK.

Hutchings, M.J. (1979). Weight - density relationships in ramet populations of clonal perennial herbs, with special references to the -3/2 power law. *J. Ecol.* 67, 21-33.

Huxley, P.A. (1967). The effects of artificial shading on some growth characteristics of Arabica and Robusta coffee seedlings. I. The effects of shading on dry weight, leaf area and derived growth data. *J. appl. Ecol.* 4, 291-308.

Huxley, P.A. (1979). The need for agroforestry and special consideration regarding field research. ICRAF, Nairobi, Kenya.

Huxley, P.A. (1980). The value of existing data appraisal. *In* "International Cooperation in Agroforestry" (T. Chandler and D. Spurgeon, eds), pp.297-315. ICRAF, Nairobi, Kenya.

Huxley, P.A. (1981). Some critical topics for plant research in agroforestry. *In* "Proc. Kenya National Seminar on Agroforestry" (L. Buck, ed.), pp.85-92. ICRAF, Nairobi, Kenya.

Huxley, P.A. and Maingu, Z. (1978). Use of a systematic spacing

design as an aid to the study of intercropping: some general considerations. *Expl. Agric.* 14, 49-56.

Jackson, J.E. and Palmer, J.W. (1977). Effects of shade on the growth and cropping of apple trees. II. Effects on components of yield. *J. hort. Sci.* 52, 253-266.

Jarvis, P.G., James, G.B. and Landsberg, J.J. (1976). Coniferous forests. *In* "Vegetation and the Atmosphere" (J.L. Monteith, ed.), pp.171-240. Academic Press, London and New York.

Landsberg, J.J. and Cutting, C.V. (1977). "Environmental Effects on Crop Physiology". Academic Press, London and New York.

Luckwill, L.C. (1970). The control of growth and fruitfulness of apple trees. *In* "Physiology of Tree Crops" (L.C. Luckwill and C.V. Cutting, eds.), pp.237-254. Academic Press, London and New York.

Luckwill, L.C. and Cutting, C.V. (Eds)(1970). "Physiology of Tree Crops". Academic Press, London and New York.

Madgwick, H.A.I. (1975). Effects of partial defoliation on the growth of *Liriodendron tulipifera* L. seedlings. *Ann. Bot.* 39, 1111-1115.

Madgwick, H.A.I., Jackson, D.S. and Knight, P.J. (1977). Above-ground dry matter, energy and nutrient contents of trees in an age series of *Pinus radiata* plantations. *N.Z. J. For. Sci.* 7, 445-468.

Magambo, M.J.S. and Cannell, M.G.R. (1981). Dry matter production and partition in relation to yield of tea. *Expl Agric.* 17, 33-38.

Maggs, D.H. (1960). The effect of number of shoots on the quantity and distribution of increment in young apple trees. *Ann. Bot.* 24, 345-355.

Maggs, D.H. (1962). A constant pattern of growth in young apple trees. *Nature, Lond.* 1[illegible], 250-252.

Maggs, D.H. (1963). The reduction in growth of apple trees brought about by fruiting. *J. hort. Sci.* 38, 119-128.

Maggs, D.H. (1964). The distance from tree base to shoot origin as a factor in shoot and tree growth. *J. hort. Sci.* 39, 298-307.

Maggs, D.H. (1965). Growth rates in relation to assimilate supply and demand. II. The effect of particular leaves and growing regions in determining the dry matter distribution in young apple trees. *J. expt. Bot.* 16, 387-404.

Maggs, D.H. and Alexander, D.McE. (1967). A topophysic relation between regrowth and pruning in *Eucalyptus cladocalyx* F. Muell. *Aust. J. Bot.* 15, 1-9.

Mohler, C.L., Marks, P.L. and Sprugel, D.G. (1978). Stand structure and allometry of trees during self-thinning of pure stands. *J. Ecol.* 66, 599-614.

Molisch, H. (1916). Pflanzenphysiologie als Theorie der Gärtnerei. [Plant Physiology as Horticultural Theory.] pp.256-262. Jena.

Mongi, H.O. and Huxley, P.A. (1979). Soils research in agroforestry: proceedings of an expert consultation held at ICRAF in Nairobi. ICRAF, Nairobi, Kenya. 584 pp.

Moss, G.I. (1971). Effect of fruit on flowering in relation to biennial bearing in sweet orange (*Citrus sinensis*). *J. hort. Sci.* 46, 177-186.

Mullins, M.G. and Rogers, W.S. (1971). Growth of horizontal

apple shoots: effects of stem orientation and bud position. *J. hort. Sci.* 46, 313-321.

Ogawa, H. and Kira, T. (1977). Methods of estimating forest biomass. *In* "Primary Productivity of Japanese Forests" (T. Shidei and T. Kira, eds), pp.15-25. JIBP Synthesis Vol.16, University of Tokyo Press.

Okigbo, B.N. (1980). The importance of mixed stands in tropical agriculture. *In* "Opportunities for Increasing Crop Yields" (R.G. Hurd, P.V. Biscoe and C. Dennis, eds), pp.233-246. Pitman, Boston, London and Melbourne.

Osiru, D.S.O. and Willey, R.W. (1972). Studies on mixtures of dwarf sorghum and beans (*Phaseolus vulgaris*) with particular reference to plant population. *J. agric. Sci. Camb.* 79, 531-540.

Ovington, J.D. (1957). Dry matter production by *Pinus sylvestris* L. *Ann. Bot.* 31, 287-316.

Parry, M.S. (1974). The control of biennial bearing of Laxton's Superb apple trees. *J. hort. Sci.* 49, 123-130.

Pereira, H.C. (1975). Climate and the orchard. Effects of climatic factors on fruit tree growth and cropping in south-east England. *CAB Research Review* 5. East Malling, Kent, UK.

Pillay, A.R. and Mamet, J.R. (1970). Intercropping sugarcane with maize. *Expl Agric.* 11, 161-165.

Plucknett, D.L., Evenson, J.P. and Sanford, W.G. (1970). Ratoon cropping. *Adv. Agron.* 22, 286-331.

Quinlan, J.D. and Preston, A.P. (1971). The influence of shoot competition on fruit retention and cropping of apple trees. *J. hort. Sci.* 46, 525-534.

Radke, J.K. and Hagstrom, R.T. (1976). Strip intercropping for wind protection. *In* "Multiple Cropping", pp.201-222. ASA Special Publication No 27. American Society of Agronomy, Madison, Wisconsin, USA.

Reineke, L.H. (1933). Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46, 627-638.

Rennie, J.L. (1974). Some effects of competition and density of plants on dry weight produced. *Ann. Bot.* 38, 1003-1012.

Richards, D. and Rowe, R.N. (1977). Effects of root restriction, root pruning and 6-benzylaminopurine on the growth of peach seedlings. *Ann. Bot.* 41, 729-740.

Richards, D., Goubran, F.H. and Collins, K.E. (1979). Root-shoot equilibria in fruiting tomato plants. *Ann. Bot.* 43, 401-404.

Rogers, W.S. and Booth, G.A. (1964). Relationship of crop and shoot growth in apple. *J. hort. Sci.* 39, 61-65.

Salisbury, E.J. (1942). "The Reproductive Capacity of Plants". Bell, London.

Scarrone, F. (1969). "Recherches sur les rythmes de croissance du Manquier et de quelques végétaux ligneux malagasy". [Studies on growth rhythms of Manquier and some other Malagasy woody plants.] Thesis, Clermont-Ferrand University.

Shinozaki, K., Yoda, K., Hozumi, K. and Kira, T. (1964). A quantitative analysis of plant form - the pipe model theory. I. Basic analyses. *Jap. J. Ecol.* 14, 97-105.

Sweet, G.B. (1966). "Some factors affecting the production of dry matter in forest tree species". PhD Thesis, University College of Wales, Aberystwyth.

Tai, E.A. (1977). Banana. *In* "Ecophysiology of Tropical Crops" (P. de T. Alvim and T.T. Kozlowski, eds), pp.441-460. Academic Press, New York, San Francisco and London.

Tejwani, K.G. (1979). Soil fertility status, maintenance and conservation for agroforestry systems on wasted lands in India. *In* "Soil Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.141-174. ICRAF, Nairobi, Kenya.

Tomlinson, P.B. and Zimmermann, M.H. (1978). "Tropical Trees as Living Systems". Cambridge University Press, London, New York.

Trenbath, B.R. (1974). Biomass productivity in mixtures. *Adv. Agron.* 26, 177-210.

Trenbath, B.R. (1976). Plant interactions in mixed crop communities. *In* "Multiple Cropping", pp.129-170. ASA Special Publication No.27. American Society of Agronomy, Madison, Wisconsin, USA.

Wareing, P.F. (1968). The physiology of the whole tree. *Ann. Rep. E. Malling Res. Stn*, pp.55-68. East Malling, Kent, UK.

Wareing, P.F. (1977). Growth substances and integration in the whole plant. *In* "Integration of Activity in the Higher Plant" *Symp. Soc. Expt. Biol.* 31, pp.337-365. Cambridge University Press, Cambridge, London, New York and Melbourne.

Wareing, P.F. and Nasr, T.A.A. (1961). Gravimorphism in trees. I. Effect of gravity on growth and apical dominance in fruit trees. *Ann. Bot.* 25, 321-340.

Weaver, P. (1980). Agri-silviculture in tropical America. *Unasylva* 31, 2-12.

Westoby, M. (1977). Self-thinning driven by leaf area not weight. *Nature, Lond.* 265, 330-331.

Wholey, D.W. and Cock, J.H. (1974). Onset and rate of root bulking in cassava. *Expl Agric.* 10, 193-198.

Willey, R.W. (1975). The use of shade in coffee, cocoa and tea. *Hort. Abstracts* 45, 791-798.

Willey, R.W. and Heath, S.B. (1969). The quantitative relationships between plant population and crop yield. *Adv. Agron.* 21, 281-321.

Willey, R.W. and Osiru, D.S.O. (1972). Studies on mixtures of maize and beans (*Phaseolus vulgaris*) with particular reference to plant population. *J. agric. Sci. Camb.* 79, 517-529.

Williams, C.N. (1975). "The Agronomy of the Major Tropical Crops". Oxford University Press, London and New York.

Williams, R.R. (1970). Factors affecting pollination in fruit trees. *In* "Physiology of Tree Crops" (L.C. Luckwill and C.V. Cutting, eds), pp.193-207. Academic Press, London and New York.

Wit, C.T. de (1960). On competition. *Versl. Landbouwk. Onderz.* 66, 1-82.

Zavitkovski, J., Isebrands, J.G. and Crow, T.R. (1974). Application of growth analysis in forest biomass studies. *In* "Proc. Third North American Forest Biology Workshop" (C.P.P. Reid and G.H. Fechner, eds), pp.196-226. Colorado State University, Fort Collins, USA.

DISCUSSION

KOZLOWSKI - When trees are widely spaced they produce conical stems. They should, therefore, be closely spaced, so that they

produce cylindrical stems, then thinned.

CANNELL - Wide spacing and basal pruning have proved beneficial in agroforestry situations where other products are also required.

BUDOWSKI - Studies in South Africa have shown wide spacing and intensive pruning to be preferable to thinning, but the decision depends on the labour available.

LOOMIS - Dr Cannell's presentation is a most elegant demonstration of a systems type analysis for cause and effect.

CONNOR - Dr Cannell previously asked how systems analysis could handle situations where there was a range of objectives. Systems analysis is the only way in which all the objectives can be met, but for any particular system the objectives must be specified clearly. For example, to maximize the yield of one particular component, with the constraint of no soil erosion and some element of aesthetic function.

BRUNIG - If you take the information of Figure 5 of your paper to infer in Figure 9(b) that options are narrower, you disregard the interactions between the various compartments of the stand as an ecosystem. For example, if you keep your tree density in the early phases as low as possible with respect to your objective functions, you will change the structure and functions of the trees. At the same time, you will change the understorey, and the nutrient, water and energy regimes. There are means available to describe and predict these reactions of the system in ecological and economic terms which would also be useful to agroforestry. An example is the model hierarchy which I described in my paper.

HUXLEY - It is necessary to consider the optimum populations of mixtures separately from optimum populations of sole crops. The optimum population of a mixture is not necessarily the mean of its two components.

RAINTREE - Linear programming is another good tool for handling situations with multiple constraints and multiple variables.

NAIR - The cultivars used in agroforestry are often not those applicable to marginal areas. Experience with high input cultivars has to be used in the agroforestry context because there is as yet no other experience available. This could, however, easily lead to wrong conclusions.

ALVIM - There is now a tendency to use wide spacings, for example box planting in Malaysia. Economic species are not currently used for the box, but this could be done. Planting patterns of this type are necessary for crops which do not withstand much wind, such as cacao.

CANNELL - There are many constraints on spatial arrangements of trees other than those which I mentioned, as you rightly point out.

PLANT POPULATION AND YIELD OF TREE AND HERBACEOUS CROPS

M.G R. CANNELL
Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian, Scotland.

ABSTRACT. A review is given of the effects of plant population in monoculture on the biomass production, yield, and components of yield in a range of crop types used in tropical agroforestry systems. These include timber trees, fuelwood trees, fruit trees, palms, bananas, various root crops, grain legumes and cereals.

INTRODUCTION

Information on the effects of plant population on the performance of different tree and herbaceous crops is widely scattered in the literature on forestry, horticulture and agriculture. Reviews such as those by Willey and Heath (1969) and Harper (1977) explain the principles concerned, but they do not bring together data on the diverse range of tropical crops that are grown together in agroforestry systems. An attempt has therefore been made to summarize such data for (a) forest trees, (b) fruit trees and palms, (c) storage root crops, (d) grain legumes, and (e) cereals. For each crop, the effects of plant population are described in the figures and/or text on (i) biomass production (or leaf area index) per unit area of land, (ii) yield per hectare and per plant and (iii) the components of yield. The sources of information are quoted mainly in the figure legends.

TREE CROPS

Forest trees (Fig. 1)

Per hectare yields of trees have to be averaged over the years since planting, giving the mean annual increment (MAI), which, like the current annual increment (CAI), increases after planting as the stand leaf area index increases, but *decreases* when the trees age. MAI is greatest at the age when it equals CAI, by which time there is often competition-driven mortality. The plant population ('stocking density') and age giving maximum

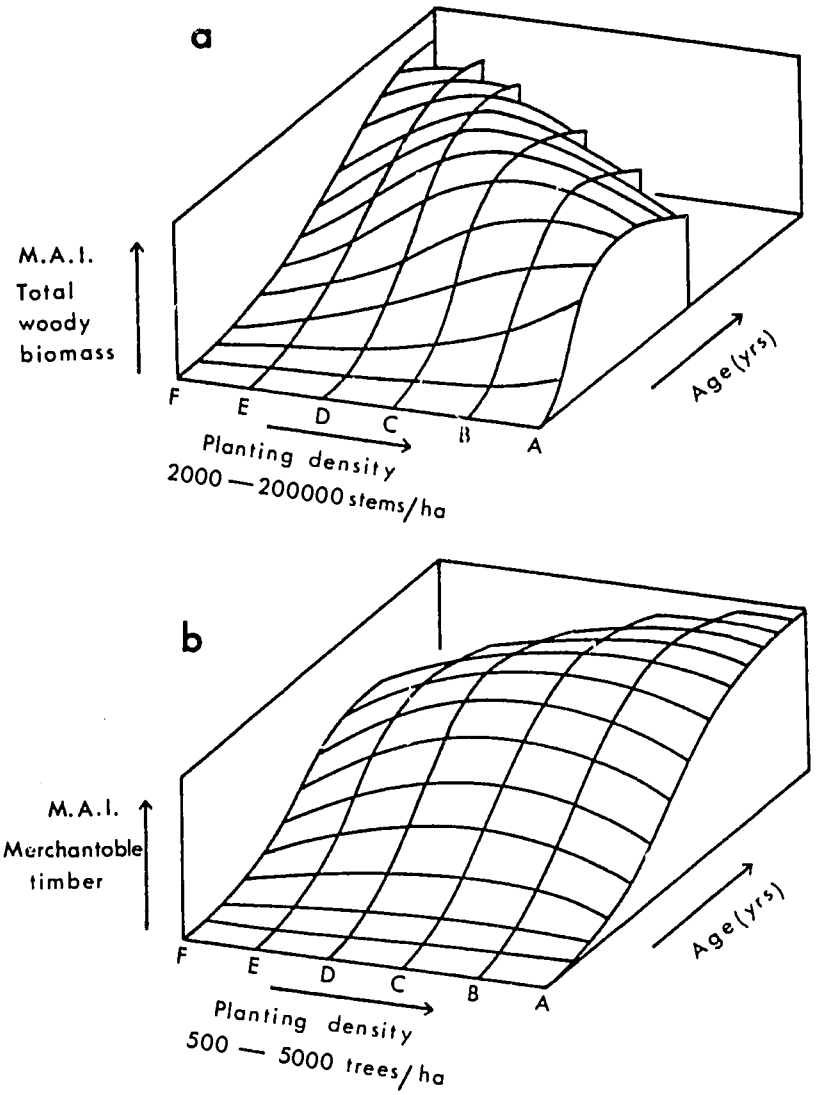


Fig. 1. Effect of planting density on the mean annual increment (MAI) of trees grown for woody biomass (branches and stems of any diameter) and merchantable timber (stems above a given diameter). Note that there is an optimum density for woody biomass as well as timber production, and that thinning will move the population in the direction A to F. Remember that closely spaced trees will be small in diameter, but not necessarily height, and that, in unthinned stands, the number of trees at harvest will be less than at planting owing to self-thinning.

MAI depend on the environmental resources, species and product (Assman, 1970; Hamilton and Christie, 1974; Baskerville, 1965; Cannell and Smith, 1980).

If the product is woody biomass of branches and stems, without regard to individual tree diameter, then MAI maximizes ('culminates') at a younger age with increase in plant population, but the greatest MAI is achieved at a *particular density and age* (density D in Figure 1a). This is because, at very wide spacings the trees age physiologically and so produce less total dry matter per hectare, before they reach maximum MAI, whereas at very close spacings maximum MAI occurs before the stand has developed its full height, cambial surface and canopy depth, and the stand 'stagnates'. Thus in pulpwood plantations the asymptotic yield-density relationship does not hold over a *wide* range of densities, although it does hold approximately over the range of densities included in most studies (Cannell, 1979).

If the product is boles above a given diameter, that is merchantable timber, or fuelwood with a certain minimum volume/surface ratio, then stands at *wide* spacings become productive soonest because they produce large individuals quickly. Stands at close spacings will have small diameter stems to begin with, but after considerable thinning or self-thinning these closely-spaced stands may eventually reach maximum MAI values (including only large diametered stems) similar to those of stands initially planted at wider spacings. In Figure 1b thinning the trees moves the population from lines B to C to D to E and is desirable because it *brings forward* the time of maximum MAI and also salvages the smaller individuals that would otherwise die and rot. Foresters normally prefer this policy - close initial planting and successive thinning (even 'precommercial' thinnings) - because density stress suppresses branching (and weeds) and encourages self-pruning, which in turn increases the proportion of above-ground dry matter going to the boles, decreases knot number and size, and decreases stem taper. Because of these effects, the small tree crowns of density-stressed trees (at desirable spacings) are efficient producers of merchantable bole wood per unit of foliage and ground area (Assman, 1970).

In short, the forester's aim is to keep the degree of density stress at a desirable level, balancing the benefits of density stress on weed and branch suppression against its undesirable effect on decreasing mean bole diameter (and eventually inducing mortality) and a delay in reaching maximum MAI. And at the same time the forester recovers saleable thinnings as soon as he can.

Fruit trees and palms (Fig. 2)

Tree populations giving maximum fruit yields per hectare are much lower than those producing maximum dry matter per hectare, whether the yield is fleshy fruits, seeds, or palm fruits. This is because there is a precipitate decrease in numbers of fruits per tree with increase in mutual shading resulting, at a critical plant population, in decreased yield per hectare above, for instance, leaf area indices of 1 to 2 in shade intolerant apple in England, and above leaf area indices of 3 to 4 in shade tolerant coffee in Kenya. Also, shaded fruits may not ripen

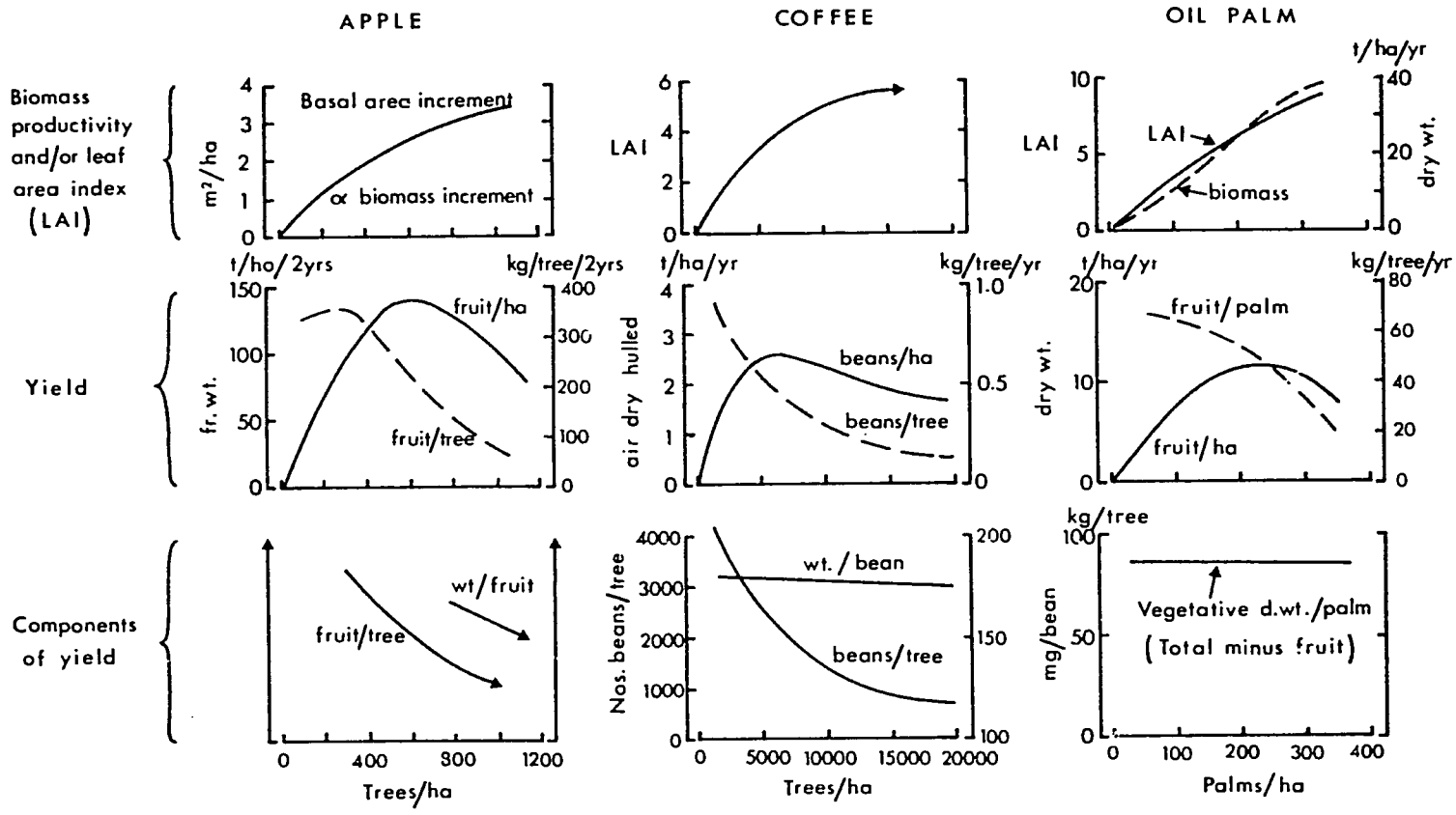

APPLE
COFFEE
OIL PALM
Biomass productivity and/or leaf area index (LAI)
Basal area increment
∝ biomass increment
m²/ha
LAI
t/ha/yr
dry wt.
biomass
Yield
t/ha/2yrs
kg/tree/2yrs
fr. wt.
fruit/ha
fruit/tree
t/ha/yr
kg/tree/yr
air dry hulled
beans/ha
beans/tree
dry wt.
fruit/palm
fruit/ha
Components of yield
wt/fruit
fruit/tree
Trees/ha
Nos. beans/tree
wt. / bean
beans/tree
Trees/ha
kg/tree
mg/bean
Vegetative d.wt./palm
(Total minus fruit)
Palms/ha

Figure 2.

properly and may be small, but there may not be much decrease in the mean weights of individual seeds or shelled nuts.

The effects of plant population on dry matter distribution in fruit trees depend on the species. In apple, very widely spaced trees may produce few fruit because cross-pollination is hampered. The optimum proportion of the total dry matter is devoted to apple fruits at an intermediate plant population which decreases as the trees get bigger (Cripps *et al.*, 1975). In self-pollinated Arabica coffee a very large proportion of the total dry matter is apportioned to seeds when the trees are widely spaced and well-illuminated, indeed so much so on young trees that they can 'overbear' (for reasons given by Cannell, 1975). So, for coffee too, the optimum lies at some intermediate population, depending on how the trees are pruned.

Oil palm is quite different; the proportion of dry matter devoted to fruits increases as the palms get bigger, will decrease if some leaves are pruned off, and will diminish with an increase in plant population because the amount of dry matter produced per palm will be smaller. However, the absolute dry weight of the vegetative parts per palm is surprisingly constant over a wide range of densities, showing that the size of individual palms and their individual dry matter productivities have to exceed a certain minimum before they will produce large amounts of fruits (Corley, 1973). Consequently palms need to be grown at relatively wide spacings and plantations often have only about 200 plants per hectare, as compared with over 400 for apple and well over 1000 for coffee.

HERBACEOUS CROPS

Bananas

Bananas seem to be quite tolerant of increases in density stress, largely because they produce suckers. Unreported 'fan' trials in Jamaica have shown that tetraploid clones will yield similar amounts per hectare over the range 1077 to 2389 plants per hectare. At close spacings the individuals produced fewer suckers, fewer branches, fewer fruits per branch, but similarly sized bananas, and only marginally greater yields per hectare (pers. comm. K. Shepherd, Banana Company of Jamaica). However, at very close spacings ratoon yields could decline.

Fig. 2 (*Opposite*) Effects of planting density on the biomass* and yield of tree crops. *Apple*: from Verheij (1968, quoted by Harper, 1977, his Fig. 7/17); values for 11th to 13th year after planting in Hungary. Stem base cross-sectional areas are linearly related to above-ground biomass (Westwood and Roberts, 1970). The trees were pruned to bush and spindle shapes. *Coffee*: from Browning and Fisher (1976), Kuguru *et al.* (1977) and Cannell (1972); values for 4-year-old *Coffea arabica* L. in Kenya. Bean (=seed) yields differed greatly between sites, but the trends with planting density were similar. *Oil palm*: from Corley (1973); values for 7-year-old *Elaeis guineensis* Jacq. in southern Malaya.
*Biomass values refer to the dry weight above ground, omitting roots and fallen leaves.

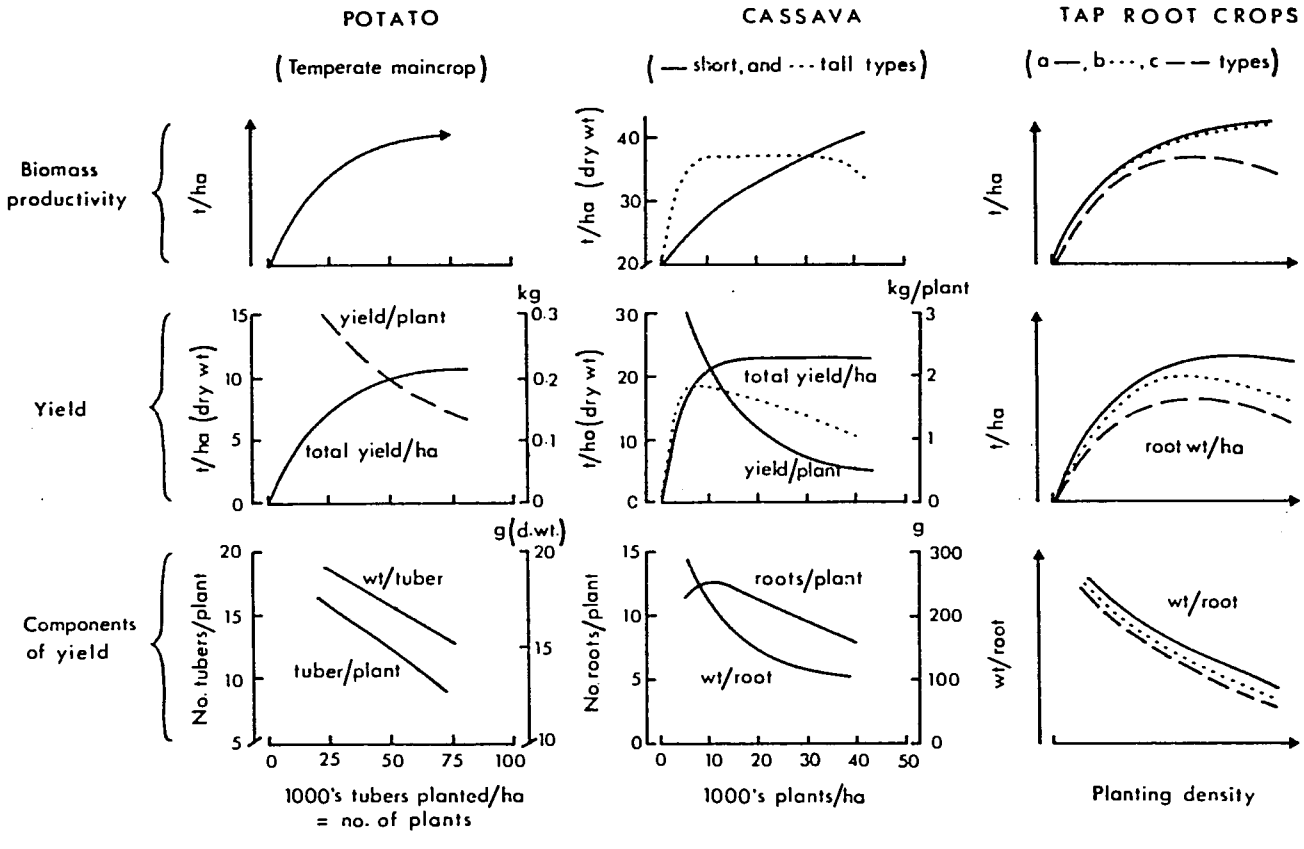

POTATO
(Temperate maincrop)
CASSAVA
(— short, and --- tall types)
TAP ROOT CROPS
(a —, b ···, c — — types)
Biomass productivity
t/ha
t/ha (dry wt)
Yield
yield/plant
total yield/ha
kg
kg/plant
root wt/ha
Components of yield
wt/tuber
tuber/plant
roots/plant
wt/root
No. tubers/plant
No. roots/plant
g (d.wt.)
g
1000's tubers planted/ha = no. of plants
1000's plants/ha
Planting density

Figure 3.

Storage root crops (Fig. 3)

The per hectare yields of storage root crops usually increase to a plateau with increase in plant, or rather *stem*, population (cassava, Enyi, 1973b; potato, Ifenkwe and Allan, 1978a, b), following a similar trend to the increase in total dry matter per hectare. Although there are instances, such as in some tall cassavas, where total dry matter and harvest indices decline at high plant populations, this is not the rule. Increasing cassava plant populations only slightly decreased the harvest index, from 58 to 56 per cent in Tanzania (Enyi, 1973b), had no effect in Malaya (harvest index 55 per cent; Williams, 1972), and increased it from 44 to 58 per cent in Sierra Leone (Godfrey Sam-Aggrey, 1978). In tap root crops (beets, turnips, etc.) there is only a small decrease in storage root/top ratio, or no change at all (Bleasdale, 1966; Currah and Barnes, 1979). The most important factors affecting harvest indices in root crops are: (a) genotype: those varieties which divert a large proportion of their dry matter to storage roots tend, unfortunately, to increase their foliage canopies, and hence total dry weights, rather slowly (for example, cassava, Cock, 1976; Cock *et al.*, 1977); and (b) size-grading, because in all root crops increasing population density decreases the size of individual roots (or tubers, etc.). Thus relatively high plant populations will be desired for single-stemmed root crops, for an early harvest, or small roots, whereas lower populations would be better for multistemmed branching or trailing types, a delayed harvest, or large roots.

Grain legumes (Fig. 4)

The examples given in Figure 4 are *not* necessarily typical of the three species represented; they show only a part of the variation in response to plant population within this diverse group of crops. Note that the greatest yields per hectare typically occur at populations much below those giving greatest total dry matter, but not always (see bush type cowpeas). Also the economic optimum populations are typically less than those giving greatest yield (because the seed is expensive), but not invariably. Plant habit is all important. The optimum population

Fig. 3 (*Opposite*) Effect of planting density on the growth and yield* of storage root crops. Potato (*Solanum tuberosum*) from Ifenkwe and Allen (1978 a, b) taking means for cvs Désirée and Maris Piper main crops grown in west Wales at varying within-row spacings, averaged for rows 66 cm and 132 cm apart. Cassava (*Manihot esculenta* Crantz) from Cock *et al.* (1977) for cvs M Col 1080 (tall) and M Col 22 (short) growing in Colombia. Tap root crops: (a) *carrot* (Bleasdale, 1967; Currah and Barnes, 1979; Salter *et al.*, 1979); *parsnip* (Bleasdale and Thompson, 1966); *radish* (Bleasdale, 1967); *turnip* (Hozumi and Ueno, 1954); and *onion* (Frappel, 1973). (b) Size-graded yield of most root crops (including potatoes and cassava). (c) *Red beet* (Bleasdale, 1966); *globe beet* (see Willey and Heath, 1969). *Similar scales are used in the graphs of total biomass (total above ground plus storage root) and storage root weights so that trends in the harvest indices can be judged.

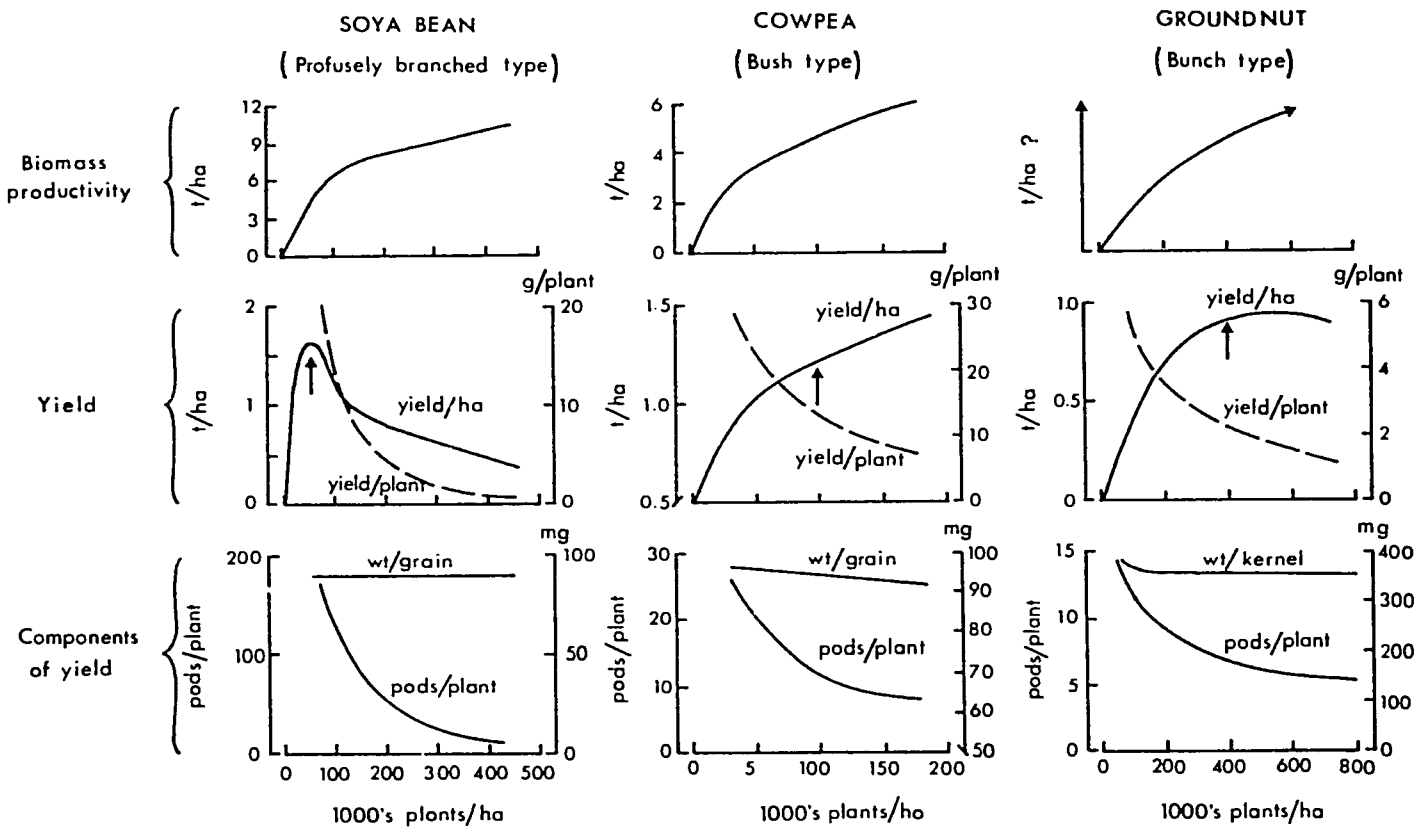

SOYA BEAN
(Profusely branched type)
COWPEA
(Bush type)
GROUNDNUT
(Bunch type)
Biomass productivity
Yield
Components of yield
t/ha
t/ha ?
g/plant
mg
yield/ha
yield/plant
wt/grain
wt/kernel
pods/plant
1000's plants/ha

Figure 4.

for soya bean, by far the most studied species, varies from 70,000 per hectare for profusely branched types in Tanzania (Enyi, 1973a) to almost a million per hectare from determinate, poorly branched types in the USA (Wiggans, 1939). Similarly, the optimum population for groundnuts in East Africa varies from about 90,000 for prostrate, alternately branched types, to over 150,000 for erect, sequentially-branched types (Laurence, 1974; Enyi, 1977).

The main reason for this variation in response lies in the fact that legumes which are indeterminate and spreading, yield by the continued production of branches and flowers over a long time period, whereas determinate types do not. The indeterminate types suffer a profligate loss of flowers if there is substantial mutual shading. Density stress does not necessarily hasten or synchronize flowering (cowpea, Erskine and Khan, 1976; groundnuts, Gopalaswamy *et al.*, 1979); so if indeterminate types are planted at high densities they develop few fruiting nodes (because they develop few branches) and, because self-shading occurs early in their development, they develop few flowers per node. Relatively few of these may survive, or develop filled pods, because mutual self-shading increases as the crop grows. Determinate, erect types suffer less of these adverse effects. In both cases mean grain weights remain relatively unaffected.

Cereals and maize (Fig. 5)

Cereals such as wheat, barley, and especially rice (Yoshida, 1972) give similar yields over 2- to 10-fold ranges in planting density, mainly because they can produce variable numbers of tillers to fill the space available. The plant population at which total dry matter production begins to plateau is usually also the population giving within 5 per cent of the greatest grain yield (Donald, 1963; Fischer *et al.*, 1976). For wheat, this plant population is lower for profusely tillering, or dwarf Norin 10 derivatives, grown with large fertilizer inputs in the tropics, than for poorly tillering or tall varieties grown with small application of fertilizer in temperate regions (see Figure 5). The greatest yield seems to occur when the crop growth rate peaks just before spike dry matter accumulation (Fischer *et al.*, 1976). At higher plant populations yields decrease, at least slightly, because mutual shading leads to (i) wasteful tiller self-thinning; (ii) fewer ears being produced per tiller; (iii) leaf senescence; and (iv) a smaller number of grains being produced per ear and per hectare (Puckridge and Donald, 1967; Willey and Holliday, 1971). The harvest index decreases gradually as plant population increases (Donald and Hamblin, 1976)

Fig. 4 (*Opposite*) Effect of planting density on the growth and yield of grain legumes. Soya bean (*Glycine max* L.) from Enyi (1973a) for a cultivar which produced most of its pods on side branches, grown in Tanzania. Cowpea (*Vigna unguiculata* L.) from Erskine and Khan (1976); the means of two bush type cultivars grown in Papua New Guinea. Groundnut (*Arachis hypogaea* L.) from Gopalaswamy *et al.* (1979); a bunch Spanish type cultivar grown on rainfed lands at Tamil Nadu, India. Arrows mark the economic optimum planting density in each case

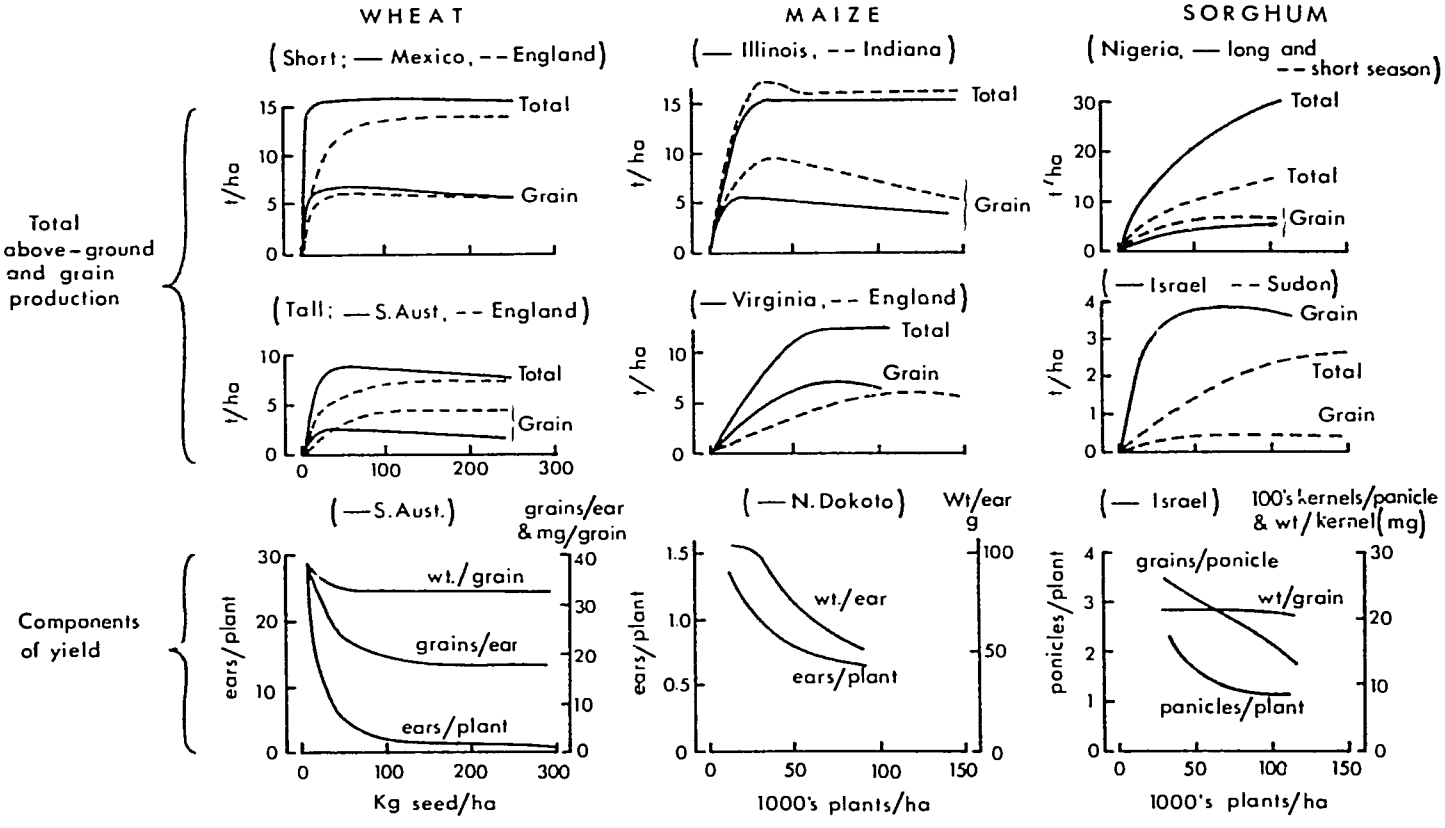

WHEAT
MAIZE
SORGHUM
(Short; — Mexico, -- England)
(— Illinois, -- Indiana)
(Nigeria, — long and -- short season)
Total
Grain
t/ha
Total above-ground and grain production
(Tall; — S.Aust, -- England)
(— Virginia, -- England)
(— Israel -- Sudon)
(—S.Aust.)
grains/ear & mg/grain
(— N.Dokoto)
Wt/ear g
(— Israel)
100's kernels/panicle & wt/kernel (mg)
Components of yield
wt./grain
grains/ear
ears/plant
wt./ear
ears/plant
grains/ponicle
wt/grain
panicles/plant
ponicles/plant
Kg seed/ha
1000's plants/ha
1000's plants/ha

Figure 5.

and at high plant populations net total dry matter production may decrease (Willey and Holliday, 1971).

Sorghum behaves similarly, except that in long-season types the greatest grain yield is obtained at much lower populations than those giving maximum dry matter per hectare.

Maize is somewhat different, because it produces few tillers, and because its inflorescences are held low down on the plant where they are easily shaded. Consequently, maize generally exhibits a more distinct optimum population for yield than other cereals. Mutual shading decreases both the number and size of ears, and the optimum population is lower in countries with high solar radiation receipts than in northwestern Europe (compare USA and England, Figure 5). The search for high yielding hybrid maize varieties has largely been for types which maintain a high harvest index at high plant populations (Bonaparte and Brown, 1975; Donald and Hamblin, 1976).

REFERENCES

Allessi, J. and Power, J.F. (1974). Effects of plant population, row spacing, and relative maturity on dryland corn in the northern plains. I. Corn forage and grain yield. *Agron. J.* 66, 316-319.

Assman, E. (1970). "The Principles of Forest Yield Study". Pergamon Press, Oxford, New York, Toronto and Sydney.

Baskerville, G.L. (1965). Dry matter production in immature balsam fir stands. *For. Sci. Monograph* No.9. 41 pp.

Bleasdale, J.K.A. (1966). Plant growth and crop yield. *Ann. appl. Biol.* 57, 173-182.

Bleasdale, J.K.A. (1967). The relationship between the weight of a plant part and total weight as affected by plant density. *J. hort. Sci.* 42, 51-58.

Fig. 5 (*Opposite*) Effects of planting density on the growth and yield of cereal crops. *Wheat*: short (that is, dwarf and semi-dwarf cultivars derived from Norin 10) spring cultivars growing in Mexico, from Fisher *et al.* (1976, their experiment 8), and a winter cultivar ('Gaines') growing in England, from Thorne and Blacklock (1971, their Table 4); tall cultivars growing in South Australia from Puckridge and Donald (1967) and England from Holliday (1960). 1 kg seed $ha^{-1} \equiv 2$ plants m^{-2}. Yield component data from Puckridge and Donald (1967). *Maize*: data from Illinois for an old cultivar from Morrow and Hunt (1891, quoted by Donald and Hamblin, 1976); Indiana cv. PAGSX29 (Fery and Janick, 1971); Virginia early maturing cv. Va4 (Bryant and Blazer, 1968); England mean of three early maturing hybrids (Milbourn *et al.*, 1978). The yield component data are from North Dakota for early maturing hybrids (Alessi and Power, 1974). *Sorghum*: Nigeria data are for a local long-season cv. Farfara and for the American short-season hybrid NK300 (Goldsworthy and Taylor, 1970). The Israeli data are averages for 2 years and 2 row spacings, for cv. RS610 grown on soil water reserves (Karachi and Rudich, 1966). The Sudanese data refer to unirrigated dwarf cvs 'Wad Akr 51/3' and 'Plainsman' (Gerakis and Tsangarakis, 1969).

Bleasdale, J.K.A. and Thompson, R. (1966). The effects of plant density and pattern of arrangement on the yield of parsnips. *J. hort. Sci.* 41, 371-378.

Bonaparte, E.E.N.A. and Brown, R.I. (1975) The effect of intra-specific competition on the phenotypic plasticity of morphological and agronomic characters of four maize hybrids. *Ann. Bot.* 39, 863-869.

Browning, G. and Fisher, N.M. (1976). High density coffee: yield results for the first cycle from systematic plant spacing designs. *Kenya Coffee* 41, 209-217.

Bryant, H.T. and Blaser, R.E. (1968). Plant constituents of an early and a late corn hybrid as affected by row spacings and plant population. *Agron. J.* 60, 557-559.

Cannell, M.G.R. (1972). Primary production, fruit production and assimilate partition in Arabica coffee: a review. *Ann. Rep. Coff. Res. Stn, Ruiru, Kenya*, pp.6-24.

Cannell, M.G.R. (1975). Crop physiological aspects of coffee bean yield: a review. *J. Coffee Res.* 5, 7-20.

Cannell, M.G.R. (1979). Improving per hectare forest productivity. *In* "Proceedings of 5th North American Forest Biology Workshop" (C.A. Hollis and A.E. Squillace, eds) pp.120-168. University of Florida, Gainsville, USA.

Cannell, M.G.R. and Smith, R.I. (1980). Yields of mini-rotation closely spaced hardwoods in temperate regions: review and appraisal. *For. Sci.* 26, 415-428.

Cock, J.H. (1976). Characteristics of high yielding cassava varieties. *Expl Agric.* 12, 135-143.

Cock, J.H., Wholey, D. and Gutierrez de las Cassas, O. (1977). Effects of spacing on cassava. *Expl Agric.* 13, 289-299.

Corley, R.H.V. (1973). Effects of plant density on growth and yield of oil palm. *Expl Agric.* 9, 169-180.

Cripps, J.E.L., Melville, F. and Nicol, H.I. (1975). The relationship of Granny Smith appletree growth and early cropping to planting density and rectangularity. *J. hort. Sci.* 50, 291-299.

Currah, I.E. and Barnes, A. (1979). Vegetative plant part relationships. I. Effect of time and population density on the shoot and storage root weights of carrot (*Daucus carota* L.). *Ann. Bot.* 43, 475-486.

Donald, C.M. (1963). Competition among crop and pasture plants. *Adv. Agron.* 15, 1-118.

Donald, C.M. and Hamblin, J. (1976). The biological yield and harvest index of cereals as agronomic and plant breeding criteria. *Adv. Agron.* 28, 361-405.

Enyi, B.A.C. (1973a). Effect of plan population on growth and yield of soya bean. *J. agric. Sci. Camb.* 81, 131-138.

Enyi, B.A.C. (1973b). Growth rates of three cassava varieties (*Manihot esculenta* Crantz) under varying population densities. *J. agric. Sci. Camb.* 81, 15-28.

Enyi, B.A.C. (1977). Physiology of grain yield in groundnuts (*Arachis hypogea*). *Expl Agric.* 13, 101-110.

Erskine, W. and Khan, T.N. (1976). Effects of spacing on cowpea genotypes in Papua New Guinea. *Expl Agric.* 12, 401-410.

Fery, R.L. and Janick, J. (1971). Response of corn (*Zea mays* L.) to population pressure. *Crop Sci.* 11, 220-224.

Fischer, R.A., I. Aquilar, M., R. Maurer, O. and S. Rivar, A.

(1976). Density and row spacing effects on irrigated short wheats at low latitude. *J. agric. Sci. Camb.* 87, 137-147.

Frappell, B.D. (1973). Plant spacing of onions. *J. hort. Sci.* 48, 19-28.

Gerakis, P.A. and Tsangarakis, C.Z. (1969). Response of sorghum, sesame, and groundnuts to plant population density in the Central Sudan. *Agron. J.* 61, 872-875.

Godfrey Sam-Aggrey, W. (1978). Effects of plant population on sole-crop cassava in Sierra Leone. *Expl Agric.* 14, 239-244.

Goldsworthy, P.R. and Taylor, R.S. (1970). The effect of plant spacing on grain yield of tall and short sorghum in Nigeria. *J. agric. Sci. Camb.* 74, 1-10.

Gopalaswamy, N., Elangovan, R. and Rajah, C. (1979). Agronomic and economic optimum plant densities for rainfed groundnut. *Indian J. agric. Sci.* 49, 17-21.

Hamilton, G.J. and Christie, J.M. (1974). Influence of spacing on crop characteristics and yield. *For. Comm. Bull.* 52. HMSO, UK.

Harper, J.L. (1977). "Population Biology of Plants". Academic Press, London, New York and San Francisco.

Holliday, R. (1960). Plant population and crop yield: part I. *Field Crop Abstracts* 13, 159-167.

Hozumi, K. and Ueno, Y. (1954). Spacing experiments on the growth of root vegetables. *Mem. Coll. Agric. Kyoto Univ.* 10 (*Hort. Ser.* No.3), pp. 1-20.

Ifenkwe, O.P. and Allen, E.J. (1978a). Effects of row width and planting density on growth and yield of two maincrop potato varieties. I. Plant morphology and dry matter accumulation. *J. agric. Sci. Camb.* 91, 265-278.

Ifenkwe, O.P. and Allen, E.J. (1978b). Effects of row width and planting density on growth and yield of two maincrop potato varieties. II. Number of tubers, total and graded yield and their relationships with above-ground stem densities. *J. agric. Sci. Camb.* 91, 279-289.

Karachi, Z. and Rudich, Y. (1966). Effects of row width and seedling spacing on yield and its components in grain sorghum grown under dryland conditions. *Agron. J.* 58, 602-604.

Kuguru, F.M., Fisher, N.M., Browning, G. and Mitchell, H.W. (1977). The effect of tree density on yield and some yield components of Arabica coffee in Kenya. *Coffee Res. Stn, Ruiru, Kenya.* Mimeo.

Laurence, R.C.N. (1974). Population and spacing studies with Malawian groundnut cultivars. *Expl Agric.* 10, 177-184.

Milbourn, G.M., Tiley, G.E.D. and Carr, M.K.V. (1978). Plant density for grain maize in southeast England. *Expl Agric.* 14, 261-268.

Morrow, C.E. and Hunt, T.F. (1891). Effect of plant population on the corn yields. *Ill. Agr. Expt Sta. Bull.* No.13.

Puckridge, D.W. and Donald, C.M. (1967). Competition among wheat plants sown at a wide range of densities. *Aust. J. agric. Res.* 18, 193-211.

Salter, P.J., Currah, I.E. and Fellows, J.R. (1979). The effects of plant density, spatial arrangement and time of harvest on yield and root size in carrots. *J. agric. Sci. Camb.* 93, 431-440.

Thorne, G.N. and Blacklock, J.C. (1971). Effects of plant density

and nitrogen fertilizer on growth and yield of short varieties of wheat derived from Norin 10. *Ann. appl. Biol.* 78, 93-111.

Verheij, E.W.M. (1968). Yield-density relationships in apple: results of a planting system experiment in Hungary. *Inst. voor Tuinbouwtechniek, Wageningen* 37, 1-31.

Westwood, M.N. and Roberts, A.N. (1970). The relationship between trunk cross-sectional area and weight of appletrees. *J. Am. Soc. hort. Sci.* 95, 28-30.

Wiggans, R.G. (1939). The influence of space and arrangement on the production of soyabean plants. *J. Amer. Soc. Agron.* 31, 314-321.

Willey, R.W. and Heath, S.B. (1969). The quantitative relationships between plant population and crop yield. *Adv. Agron.* 21, 281-321.

Willey, R.W. and Holliday, R. (1971). Plant population, shading, and thinning studies in wheat. *J. agric. Sci. Camb.* 77, 453-461.

Williams, C.N. (1972). Growth and productivity of tapioca (*Manihot utilissima*). III. Crop ratio, spacing and yield. *Expl Agric.* 8, 15-23.

Yoshida, S. (1972). Physiological aspects of grain yield. *Ann. Rev. Plant Physiol.* 23, 437-464.

See previous paper for DISCUSSION.

PHENOLOGY OF TROPICAL WOODY PERENNIALS AND SEASONAL CROP PLANTS WITH REFERENCE TO THEIR MANAGEMENT IN AGROFORESTRY SYSTEMS

P.A. HUXLEY
International Council for Research in Agroforestry,
Nairobi, Kenya.

ABSTRACT. Adapted plant species should be 'matched' in agroforestry so that they complement one another in their time dependence for environmental and management resource sharing. A knowledge of phenological mechanisms and responses has, therefore, considerable practical value.

With tropical woody species the onset of rest may be decided, primarily, by the ageing of leaves. It will thus be regulated by *any* environmental or endogenous stresses that hasten leaf senescence: for example by drought or by fruiting. With such a system renewed vegetative growth can then be centred on times when the environment best suits it, and a generalized growth regulating mechanism of this type is well adapted to the vagaries of tropical climates. It does not preclude additional specific regulation through, for example, photoperiodic control. Tropical herbaceous crop species, or cultivars, need to be selected for particular growing seasons and with special reference to the water budget and to day and night temperatues. Cotton, maize and cowpea are given as examples. Matching the woody and herbaceous components is the final stage of finding effective plant combinations.

Recording plant phenophases in relation to environmental change in the natural, indigenous state is easily accomplished; it provides information about adaptability, as well as possible phenological complementarity. Once genotypes are chosen the next most important concern is plant manipulation and how this modifies phenology. For woody perennials manipulations are limited to relatively few processes; removal of plant parts at appropriate times in order to entrain subsequent phases of growth and flowering is likely to be the most effective. For herbaceous annuals time-of-sowing is the most influential time-related procedure. The need for more information about juvenility - maturity - ageing sequences, and about 'below-ground' phenology for the wide range of multipurpose tree species being used in agroforestry is noted. All agroforestry field research should include simple plant phenological studies wherever possible.

INTRODUCTION

Phenology is the descriptive study of the behavioural characteristics of organisms in relation to their environment. Phenometry being the quantitative measure of life cycles or specific phenophases. Their value with regard to ecosystems analysis lies particularly in the understanding they provide of plant responses to climate (Lieth, 1970, 1974).

Stone Age man was a good practising phenologist — he had to be in order to gather plant products effectively, and to know where and when the animals he hunted would be feeding. For more modern land users a knowledge of phenological relationships also affords the opportunity to select plant genotypes and management practices in a way which will optimize plant productivity, and/or obtain particular products from the land at the time of season at which they are required.

When plants of different kinds grow together the effective sharing of environmental resources depends on both their spatial and temporal patterns of distribution and actitivy. The spatial relationships have been dealt with in detail by Cannell (see p. 489, this volume). My contribution deals with temporal relationships, but it is not intended as an in-depth review of tropical plant phenology as such (for example, see extensive references in Alvim, 1964; Huxley and Van Eck, 1974; Lieth, 1974; Whitmore, 1975; Borchert, 1976; Alvim and Alvim, 1978; Hallé *et al.*, 1978; Putz, 1979). It is, rather, a summary of some relevant aspects which are briefly related to the design and management of agroforestry land use systems in the tropics and subtropics.

THE BACKGROUND

Different plant species have evolved a wide range of behavioural strategies to enable them to occupy various ecological niches in all kinds of climates. However, in over 200 years of continuing investigations on climate and plant productivity it is only recently that our knowledge of the effects of individual climatic factors on particular plant processes has taken a significant step forward (for example see Rees *et al.*, 1972; Evans, 1975; Monteith, 1975; Cannell and Last, 1976; Alvim and Kozlowski, 1977; Goodall *et al.*, 1979). Much remains to be learnt, however, especially concerning the interactions of climatic factors (see also Kozlowski and Huxley, this volume), and the effects of climatic 'noise'. There is also a dearth of specific information for hundreds of useful species, including many of the multipurpose trees which can be valuable in agroforestry systems.

The tropics and subtropics are exciting places in which to study phenology because of the very wide range of climatic zones which exist, involving aseasonal, wet tropics to highly-seasonal, semiarid and arid regions, with either winter or summer rainfall and a variety of temperature regimes. These provide a complex climatic matrix within which to investigate the behaviour of vegetation or of particular component species. Climatic complexity is increased further by the large season-to-season variations which often exist, as well as the wide range of topoclimatic changes which may occur within a comparatively short distance in broken or undulating land (Huxley and Beadle, 1964).

Against this background it is not surprising that a number of different hypotheses have arisen to account for the recorded behavioural responses of tropical vegetation to changes in particular climatic variables — especially with regard to tropical trees. In the next section I want first to summarize these.

TROPICAL TREES AND SHRUBS: PHENOLOGICAL TACTICS FOR ENVIRONMENTAL STRATEGIES

Exogenous/endogenous controls

Some degree of vegetative growth regulation is a feature of many ligneous tropical species. The initiation of growth has been attributed to the occurrence of rain (Richards, 1952; Holttum, 1953), an increase in air temperature (Murray, 1961; Sale, 1970) or an increase in the level of incoming solar radiation (Alvim, 1964), a decrease in air temperature followed by a rise (Jeffers and Boaler, 1966), and to fire (Hopkins, 1970b). As well as to combinations of these factors which, in any case, are sometimes confounded. The onset of rest has been attributed also to numerous climatic factors. For example, to seasonal drought (Koriba, 1958; Alvim, 1964; Hopkins, 1970a, b), low atmospheric humidity (Wright, 1905), photoperiod (Njoku, 1964; Longman, 1969; Hopkins, 1970a, b) and thermoperiodism — more particularly low night temperatures (Longman, 1969).

Many early workers, in addition to evoking exogenous 'cues' for particular growth and development phenomena, pointed to the apparent existence of endogenous rhythms in tropical woody perennial species (Richards, 1952). A premise which we know, from experimental work in uniform environmental conditions, to be valid (for example, Greathouse *et al.*, 1971, with cacao). Models of plant growth have since been proposed (Thornley, 1972a, b; Borchert, 1973) which would result in such rhythms, based on feedback mechanisms between shoots and roots. Finally, the dependence of many species on photoperiod to promote flowering, even within the relatively small daylength changes which occur in tropical regions, is very well documented (for example, Vince-Prue, 1975).

A flexible strategy for the tropics

What we have been outlining up to now are the tactics which plants adopt to achieve particular adaptive life strategies, that is patterns of growth and development which enable them to survive and to retain their share of resources in association with other plant species. To be successful in many tropical regions with year-to-year climatic variations, these strategies may best depend on alternative sets of tactics. Or at least not be too inflexible if the timing of growth and flowering is to be optimally adjusted to tropical climatic vagaries. Huxley and Van Eck (1974) suggested that such a scheme is fulfilled if there is a general underlying control of vegetative growth which is regulated by the physiological ageing of the leaf canopy as influenced by *any* environmental stress factor, as well as by endogenous factors. Effectively this will regulate the activity of shoot apices by controlling the balance of growth promoting and growth retarding hormones (Borchert, 1978). After the onset of

rest, renewed growth may depend, at least for some species, on no more than the occurrence of the next set of favourable climatic circumstances. This sequence will tend to centre periods of maximum vegetative growth on times when the environment best suits it, either for individual species (see details in Huxley and Van Eck, 1974) or for the woody vegetation as a whole (Fig. 1).

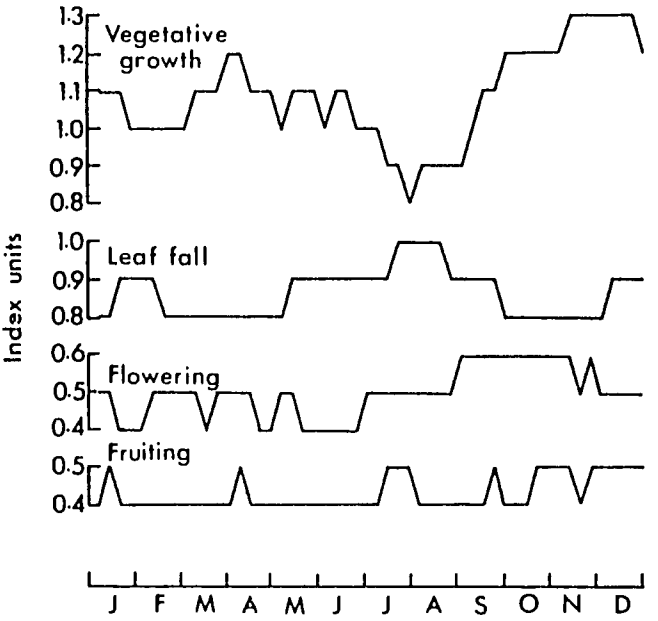


Fig. 1. Overall seasonal trends in vegetative growth, leaf fall, flowering and fruiting of woody perennial species near Kampala, Uganda. Mean values of all recorded specimens from Huxley and Van Eck (1974). The phenology of individual species varied considerably even to the extent of different specimens being out of phase with one another (see original paper for details).

Such a generalized scheme in no way precludes further regulation by additional mechanisms involving specific environmental requirements. For example, daylength (*Hildegardia barteri*, Njoku, 1964) or relief of high plant water potentials (*Coffea arabica*, Browning, 1973).

Many tropical and subtropical species of trees and shrubs flower on current season's wood, and subsequent fruit development is, therefore, supported by a relatively fresh canopy of photosynthetically active leaves. The exhaustion of the plant's carbohydrate and nutrient reserves during fruit maturation will itself then bring on leaf senescence; a sequence which 'entrains' the subsequent cycles of vegetative growth and fruiting (for example, in coffee, Cannell, 1971).

Manipulating woody plants in tropical climates so as to optimize production through 'entrainment' is one of the most demanding of management techniques, and one which is very relevant to the proper use of trees and shrubs in agroforestry systems.

Evergreen/deciduous habits

What has been said above helps us to relate the behaviour of widely distributed woody species which, according to the climatic stress imposed, may appear evergreen in one ecozone but semi-deciduous, or fully deciduous, in another. The same applies to individuals of species situated in the same ecozone but at different sites, and, in some cases, for example mango, even to parts of the same tree.

The coincidence in any particular zone of species which adopt an evergreen strategy, and others which are deciduous, is commonplace (Ellenburg, 1979) and, where it does occur, must be the evolutionary outcome of many physiological factors. For example, in Mediterranean-type climates both drought deciduous and sclerophyllous evergreen species coexist, depending in part, it has been suggested, on the net carbon economy for individual species of either shedding and regrowing a leafy canopy, as compared with sustaining the respiratory load through the unfavourable season (Mooney and Dunn, 1970).

If we are going to introduce new woody agroforestry species it will clearly pay to study their phenology in their natural habitats and compare this with what happens in new ones. This takes a little time but it will well repay the effort. There is now, for example, growing literature on jojoba phenology (*Simmondsia chinensis*) (Humphrey, 1975; Haase, 1976; Brooks, 1978a, b; Forti, 1978; Hogan, 1979) which can help provide guidance in choosing suitable zones for this interesting new crop species.

HERBACEOUS SEASONAL PLANTS

Entrainment of growth and development so as to take advantage of favourable climatic periods is much simpler with herbaceous seasonal plants. In the natural state this is often resolved initially by some form of growth regulation imposed through the seed (Roberts, 1972). As this creates difficulties for the farmer such seed dormancy mechanisms have, in the main, been eliminated by plant breeders for the major agricultural crops; although foresters often still have to contend with them

In order to maximize productivity at any particular level of inputs, and in any chosen place, appropriate cultivars of any crop species must be selected so as to match closely the environmental resources available throughout the growing season. Thus the overall and specific characteristics of the climate must fit the plants' requirements for germination, early seedling growth, branching and development of main vegetative structures, flowering and fruit growth and maturation. Of course, this applies to trees and shrubs also, but a key difference is the greater management flexibility for herbaceous crops which manipulation of time of sowing allows. Changing the plant population is also a powerful management tool which is more flexibly and cheaply applied to herbaceous crops, but this is dealt with by Cannell elsewhere in the volume (see p.489).

There is only room here to select three examples from the considerable work which has been done on tropical crops. Cotton is chosen to illustrate a relatively limited but useful approach to climatic fit; maize, because there has been a particular

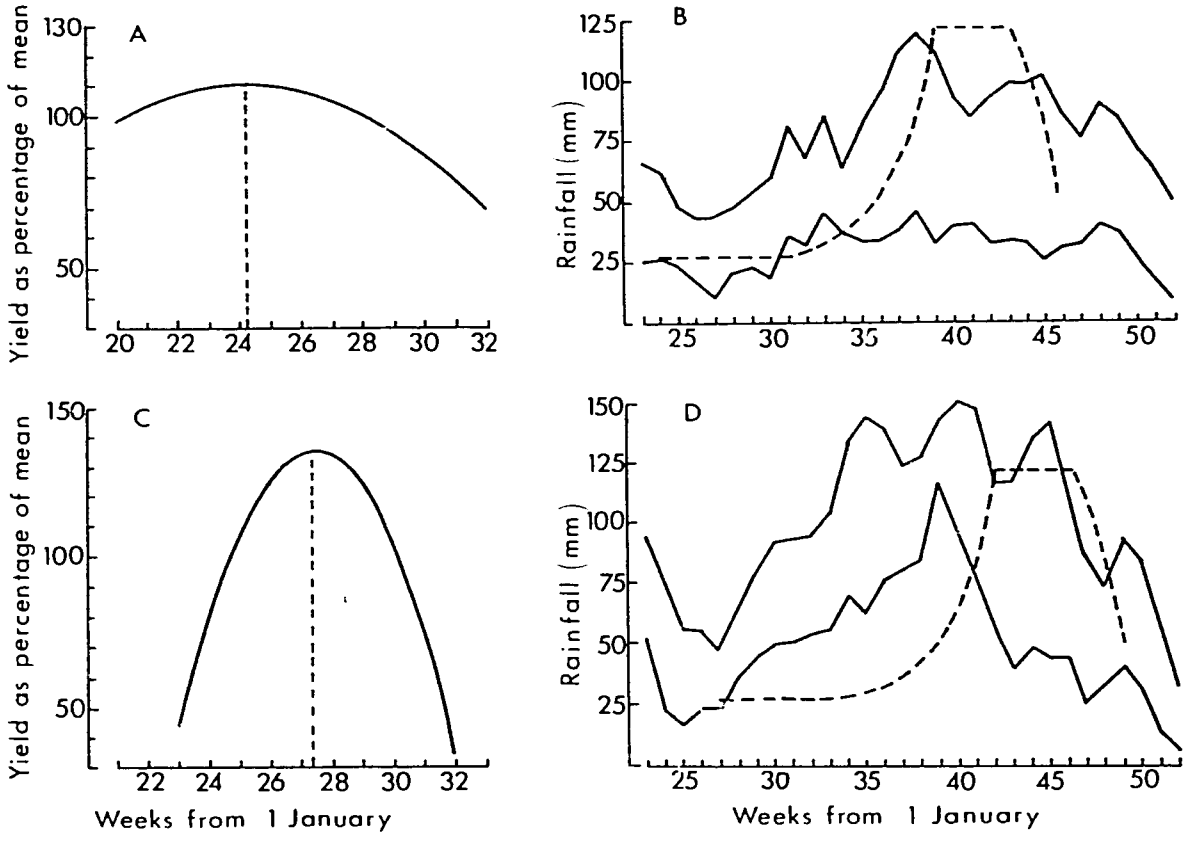

A
B
C
D
Yield as percentage of mean
Rainfall (mm)
Weeks from 1 January
130
100
50
150
125
75
25
20
22
24
26
28
30
32
35
40
45

Figure 2.

problem to resolve (late planting yield loss); and cowpea, to note the very detailed studies of the climatic factors affecting all stages of growth and development which need to be investigated, through both field and controlled environment studies, if a thorough understanding of the effects of climate are to be achieved.

Cotton and water availability

The classical work done at Namulonge, Uganda, during the 1950s to relate cotton growth and development with water use and availability is a well-known example of matching a crop's needs to a major climatic factor (water), using a stochastic approach (Rijks, 1967).

Rijks defined the optimum sowing date, or period, as the time during which a crop must be sown in order to be likely to experience the most favourable combination of factors that are relevant in obtaining maximum yield. In agroforestry the complex of factors involved must of course also include the interactions — biological and managemental — with one or more woody perennials and, perhaps, with other crop species. In fact, no single environmental factor decides yield and even if the rainfall/evaporation regime is seen as a major influence, there are others of considerable significance. For example, with cotton, the incidence of pests and diseases and the effect of climate on these is always a crucial issue; and solar radiation and the temperature regime are clearly important, even though they have been less well studied.

Figure 2 shows, from some of the earlier work, how yield and the water regime were related at two specific sites; presenting the data in such a way that the probability of receiving rainfall at these sites is clearly brought out. The result of this work, by the then Empire Cotton Growing Corporation, enabled cotton breeders and agronomists to select cultivars for particular climatic areas with much more precision and understanding then would otherwise have been the case.

Maize and heat units

Maize provides another good example of a crop species where yield is highly dependent on timely sowing, as numerous field studies have shown (Cooper, 1975). Indeed, this restraint is commonly found with many long-season tropical crops grown under summer rainfall regimes. With maize, at least, this is partly due to the plants' needs for continuous, relatively high, ambient air temperatures, and partly due to the adverse effects of cool soil temperatures, especially in the seedling stage (Cooper, 1979).

Fig. 2 (Opposite) Change in yield with change in sowing date and rainfall pattern at a station with unreliable (Kawanda) and reliable (Bulindi) second rains. A - yield and sowing date for Kawanda. B - 1:1 confidence limits of rainfall at Kawanda during the cotton season and estimated crop water requirement (broken line). C - as A, for Bulindi. D - as B, for Bulindi. After Manning, unpublished. From Rijks (1967).

Growth, development and maturation of maize have been found to be broadly correlated, for any particular cultivar, with the number of 'heat units' received. In view of the complex relationships between climatic factors and plant growth and development which detailed investigations invariably uncover (see cowpea, below), it seems remarkable that the relatively simple integration with time of mean temperature above a base can provide a means for predicting the duration of various stages of plant development and the time to final maturation. Even more so when it is clear that in tropical areas the heat balance is very variably correlated with incoming solar radiation, because this relationship depends on the weather in the previous period and factors affecting net radiation and its partition into sensible heat and evapotranspiration (Huxley, 1973). Nevertheless, for maize and other crops, agriculturists do find the heat unit concept a useful albeit somewhat crude tool, and it has been the subject of much evaluation (Arnold, 1959; Wang, 1960; Allison, 1963; Brown, 1963, 1969; Dijkhuis, 1971; Caprio, 1974; Carr, 1977).

Measuring the integration of temperature with time can be both cheap and efficient, for example by using the sucrose inversion technique (Berthet, 1960; Lee, 1969; Jones, 1972) with, perhaps, a 'roving' statistical sampling as suggested by Wilm (Rieley *et al.*, 1969). There is much to be said for such a pragmatic approach to measurements in predictive phenology and we need to simplify techniques and adapt them to be less costly.

In agroforestry the effect of the trees or shrubs on the environment of the associated agricultural crop species can be highly relevant. Changes in soil temperature being a case in point. However, each situation has to be considered carefully. For example, although low soil temperatures can be detrimental to the early growth stages of maize, with soya and other grain legumes unduly high soil temperatures at germination are to be avoided (Singh, 1975). The situation in any agroforestry system will be complex, and it requires detailed study in relation to time of season and the stage of growth of accompanying crops, using all the available information that can be gleaned from the literature.

Cowpea and integrated climatic response

Extensive studies both in the field and in controlled environments have contributed to our knowledge of phenological responses to climatic factors for this species. It provides a good example of the value of combining these two experimental approaches (see Kozlowski and Huxley, this volume). Yield potential in cowpea, as with other grain legumes, is critically affected both by the development of the plant's vegetative structure and the initiation, growth and maturation, at the appropriate times, and for the optimum duration, of the reproductive elements. These processes are markedly affected by daylength, day temperature and night temperature (Huxley and Summerfield, 1976) (see Figure 3).

Daylengths below the critical will shorten the vegetative phase of the plant affecting adversely the potential number of fruiting points which can develop; warm day temperatures can increase vegetative growth in the period up to flower initiation

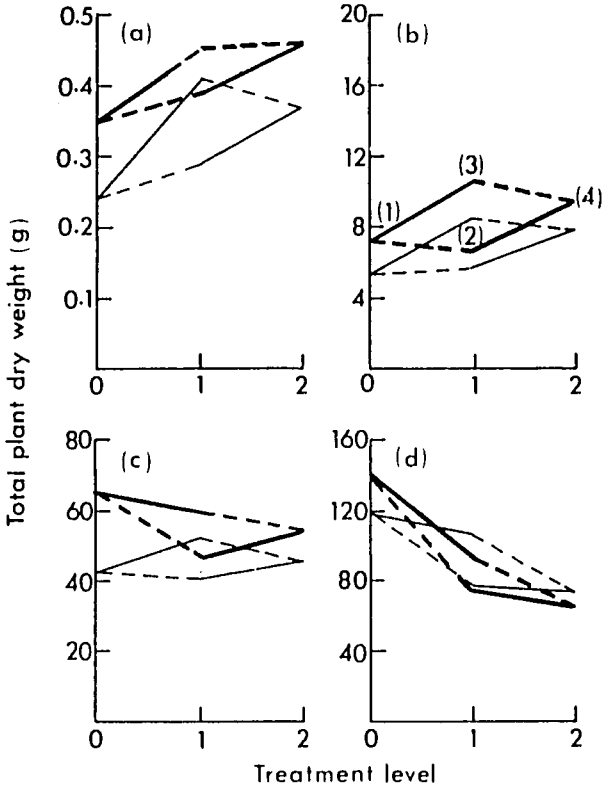


Fig. 3. Effects of treatments on dry matter production (g plant^{-1}) of cowpea cv. K 2809 at various stages of growth. (*a*) and (*b*) - Pre-flowering 11 and 25 days after sowing. (*c*) - Early/mid podfill 47 days after sowing. (*d*) - Final harvest 77 to 105 days after sowing. In these interaction diagrams the solid thick lines represent the effect of raising the night temperature (——) and dashes that of raising the day temperature (---) in the 13 h 20 daylength. Equivalent thin lines represent these effects in the 11 h 40 daylength, thus the relative positions of the various day - night temperature combinations (°C) are denoted by (1) for 27-19, (2) for 33-19, (3) for 27-24 and (4) for 33-24, as indicated in (*b*). From Huxley and Summerfield (1976). This was one of the early, significant results of a programme initiated by P.A. Huxley and the late A.P. Hughes in 1971 at the Plant Environment Laboratory (PEL), University of Reading, UK, (funded by the British Overseas Development Ministry), which has subsequently expanded to cover investigations on the climatic responses and the nitrogen nutrition of several grain legume species. Readers interested should write direct to the PEL.

but also shorten the period of seed maturation; warm night temperatures can reduce the period to flower initiation. Further work (for example, Stewart *et al.*, 1980) has helped to explain the detailed effects of climate on flower and fruit development. Warm days can reduce the number of nodes at which peduncles are

formed, they increase the number of peduncles aborting or growing poorly, as well as the number of flowers and pods which abscise. Cool nights following warm days increase flower abscission, but cool days followed by cool nights enhance flower retention.

Resolving the climatic needs for all the complex stages of growth and development of plants as complicated as the grain legumes, in which nitrogen supply is additionally dependent on a symbiotic association and interaction with rhizobium may seem a hopeless task. But the results of a combined approach of laboratory, controlled environment and field work has now enabled us to determine the pattern of programming and response for this group of plants to a point where it is feasible to fit the species and cultivars so far investigated to specific environments and production systems. Or, conversely, to arrive at reasoned explanations for their climate-related success or failure on any one site, or in any one season (Summerfield and Bunting, 1981). This type of detailed knowledge will clearly not be available for all but a few of the species of interest, but whenever such information can be obtained it will help to make the design of agroforestry systems infinitely more precise, their management more rational, and the outcome more predictable.

The agroforestry situation

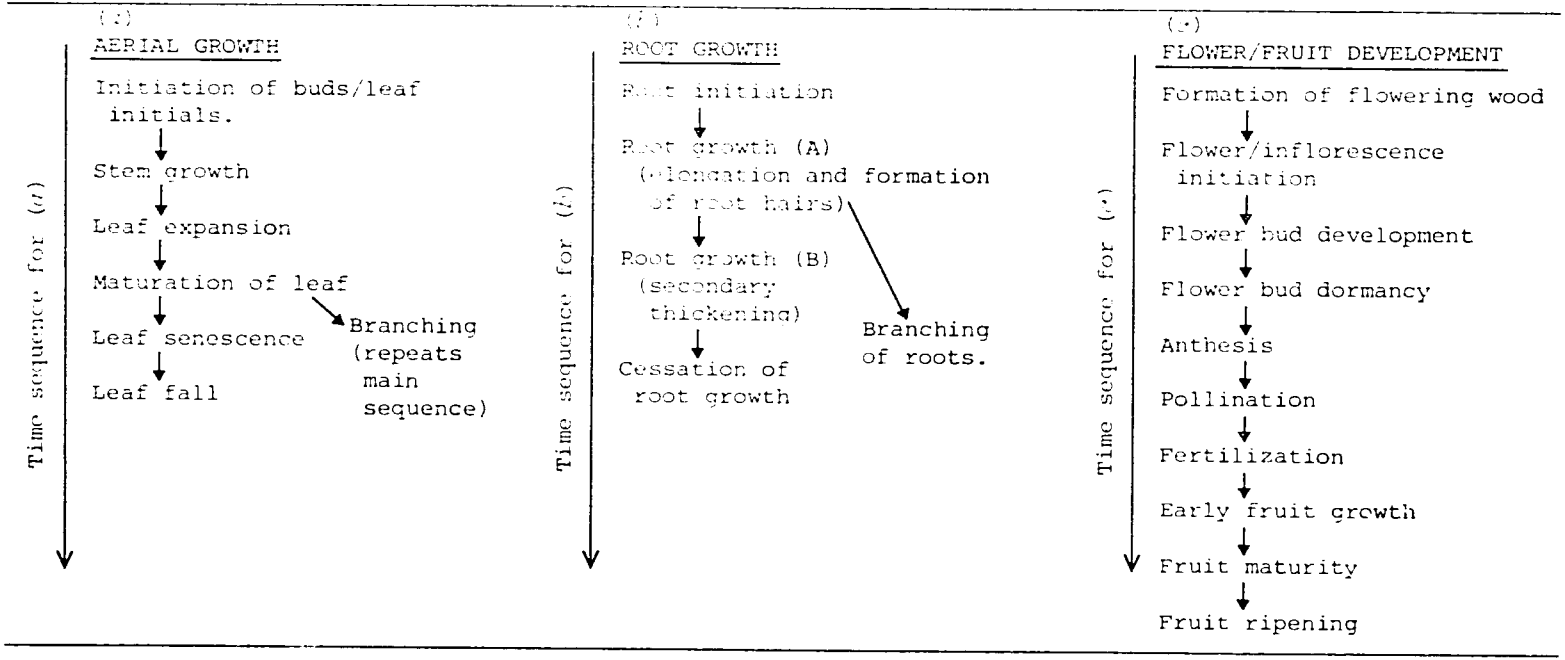
These three examples — cotton, maize, and cowpea — illustrate, in increasing detail, how complex the many stages of growth and development are and, in no small measure, the reason why in the field it is often far from easy to explain the gross effects of weather. Furthermore, the *time* at which environmental changes are imposed is, in many cases, critical in relation to particular development phases of the plant. Thus the complex environmental interrelationships affecting the phenology of the woody and herbaceous species in an agroforestry mixture will not always be easy to identify or to quantify. Nevertheless, as our knowledge of the influence of one agroforestry plant component on another builds up, through tree/crop interface studies, a useful level of prediction is likely.

One other point. Many of our most successful crop plant selections are not just those well adapted to grow, flower and fruit vigorously in any particular climate but probably, also, those less likely to suffer from environmental stress. For example, with cowpea growth cabinet studies have shown that, in terms of overall seed yield, some cowpea cultivars are insensitive to daylength changes, or to night temperatures, or to both (Huxley and Summerfield, 1976; Summerfield and Wien, 1979). Cultivars of herbaceous crop plants which are high yielding but have a small genotype × environment interaction (G × E) could, perhaps, be the safest choice for agroforestry systems, particularly where marked temporal microenvironmental changes are likely to be imposed on the lower storeys.

THE VALUE OF STUDYING NATURAL PHENOLOGICAL STATES

Plant phenological studies can be of the simplest kind, involving only a series of observations of the plant accompanied by meteorological and soil data (soil water status and soil temperatures, if possible). Obviously more sophisticated measurements

Table 1. Although completely interdependent (a) aerial growth, (b) root growth, and (c) flower and fruit development can usefully be considered as each progressing through separate steps of phenophases. These will occupy different real-time periods and sequences will overlap. In agroforestry phenological complementarity involving the tree/agricultural crops implies optimizing the sharing of environmental resources throughout the growing season so that minimum stress is imposed on any plant component at critical stages of its growth and development as represented by the steps listed.



can be made to help elucidate specific plant responses. For example, one might wish to check plant water potentials, or bud temperatures, and so on. For the current level of agroforestry research a weekly or fortnightly record of the state of vegetative growth (shoot growth occurring or not), leaf fall, flowering, the presence of fruit and whether or not root extension is occurring in the topsoil, may well be sufficient. Table 1 gives a more complete list of phenophases and it serves also to remind us of the complex and parallel series of steps which have all to be completed for any plant to achieve maturity.

There is a very extensive literature relating types of tropical vegetation to particular climates (e.g. Ellenburg and Mueller-Dombois, 1967; Walter, 1973, 1977) and, apart from hot, wet, aseasonal climates, a rather important division needs to be made between climates with rain during the cool season, and those receiving mono- or bimodal rainfall in the hottest part of the year; either as a consequence of a true monsoon-type air circulation, or through the north-south transition of a convergence zone (winter or summer rainfall climates). This is because a considerable body of evidence suggests that perennial woody species, and grasses from these two types of climate may often possess somewhat different growth regulation syndromes.

Woody species adapted to winter rainfall regions have often developed a vegetative growth regulation mechanism which is broken, naturally, by a greater or lesser amount of winter chilling. Chemical means (for example, using di-nitro ortho-cresol), or end-of-season defoliation can sometimes achieve the same effect (see Ruck, 1975 for fruit trees). Moving such species to summer rainfall areas may, obviously, bring problems. Some of our promising species of multipurpose trees (for example, *Ceratonia siliqua*, *Brosimum alicastrum*) originate in winter rainfall areas and this should be taken into account when including them in trials in summer rainfall climates. Some simple comparative phenology should quickly indicate whether there are any difficulties.

The reverse process of moving summer rainfall species to winter rainfall areas involves less a problem of growth regulating mechanisms than of achieving optimum temperatures for carbon fixation, distribution and utilization during the time of available water supply.

Some tree species useful in agroforestry appear to be very widely adapted. For example, species of *Acacia* such as *A. tortilis*, see Kazmi (1979), or *A. albida*, see Halevy (1971); *Ficus benjamina*, *Schinus molle*, *Grevillea robusta*, and some *Eucalyptus* species, see Food and Agriculture Organization (1976), to name but a few. Foresters are well versed in 'provenance testing' but appropriate selection procedures for multipurpose species to be used in agroforestry should be carefully borne in mind, and some evaluation of the genetic fitness or flexibility of different species needs to be undertaken. The separation of genetically and environmentally induced phenological responses is critical (Flint, 1974), but work on potential agroforestry tree components is not well advanced and only fragments of information are available (for example, Peacock and McMillan (1965) for American *Prosopis* and *Acacia*, and Halevy (1971) for *Acacia albida* in Israel).

In such investigations not all woody species will show obvious indications of non-adaptability in the form of an out-of-sequence vegetative dormancy or growth flush, but their phenological behaviour may still provide some evidence of unsuitability. For example, an increase in frequency of growth flushes (for cacao, Sale, 1970) is just such an indicator. As may be early leaf senescence/leaf fall, early or intermittent flowering/fruiting, and either premature or unduly delayed fruit maturation. All that is needed to obtain such data is a carefully conducted set of field observations and some meteorological data. If the phenology of a woody species is carefully studied in relation to the climate in its area of natural distribution some useful pointers immediately become available as to its management in other, supposedly suitable climatic zones.

PHENOLOGY AND PLANT MANAGEMENT IN AGROFORESTRY SYSTEMS

Phenological complementarity

Much of what has been said so far has emphasized the importance of the behaviour of the woody component in an agroforestry system. Because at maturity these are, almost invariably, the dominant partners in an intercropping situation with herbaceous crops the selection of appropriate genotypes is a crucial one. This choice, with an eye both to possible resource sharing capabilities as well as the potential for microsite enrichment and environmental amelioration is, clearly, the first management consideration once production outputs have been decided upon.

The choice of an agricultural crop is, in practice, likely to be limited to that which the local population, or established markets, require. But within these limitations, phenological compatibility can be sought. The important variables being the length of the growing season, the time of sowing in relation to the environmental resources likely to be available, and the natural phenophases and/or potential management treatments (such as lopping) of the trees and shrubs. The various kinds of temporal relationships which can occur (crop sequences) are set out in Figure 2 of the paper 'Comments on agroforestry classification: with special reference to plant aspects' (see p.161, this volume).

Some tree species, for example *Acacia albida*, produce a leafy canopy *prior* to the onset of rains and lose these leaves during the early part of the rainy season (Felker, 1978). This enables crops such as millet and groundnuts to be grown around or even beneath the trees, where they can derive benefit from top soil microenrichment, but environmental resource sharing is otherwise separated in time. This almost complete temporal separation of growth periods is an ideal one, but there are probably only limited opportunities to modify the natural phenology of most woody species to any extent through management practices in order to simulate this.

Optimum yield of vegetative parts will be obtained if flowering and fruiting are avoided. For example, the usable yield of *Leucaena leucocephala* (fodder, fuelwood) could, perhaps, be increased by some 20 to 30 per cent if sterile or scantily-fruiting cultivars could be found. However, to maximize total yield, including fruits and seeds, it is necessary to optimize early

vegetative growth and synchronize the time at which adequate numbers of relevant sinks are created (that is for carbon, nutrients and hormones) in relation to the development of the appropriate sources. This can be done only within the limits of genetic control, and by a limited number of management practices. The first requirement is an appraisal of the 'natural' phenology of the various plant components in the system, the second a stochastic analysis of the extent of between-season climatic variability, the third is an understanding of the degree to which various management practices can affect particular phenophases in the species concerned, and the fourth a knowledge of species interaction. At this stage trying to optimize source/sink relationships in the individual species in agroforestry mixtures, by simple deflowering/defruiting, or by lopping vegetative parts at carefully chosen times, is probably all that can be done.

A major feature of management in agroforestry must be to maintain the appropriate balance between output of products from the woody and herbaceous components. To do this the population and arrangement of woody plants has to be chosen with the future management of the trees/shrubs firmly in mind. The capacity of the chosen woody species to tolerate pruning, lopping, pollarding and browsing, or some other form of removal of leafy twigs or leaves, is fundamental to this. Here the question is not only what to remove, and how much, but when? Removal of apical buds from deciduous trees/shrubs which show some form of growth regulation will interrupt natural growth phases least if it is done just prior to a growth extension phase. And the same applies to evergreen species. Such removal of apical dominance during a rest phase can, depending on the species and the timing, bring about renewed growth, although shoot removal in a severely dry season can sometimes result in branch dieback. Species will differ considerably in their response to this treatment depending on the environment they are in, and simple but extensive field tests are necessary. Cultivators of our major tropical woody perennial fruit and beverage crops are well aware of the optimum season for pruning, according to their particular climatic expectations, but this has been optimized only after a good deal of research (for example for tea, Carr, 1972; coffee, Maestri and Santas Baros, 1977).

Removal of leafy shoots or leaves (particularly old ones, Browning, 1973) during a natural vegetative growth period may sometimes help extend the period during which a tree or shrub maintains shoot extension and hence a greater proportion of actively photosynthesizing canopy. Alleviating stress by irrigating and/or applying fertilizers, particularly nitrogen, can also do this.

All these management procedures demand increased inputs, however. Either in terms of skills, or materials. And results depend very much on the timeliness of application. Woody plants can sometimes be grown successfully completely outside their normal climatic range providing sufficiently skilled management is applied. A good example of this is the vine. Cultivars differ but in its natural habitat in Europe or America it is subjected to winter rainfall and winter chilling, and the dormancy of the apical bud in each bud series is broken by a period of cold. Fruiting then occurs on the lateral leafy shoots arising from

these apical buds. In summer rainfall tropical regions fruiting can be brought about on the shoots arising from lateral buds in the axillary series, if apical dominance is removed by pinching out shoot tips (Shalitin, 1973). Such complex management procedures are unlikely to be of much use in handling multipurpose trees in low input agroforestry systems, however.

Long-term changes

The changes which occur in woody plants over the longer term have also to be considered. That is, the changes from juvenility to maturity and, finally, to various stages of ageing. Borchert (1976) points out that the various aspects of physiological ageing can best be understood by considering them as consequences of the increasing complexity which arises when viewing the tree as a growing system.

Although the onset of flowering in herbaceous plants is related to early growth rate (number of leaves), the extent of the juvenile phase in woody perennials can, in practice, be unduly delayed by such practices as early pruning or an excessive supply of nitrogen. Some degree of environmental stress is therefore likely to promote early flowering. The process of ageing in plants in general (Wareing and Seth, 1967; Carr and Pate, 1972; Woolhouse, 1972) and its morphological expression in trees in particular (see Wareing, 1968) is now fairly well appreciated. In agroforestry systems it is the juvenile phase of the woody component(s) which is most likely to be dominated by associated agricultural crops and, during this period, special care is needed to ensure phenological compatibility, as well as spatial regulation, if the trees, shrubs or vines are to be properly established. 'Taungya' practices take these facts into account (for example, Buchele and Conn, 1981). In some circumstances, an optimum solution may be reached by adjusting the geometry of the system with time. For example, by sequential whole-plant thinning, or the increasing removal of stems and branches from the woody species in an originally thickly planted stand.

BELOW-GROUND PHENOLOGY

Root systems and root growth and activity in relation to agroforestry are discussed by Huck (elsewhere in this volume), and in several recent general reviews (Lyr and Hoffman, 1967; Sutton, 1969; Cooper, 1973; Drew, 1979, 1980). Some emphasis does need to be given, however, to the *time* at which different activities occur.

A consequence of a constant allometric relationship between roots and shoots would be an alternation of root and shoot growth (see Ledig, this volume), although, in practice, a measure of overlap in time is to be expected. However, the mechanisms which initiate a phase of root elongation in tropical woody perennials are not clearly established. And whether a root elongation phase precedes a leaf flush, and is cut short by this, or whether it occurs subsequent to leaf flushing, may depend on the species concerned. Certainly, present field evidence is inconclusive (Huxley and Turk, 1976). It is a matter of considerable practical relevance in agroforestry mixed cropping because in order to understand, and optimize, such management practices as

cultivation, fertilizer application and pruning, lopping and browsing, an appreciation of the state of activity of the roots of the woody components is essential.

Another feature of below-ground phenology should be mentioned. Many of the most promising multipurpose trees are legumes (National Academy of Sciences, 1980) and effective nodulation and dinitrogen fixation is important if they are to play their full role in a productive and sustainable agroforestry system. The various factors which can help to optimize dinitrogen fixation in herbaceous legumes are well established (Roughley, 1980), but much less detail is known about the woody species of the family. In particular the extent, time and duration of nodulation and fixation phases in trees. In this respect we have to consider, also, the possible symbiosis with mycorrhizas (Redhead, 1979), the presence of which have been shown to enhance the dinitrogen fixation activity of rhizobium (Daft and El-Giahmi, 1976). Also the possibilities of free-living dinitrogen fixers associated with the rhizosphere (Dobereiner *et al.*, 1972a, b) may be of some considerable significance.

In seasonally arid regions where tree/shrub species are showing distinct growth phenophases, the activity of associated micro-organisms is also likely to be a periodic phenomenon, perhaps occurring within relatively short time scales. As with the state of activity of roots, we need to be aware of at least the broad outline of not only what is happening but *when*, if we are to make the most of compatible plant associations in agroforestry systems.

SOME CONCLUSIONS

The choice of appropriate plant genotypes which fit not only the climatic limitations of the site but also match one another's resource demands is a critical factor in optimizing both productivity and environmental benefits in agroforestry systems. This applies to all plant components, but it is especially important for the woody ones which are not easily changed. Unfortunately, many of the woody species we are now interested in are comparatively little studied. Phenological complementarity should be a major objective in the design and management of agroforestry land use systems. Once the genotypes have been chosen with this in view then herbaceous species can be regulated to some extent through manipulation of time-of-sowing and woody perennials through the removal of parts.

Phenological studies, including the collection of meteorological data, are indispensible and should accompany all agroforestry field investigations. These should be of two complementary kinds in any particular environmental situation. First, observations of the free-standing, untouched plant. Second, experiments involving various types of simple management treatments. The indiscriminate collection of data is merely time wasting, but careful observations of plant behaviour will undoubtedly help to explain both the level of environmental adaptability of the plant species concerned, as well as the opportunities they may offer for temporal resource sharing in any agroforestry system.

More detailed approaches to phenology/phenometry are

likely to have a place once preliminary plant component selection has been done. For example, treatments designed to test the capacity for changing the entrainment sequences of a woody species (or cultivars/selections) and to modify times of flowering/fruiting, timing of plant part removal in order to optimize off-take or, combined with herbaceous crops, time-of-sowing experiments. Such trials are all relatively simple to design and carry out. Table 1 reminds us that they may not be so easy to interpret, however, because of the complexity of plant growth and development. The phases of these are not only highly interdependent, of course, but may proceed along different real-time sequences. The objectives of phenological study must be clearly defined and, in the case of agroforestry, will usually be limited by practical goals rather than a desire to understand the plant's whole set of relationships with the environment.

We should always remember, too, that an appreciation of the levels of phenological adaptability to the environment, and complementarity in an agroforestry system, is but one part of the understanding required to evaluate that system holistically. The short- and long-term time dependent factors involved must include those related to management and socioeconomic considerations.

A PLATE illustrating this paper is elsewhere in this volume.

REFERENCES

Allison, J.C.S. (1963). Use of day-degree summation technique for specifying flowering times of maize varieties at different localities in southern Africa. *Rhod. J. agric. Res.* 1, 22-23.

Alvim, P. de T. (1964). Tree growth periodicity in tropical climates. *In* "The Formation of Wood in Forest Trees" (M.H. Zimmermann, ed.), pp.479-495. Academic Press, New York.

Alvim, P. de T. and Alvim, R. (1978). Relation of climate to growth periodicity in tropical trees. *In* "Tropical Trees as Living Systems" (P.B. Tomlinson and M.H. Zimmermann, eds), pp.445-464. Cambridge Univ. Press, Cambridge, UK.

Alvim, P. de T. and Kozlowski, T.T. (1977). "Ecophysiology of Tropical Crops". Academic Press, New York.

Arnold, C.Y. (1959). The determination and significance of the base temperature in a linear heat unit system. *Proc. Amer. Soc. hort. Sci.* 74, 430-445.

Berthet, P. (1960). La mesure écologique de la température par détermination de la vitesse d'inversion du saccharose. [The ecological measurement of temperature by determination of the rate of sucrose inversion.] *Vegetatio* 9, 197-207.

Borchert, R. (1973). Simulation of rhythmic tree growth under constant conditions. *Physiol. Plant.* 29, 173-180.

Borchert, R. (1976). The concept of juvenility in woody plants. *Acta Hort.* 56, 21-36.

Borchert, R. (1978). Feedback control and age-related changes of shoot growth in seasonal and non-seasonal climates. *In* "Tropical Trees as Living Systems" (P.B. Tomlinson and M.H. Zimmermann, eds), pp.497-515. Cambridge Univ. Press, Cambridge, UK.

Brooks, W.H. (1978a). Jojoba: some natural history aspects and its potential in the Sahel semiarid zone. *In* "Proc. Symp. Revegetation of the Sahel". Royal Geog. Soc. London, London,

UK. 17 pp. (Mimeograph)

Brooks, W.H. (1978b). Jojoba, a North American desert shrub: its ecology, possible commercialisation and potential as an introduction into other arid regions. *J. arid Environments* 1, 227-236.

Brown, D.M. (1963). A 'heat unit' system for corn hybrid recommendations. *In* "Proc. Fifth Nat. Conf. Agric. Meteorol.". Lakeland, Florida, US. 9 pp. (Mimeograph)

Brown, D.M. (1969). Heat units for corn in southern Ontario. *Ontario Dept. of Agric. and Food Information Leaflet* 111/31. 4 pp.

Browning, G. (1973). Hormone physiology of *Coffea arabica*. Interaction of climatic factors and gibberellins in the regulation of extension growth. *In* "Rep. Long Ashton Res. Stn for 1972", pp.46-47. Long Ashton, Bristol, UK.

Buchele, A. and Conn, G. (1981). Agroforestry, another land use alternative within the southern region of the Sudan. Paper presented at the DSE/GTZ Workshop in Agroforestry at Turrialba, Costa Rica. 11 pp. (Mimeograph)

Cannell, M.G.R. (1971). Production and distribution of dry matter in trees of *Coffea arabica* L. in Kenya as affected by seasonal climatic differences and the presence of fruit. *Ann. appl. Biol.* 67, 99-120.

Cannell, M.G.R. and Last, F.T. (Eds) (1976). "Tree Physiology and Yield Improvement". Academic Press, London.

Caprio, J.M. (1974). The solar thermal unit concept - problems related to plant development and potential evapotranspiration. *In* "Phenology and Seasonality Modelling" (H. Lieth, ed.), pp. 353-364. Springer-Verlag, Berlin, New York.

Carr, D.J. and Pate, J.S. (1967). Ageing in the whole plant. *Symp. Soc. expl Biol.* 21, 559-599.

Carr, M.K.V. (1972). The climatic requirements of the tea plant: a review. *Expl Agric.* 8, 1-14.

Carr, M.K.V. (1977). The influence of temperature on the development and yield of maize in Britain. *Ann. appl. Biol.* 87, 261-266.

Cooper, A.J. (1973). Root temperature and plant growth. *Comm. Agric. Bur. Res. Rev.* No.4. Farnham Royal, UK.

Cooper, P.J.M. (1975). Studies on the soil atmosphere composition under maize, grass and bare fallow in western Kenya. *E.A. agric. For. J.* 40, 313-331.

Cooper, P.J.M. (1979). The association between altitude, environmental variables, maize growth and yields in Kenya. *J. agric. Sci. Camb.* 93, 635-649.

Daft, M.J. and El-Giahmi, A.A. (1976). Studies on nodulated and mycorrhizal peanuts. *Ann. appl. Biol.* 83, 273-276.

Dijkhuis, F.J. (1971). The use of heat units in maize production. I. Literature review. II. Experimental results. *Fertilizer Soc. S. Afr. J.* 1, 19-43 and 45-49.

Dobereiner, J., Day, J.M. and Dart, P.J. (1972a). Nitrogenase activity in the rhizosphere of sugar cane and some other tropical grasses. *Plant and Soil* 37, 191-196.

Dobereiner, J., Day, J.M. and Dart, P.J. (1972b). Nitrogenase activity and oxygen sensitivity of the *Paspalum notatum* - *Azotobacter paspali* association. *J. gen. Microbiol.* 71, 103-116.

Drew, M.C. (1979). Root development and activities. *In* "Arid Land Ecosystems: Structure, Functioning and Management", Vol.1 (D.W. Goodall and R.A. Perry, eds), pp.573-606. IBP 16. Cambridge Univ. Press, Cambridge, UK.

Drew, M.C. (1980). Use of isotope techniques for determination of root activity patterns of cropping systems. *In* "Modern Techniques in the Development of Management Practices for Multiple Cropping Systems", pp.95-108. IAEA-TecDoc-235. Int. Atomic Energy Agency.

Ellenburg, H. (1979). Man's influence on tropical mountain ecosystems in South America. *J. Ecol.* 67, 401-416.

Ellenburg, H. and Mueller-Dombois, D. (1967). Tentative physiognomic-ecological classification of plant formations of the earth. *Ber. Geobot. Inst. EHT Zurich* 37, 21-55.

Evans, L.T. (1975). "Crop Physiology, Some Case Histories". Cambridge Univ. Press, Cambridge, UK.

Felker, P. (1978). State of the art: *Acacia albida* as a complementary permanent intercrop with annual crops. *US Agency for International Development Report* AID/afr-C-1361. USAID, Washington D.C., USA.

Flint, H.L. (1974). Phenology and genecology of woody plants. *In* "Phenology and Seasonality Modelling" (H. Lieth, ed.), pp. 83-97. Springer-Verlag, Berlin, New York.

Food and Agriculture Organization (1976). "Eucalyptus for Planting". Forestry Dept, FAO, Rome, Italy.

Forti, M. (1978). Experiments in jojoba cultivation. *Rep. Res. Dev. Authority*, Ben-Gurion Univ. of the Negev (Simmondsia Project), Beer-Sheva, Israel. 127 pp.

Goodall, D.W., Perry, R.A. and Howes, K.M.W. (1979). "Arid Land Ecosystems: Structure, Functioning and Management" Vol.1. Cambridge Univ. Press, Cambridge, UK.

Greathouse, D.C., Laetsch, W.M. and Phinney, B.O. (1971). The shoot rhythm of a tropical tree, *Theobroma cacao*. *Amer. J. Bot.* 58, 281-286.

Grouzis, M. and Sicot, M. (1980). A method for the phenological study of browse populations in the Sahel; the influence of some ecological factors. *In* "Browse in Africa" (H.N. le Houérou, ed.), pp.233-240. Intern. Livestock Centre for Africa, Addis Ababa, Ethiopia.

Haase, E.F. (1976). Phenology of some native jojoba populations in Arizona. *In* "Proc. 2nd Intern. Conf. on the Jojoba". Cons. Nac. de Ciencia y Tech., Com. Nac. de las Zonas Aridas, Mexico.

Halevy, G. (1971). A study of *Acacia albida* in Israel. *La-Yaara* 21, 89-97.

Hallé, G., Oldeman, R.A.A. and Tomlinson, P.B. (1978). "Tropical Trees and Forests". Springer-Verlag, Berlin.

Hogan, L. (1979). Jojoba: a new crop for arid regions. *In* "New Agricultural Crops" (G.A. Ritchie, ed.), pp.177-206. Westview Press, Boulder, Colorado, USA.

Holttum, R.E. (1953). Evolutionary trends in an equatorial climate. *Symp. Soc. expl Biol.* 7, 159-173.

Hopkins, B. (1970a). Vegetation of the Olokemeji Forest Reserve, Nigeria. VI. The plants in the forest site with special reference to their seasonal growth. *J. Ecol.* 58, 765-793.

Hopkins, B. (1970b). Vegetation of the Olokemeji Forest Reserve,

Nigeria. VII. The plants in the savanna site with special reference to their seasonal growth. *J. Ecol.* 58, 795-825.

Humphrey, R.R. (1975). Phenology of selected Sonoran Desert plants at Punta Cirio, Sonora, Mexico. *J. Ariz. Acad. Sci.* 10, 50-67.

Huxley, P.A. (1973). Incoming solar radiation and degree-hours of temperature near Kampala, Uganda. *Agric. Meteorol.* 11, 437-443.

Huxley, P.A. and Beadle, M. (1964). A local climatic study in typical dissected topography in the southern region of Uganda. *Met. Mag., Lond.* 93, 321-333.

Huxley, P.A. and Eck, W.A. van (1974). Seasonal changes in growth and development of some woody perennials near Kampala. *J. Ecol.* 62, 579-592.

Huxley, P.A. and Summerfield, R.J. (1976). Effects of daylength and day/night temperatures on growth and seed yield of cowpea cv. K2809 grown in controlled environments. *Ann. appl. Biol.* 83, 259-271.

Huxley, P.A. and Turk, A. (1976). Preliminary investigations with arabica coffee in a root observation laboratory in Kenya. *Ken. Coffee* 41, 349-360.

Jeffers, J.N.R. and Boaler, S.B. (1966). Ecology of a miombo site, Lupa North Forest Reserve, Tanzania. I. Weather and plant growth 1962-64. *J. Ecol.* 54, 447-463.

Jones, R.J.A. (1972). The measurement of mean temperatures by the sucrose inversion method. *Soils and Fertilizers* 35, 615-619.

Kazmi, S.M.A. (1979). Qudhac (*Acacia tortilis*). *In* "Somali Range Bull. No.6", pp.15-20. National Range Agency, PO Box 1759, Mogadishu, Somalia.

Koriba, K. (1958). On the periodicity of tree growth in the tropics, with reference to the mode of branching, the leaf fall and the function of the resting bud. *Gdn's Bull. Singapore* 17, 11-81.

Lee, R. (1969). Chemical temperature integration. *J. appl. Met.* 8, 423-430.

Lieth, H. (1970). Phenology in productive studies. *In* "Analysis of Temperate Forest Ecosystems" (D. Reichle, ed.), pp.29-46. Springer-Verlag, Heidelberg.

Lieth, H. (Ed.) (1974). "Phenology and Seasonality Modelling". Springer-Verlag, Berlin, New York.

Longman, K.A. (1969). The dormancy and survival of plants in the humid tropics. *In* "Dormancy and Survival" (H.W. Woolhouse, ed.), pp.471-488. Soc. Experimental Biology.

Lyr, H. and Hoffman, G. (1967). Growth rates and growth periodicity of tree roots. *Int. Rev. For. Res. N.Y.* 2, 181-236.

Maestri, M. and Santos Baros, R. (1977). Coffee. *In* "Ecophysiology of Tropical Crops" (P. de T. Alvim and T.T. Kozlowski, eds), pp.249-278. Academic Press, New York.

Monteith, J.L. (1975). Climate. *In* "Ecophysiology of Tropical Crops" (P. de T. Alvim and T.T. Kozlowski, eds), pp.1-27. Academic Press, New York.

Mooney, H.A. and Dunn, E.L. (1970). Convergent evolution of mediterranean climate evergreen sclerophyll shrubs. *Evolution* 24, 292-303.

Murray, D.B. (1961). Soil moisture and cropping cycles in *Cacao*.

In "Rep. Cocoa Res. Imperial College Trop. Agric., Trinidad, 1959-60, pp.18-22.

National Academy of Sciences (1980). "Firewood Crops: Shrub and Tree Species for Energy Production". National Academy of Sciences, Washington, D.C., USA.

Njoku, E. (1964). Seasonal periodicity in the growth and development of some forest trees in Nigeria. III. Observations on seedlings. *J. Ecol.* 52, 19-26.

Peacock, J.T. and McMillan, C. (1965). Ecotypic differentiation in *Prosopis* (Mesquite). *Ecology* 46, 35-51.

Putz, F.E. (1979). Aseasonality in Malaysian tree phenology. *Mal. Forester* 42, 1-24.

Redhead, J. (1979). Soil mycorrhizas in relation to soil fertility and productivity. *In* "Soils Research in Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.175-204. ICRAF, Nairobi, Kenya.

Rees, A.R., Cockshull, K.E., Hand, D.W. and Hurd, R.G. (1972). "Crop Processes in Controlled Environments". Academic Press, London.

Richards, P.W. (1952). "The Tropical Rainforest". Cambridge Univ. Press, Cambridge, UK.

Rieley, J.O., Machin, D. and Morton, A. (1969). The measurement of microclimatic factors under a vegetation canopy - a reappraisal of Wilm's method. *J. Ecol.* 57, 101-108.

Rijks, D.A. (1967). Optimum sowing date for yield; a review of work in the BP 52 cotton area of Uganda. *Cotton Grow. Rev.* 44, 247-256.

Roberts, E.H. (1972). "Viability of Seeds". Chapman Hall, London.

Roughley, R.J. (1980). Environmental and cultural aspects of the management of legumes and *Rhizobium*. *In* "Advances in Legume Science" (P.J. Summerfield and A.H. Bunting, eds), pp.97-103. Royal Bot. Gardens, Kew, London, UK.

Ruck, H.C. (1975). Deciduous fruit tree cultivars for tropical and subtropical regions. *Commonw. Agric. Bureau Hort. Reviews*, Farnham Royal, UK. 91 pp.

Sale, P.J.M. (1970). Growth, flowering and fruiting of *Cacao* under controlled soil moisture conditions. *J. hort. Sci.* 45, 99-118.

Shalitin, G. (1973). New approaches to grape growing in the tropics: grape vine training and pruning studies in Kenya. Ministry of Agriculture, PO Box 30028, Nairobi, Kenya.

Singh, T.P. (1975). Soybean improvement work at IITA. *In* "Proc. IITA Collaborators' Meeting on Grain Legume Improvement", pp.19-20. Intern. Inst. of Tropical Agriculture, Ibadan, Nigeria.

Stewart, K.A., Summerfield, R.J., Minchin, F.R. and Ndunguru, B.J. (1980). Effects of contrasting aerial environments on yield potential in cowpea (*Vigna unguiculata* (L.) Walp). *Trop. Agric. (Trinidad)* 57, 43-52.

Summerfield, R.J. and Bunting, A.H. (Eds) (1980). "Advances in Legume Science". Royal Bot. Gardens, Kew, London, UK.

Summerfield, R.J. and Wien, H.C. (1980). The effects of photoperiod and air temperature on growth and yield of economic legumes. *In* "Advances in Legume Science" (R.J. Summerfield and A.H. Bunting, eds), pp.17-36. Royal Bot. Gardens, Kew, London, UK.

Sutton, R.F. (1969). Form and development of conifer root systems. *Comm. Agric. Bur. Tech. Comm.* No.7. Oxford, UK.

Thornley, J.H.M. (1972a). A model to describe the partitioning of photosynthate during vegetative plant growth. *Ann. Bot.* 36, 419-430.

Thornley, J.H.M. (1972b). A balanced quantitative model for root:shoot ratios in vegetative plants. *Ann. Bot.* 36, 431-441.

Vince-Prue, D. (1975). "Photoperiodism in Plants". McGraw Hill, London.

Walter, H. (1973). "Vegetation of the Earth in Relation to Climate and Ecophysiological Conditions". Springer-Verlag, New York.

Walter, H. (1977). "Vegetationszonen und Klima. Die Oekologische Gliederung der Biosphäre". [Vegetation zones and climate: the ecological structure of the biosphere.] (3rd edn). Eugen Ulmer, Stuttgart.

Wang, J.Y. (1960) A critique of the heat unit approach to plant response studies. *Ecology* 41, 785-790.

Wareing, P.F. (1968). The physiology of the whole tree. *Ann. Rep. E. Malling Res. Stn*, pp.55-69. East Malling, Kent, UK.

Wareing, P.F. and Seth, A.K. (1967). Ageing and senescence in the whole plant. *Symp. Soc. expl Biol.* 21, 543-558.

Whitmore, T.C. (1975). "Tropical Rainforests of the Far East". Clarendon Press, Oxford.

Woolhouse, H.W. (1972). Ageing processes in higher plants. *Oxford biol. Readings.* (J.J. Head and O.E. Lowenstein, eds), 15 pp. Oxford Univ. Press, London.

Wright, H. (1905). Foliar periodicity of endemic and indigenous trees in Ceylon. *Rep. Bot. Gdns, Peradeniya* 2, 415-517.

DISCUSSION

CANNELL - Opportunity exists for increasing yield by avoiding competition in time. I would suggest that the emphasis is on yield as opposed to growth in agroforestry systems.

HUXLEY - Resource sharing in time is essential but with trees the first management choice is the genotype. In agricultural crops resource sharing in time is equally vital, but the additional management option of 'time-of-sowing' can help optimize this. Yield or growth, or both, may be affected by time-dependent stresses; it will depend on circumstances. Many trees seem to have conservative growth strategies. In nature, they flush or flower sooner or later than we would wish when they are cultivated. Optimum strategies for yield in cultivation may not be the same as for survival and reproduction in nature.

LEYTON - While discussing the time of flower production to what extent can you relate this to insect problems, particularly pollination?

HUXLEY - There is a need to look into when exactly the tree starts to initiate flowers and the character of the wood on which this happens before actually relating these to insect problems (pollination or pests). In coffee, for example, bud dormancy is regulated by temperature and water stress.

LAMPREY - In dry regions the great majority of the trees and

shrubs are insect pollinated. This is true for the herbaceous plants, except grasses and palm trees which are wind pollinated. Wind pollinated plants flower first and then the insect pollinated ones. Grasses also come into flower at different times and grow very quickly. Root growth is genetically programmed. It goes through stages which are related to the above-ground parts.

BRUNIG - The phenology of seemingly uniform plants is affected by fertility and climatic factors; for example by water availability. Do you consider stress to be an important factor?

HUXLEY - Individual plants have basic endogenous rhythms, but there will be a definite response to a particular stress depending on what it is, to what part of the plant it is applied, and when.

BRUNIG - Timing of events in plants is conservative and based on survival mechanisms.

HUXLEY - It is certainly important to record the phenology of untouched, free-standing plants in their natural environment before any manipulations are carried out.

BUDOWSKI - It would be useful if we could obtain a better understanding of the environmental or management triggering mechanisms which promote particular phenophases. Classification of plants on triggering effects would greatly assist in management.

CANNELL - In my view there are many more opportunities to increase yield by phasing crops so that they share environmental resources in time rather than by manipulating them in space. It is important to fill the year not just with growth but with yielding activities. To do this effectively, particularly critical stages of crop development may need to coincide with specific conditions. For example, high light intensities will be needed by most herbaceous and tree crops at the time of floral initiation in order to establish sinks for potential yield. And these critical periods of floral initiation and fruit setting will be shorter in determinate crops than in indeterminate ones.

ROOT DISTRIBUTION, GROWTH, AND ACTIVITY WITH REFERENCE TO AGROFORESTRY

M.G. HUCK
US Department of Agriculture, Department of Agronomy and Soils, Auburn University, Alabama, USA.

ABSTRACT. Agroforestry involves species mixtures of widely disparate kinds of plants one of which, at least, is a woody perennial. If such associations are to be selected and managed optimally, and if we are to fully understand the success of existing agroforestry plant associations, then what is happening below ground cannot be ignored. Finding the best ways to manipulate how below-ground resources are to be shared requires a much more detailed knowledge of root behaviour than we have hitherto attempted for monocultures.

This paper presents a brief summary of general information about roots, and illustrates how they can be studied in a rhizotron. The possibilities of using existing information about within-plant growth regulation so as to model root growth is mentioned. In mixed cropping some form of complementarity below ground is desirable, and this can be achieved in space and/or time. Some of the situations in which competition for water and nutrients can be avoided, or obviated, are mentioned and an understanding of these provides a way out of the 'trial-and-error' approach to the evaluation of the below-ground state which is the only other alternative way of investigating it.

Some characteristic problems of root growth in soils in arid zones, acid savannas and upland regions are mentioned and the need to encourage plant breeders to select for rooting characteristics for different sites is noted as a low cost way of overcoming some of the problems which will arise in agroforestry.

INTRODUCTION

Whether we are concerned with agriculture, forestry or agroforestry, usually, after preparing the soil for sowing and planting we know little of what is happening below ground. It becomes even more vital to know about roots and root systems where, as

in many agroforestry land use systems, mixtures of widely different kinds of species are grown together. Especially if we hope to be able to optimize the sustained production from such systems by the provision of logical design and skilled management, rather than by chance or guesswork. I therefore make no excuse for spending a short time briefly summarizing some facts about roots and root systems before, later in the paper, discussing mixed cropping and agroforestry situations.

Plant growth depends upon the availability of a continuous supply of water and minerals in sufficient quantity to meet the needs of the crop. In addition to forming the link by which above-ground organs obtain these essential nutrients from the soil, root systems provide support for the erect growth of the stem and have a metabolic role in hormonal regulation of overall plant growth processes as well. The mechanical stability resulting from an extensive network of embedded roots helps reduce soil erosion and facilitates percolation of rainwater. Both live and decaying root systems supply energy to meet the metabolic requirements of microbial populations whose activities aid the recycling of minerals between successive generations of flora and fauna.

ANATOMICAL / MORPHOLOGICAL EXAMINATION OF ROOT GROWTH

To obtain water and mineral nutrients from the soil in sufficient quantities to meet the requirements of a growing plant, root systems have evolved with very large surface:mass ratios (Epstein, 1973). The relatively small amount of stored water per unit volume of soil, and the difficulty with which water and dissolved ions are able to be moved through a drying soil matrix toward a stationary root segment, are such that the growth rate of an expanding root system often exceeds the rate of unsaturated soil water flow (Taylor *et al.*, 1972). Roots may grow toward stored water faster than water can move toward the root system. The amount of carbon required to build a finely divided network of roots is frequently less than that required to meet its respiratory requirement for more than a few days, so the useful life of small feeder roots is extremely brief. Extension of new roots into new soil regions, and their ageing and subsequent decay, are significant factors in assessing the spatial distribution of living root systems at any given time.

Because a real understanding of the interactions between a root system and its surroundings requires an appreciation of the dynamic aspects of growth, death, population shifts, and movement of water and dissolved ions in three-dimensional space, a number of specialized root observation laboratories have been constructed in recent years which permit repeated measurement upon the same plant. By comparing data from successive measurements, a much better understanding of the dynamic nature of the plant/soil interactions can be obtained than from individual, isolated observations or from experiments with excised plant tissue. The first such laboratory to be extensively described in published documentation was the East Malling (UK) facility (Rogers and Head, 1963; Rogers, 1968). A similar facility was constructed at Auburn, Alabama (USA) which was described by Taylor (1969) with details of a particular experiment reported

by Browning *et al.* (1975). One such root laboratory, constructed in the tropics to study arabica coffee, has also been reported (Huxley and Turk, 1967).

The interior of the Auburn, Alabama facility and a magnified view of roots are shown in Plates elsewhere in this book. An alternative means of root observation using attenuation of thermal neutrons instead of visible light energy is described by Willatt *et al.* (1978), and a number of other alternative measurement techniques have been described in recent years.

Elongation and radial expansion of individual root tips

The biological mechanisms controlling the advance of a single root tip have been extensively reviewed elsewhere (Huck, 1977; Russell, 1977). The photograph of a young branch rootlet in a Plate elsewhere in this book (after Huck, 1977) will serve to illustrate the various regions into which an expanding rootlet is usually classified (Esau, 1972). This young branch rootlet has recently emerged from an older segment of the cotton root along the right-hand edge of the photograph. Its conical tip, marked A, is designated the 'root cap'. Cells from the root cap are gradually sloughed by abrasive action of the soil particles as the root pushes its way into new soil regions, with losses replenished from the region of cell division immediately behind. This meristematic region, marked B, also produces cells which expand in the opposite direction forming the region of cell elongation marked C. The thin walled cells in this region undergo rapid vacuolar expansion, providing the necessary mechanical force to push the root tip into new regions of unexplored soil. The conical shape of the root tip serves as a wedge, increasing the mechanical advantage of osmotic forces generated in the root tip which must overcome the soil's physical resistance to deformation.

Finally, when expansion growth is completed, the cell walls begin to thicken and the forms of mature xylem elements can be distinguished in the region of maturation marked D. Here, too, the beginning of epidermal protuberances can first be seen. Root hair development occurs about 24 to 28 hours later. Uptake of water and minerals is at a maximum in this region (Kawata and Lai, 1968; Ferguson and Clarkson, 1975).

Life expectancies and root system development

Rootlets generally show signs of senility after a period of several days, or at most a week or two, the actual duration varying with species, soil temperature, and water regime. Root hairs are lost, and cortical tissue discolours and sloughs away. When a root segment is part of a contiguous conduction system leading from the shoot to an actively growing tip or cluster of tips, it is likely to remain in place and continue functioning as a pathway for long-distance transport. If the tip is not in a favourable micro-environment the connecting root tissue is, in most species, likely to die back. The plant's growth control system somehow tends to favour root tips growing in more favourable soil regions.

As root diameter increases due to secondary cambial growth, the pathway for radial movement of water from soil into mature

xylem element increases also, so that the role of active absorption of water and minerals must gradually be relegated to younger rootlets growing from the meristematic tissue, or to root tips well beyond the older tissue segment. In this way, new soil regions will be explored, and the plant will have continuous access to fresh supplies of water and nutrients, which generally move through the soil much more slowly than an active root tip can grow toward them.

The instantaneous population of roots seen when excavating a soil on a particular day, or when looking at the arrangement of living roots visible at the glass observation panel in a rhizotron experiment, represents the sum of root growth less root death. Because the smallest rootlets live only a few days, the number seen at any given time is only a small percentage of the total produced by the plant until that time. Quantitative accounting for total carbon turnover in the plant (see Brunig, this volume) will be significantly in error unless the rapid turnover of living roots is kept in mind at all times. When the amount of carbon required to sustain the respiratory requirement of a given rootlet is compared with the quantity of carbon required to regenerate a new rootlet of the same size, it will be seen that the total weight of a root will be consumed by respiration in only a few days. Thus only the 'mainline' feeder roots are maintained over extended periods of time, while laterals and small feeder roots are regenerated as required by soil conditions in each region of soil occupied by a root system. In the author's experience with herbaceous crops, the roots of grasses generally tend to live longer than those of leguminous crops. The species difference in dieback and decay rates may be due to a difference in susceptibility to microbial attack, to differences in the native enzyme systems within the roots themselves, or to a difference in cell wall structure. While the reasons are unknown, the fact of variations in life expectancy of individual rootlets is often observed, and it has a substantial influence upon the quantity of carbon required to sustain a given population of feeder rootlets. Observations on the relation of root growth to shoot growth are discussed by Ledig (see this volume).

PLANT FACTORS AFFECTING ROOT GROWTH AND BIOMASS PARTITIONING

The growth of an aggregated system of root tips may seem to resemble the growth of a population of independent organisms. All compete with one another for scarce resources such as sugars and living space within the soil. In the case of independent, biological organisms growth is generally characterized by an exponentially increasing curve, with constraints to maximum growth imposed only when some environmental component becomes limiting; space, food, light being typical examples. Individual cellular growth and proliferation are constrained within limits by some other form of control, however, and the competing roots on a plant are, as a whole, under some unified constraining mechanism which permits them to function as an integrated system. Furthermore, there is a balance between shoot and root growth, maintained even under conditions of severe pruning, or other environmental stresses (Brouwer and de Wit, 1968).

Details of these control mechanisms at the organism level are still not well known, and their elucidation represents an area in which a great deal of additional research is required (but see Ledig, this volume). Plant growth regulators have been studied for many years, and a number of active compounds have been isolated, identified, and characterized: auxins, gibberellins, cytokinins, ethylene and abscisic acid, and other growth retardants. The literature with regard to their effects on roots and rooting is extensive but our knowledge of the way that hormones interact to control the activities and functions of an established, intact root system is still incomplete. As are the interactions within the plant as a whole. For example, cytokinins represent a class of compounds known to be excreted with the xylem exudate from decapitated root systems, which have a strong effect upon protein stability and biosynthesis in the leaves of most plants. Many benzylamino purine compounds have been shown to alter m-RNA biosynthesis and the subsequent metabolic activity of leaves.

Although all the biochemical details have not yet been worked out, it is possible to write sets of general rules, formulated as mathematical expressions, which permit large computers to simulate the growth and functions of higher plants in terms of their different organs. From such computer simulation work, and from direct observations of the relevant physical processes, it is possible to draw some conclusions about what must be happening as plants grow and develop, utilizing resources obtained from soil storage by their root systems. Such systems can be aggregated at the organism level to consider competition between various species occupying the same space, perhaps separated in time, and from this approach one can begin a rational study of intercropping systems. The multivariant regression analysis reported by Taylor *et al.* (1972) or Huck (1975) described the effects of soil physical and chemical factors on the growth rate of elongating cotton radicles. By assuming similar relationships between soil chemical and physical factors and the elongation of all root tips beneath a population of cotton plants, a simulation model can be constructed which fairly accurately describes cotton root system behaviour (Baker *et al.*, 1976; Lambert *et al.*, 1976).

COMPETITION AND SCHEMES FOR AVOIDING IT IN MIXED CROPPING SYSTEMS

Complementarity at the root level

In recent years an increasing number of reports describing work with mixed cropping systems has begun to appear. Total productivity is often higher on a per unit of land basis, averaged over the year, than in monocultural cropping systems. The detailed explanations, when any are available, usually invoke the argument that solar radiation falling upon bare soil is wasted, and that by having more than one crop occupy the land it is often possible to arrange matters in such a way that each crop species fills a niche in space, or time, which is non-competitive with the others. Competition between species, and even between individuals in a monoculture, is not however limited to the above-ground portions of the plants. If water or mineral

nutrients are scarce the temporal and spatial distribution of root activity may be as important for survival as the temporal and spatial distribution of the canopy. A key to successful mixed cropping is *selection of species with complementary root system behaviour patterns as well as complementary shoot growth habits*.

Some crops, such as winter cereals, have shallow root systems. Development of the crop is generally completed during the cooler months of the year when evaporative demand is minimal and soil moisture reserves are high. Other crops, such as those adapted to summer growth under drier conditions, have large, deep root systems. They exploit water reserves not accessible to winter cereals. In southeastern USA such crops as cotton, soya beans, or perennial warm season forage grasses can be grown in rotation with winter cereals to obtain water from deeper soil layers. Because summer annuals do not grow at all during the cooler parts of the year, they are a good complement for winter cereal crops, permitting two or more crops to be harvested from the same land area each year. In tropical regions a wide range of species incorporated into different forms of agroforestry offers a rich choice of well-integrated plant systems that are highly complementary both above and below ground.

The essential feature of avoiding root competition is analogous to that required for avoiding shoot competition: the plants must exploit a different region either in space or in time. Of the two, separation in time is easier to manage with the large-scale machinery used in commercial agriculture in the USA; where profile recharge is slow, exploitation of different spatial regions is useful also.

Roots must have room to grow and seek the water and minerals required by the shoot systems they support. If the shoot water requirements of interplanted crops are separated in time, the roots' ability to meet that need will be similarly separated. Separation in space may be as effective with root systems of trees and herbaceous crops grown in combination, but experimental details are generally lacking. Harris (1967) has made a detailed study of the mechanism of root competition in range grass species, and Willey and Rao (1981) have recently presented results of an intercropping experiment with annual crops. Comparably detailed studies of intercropped trees with herbaceous species are wanting.

The distribution of a root system through space and time is influenced by both the genetic character of the crop and by localized soil conditions. Although an extensive data base is generally not available at present, it can be obtained locally for crops of interest in that region by simply excavating root systems from time to time and recording the extent of their proliferation throughout the soil. The principal requirement for such studies is the labour to excavate the roots and to record and summarize the findings. Even simple glass window observation pits such as that described by Pearson and Lund (1968) can be constructed at relatively low cost using local labour which is generally available in developing countries.

Separation in space and time is not the only element which must be considered in planning a root system strategy for multicropping agroforestry systems. One must also consider how the

roots interact with above-ground parts of the plant. A plant grown outdoors in the field may have the same number of roots as a comparably sized plant grown in the glasshouse, but its roots may extend through much greater distances in an unconfined soil. The separation distances between individual roots may be much greater, and the root system efficiency for obtaining water and minerals thereby enhanced, in the field grown plant but the biomass of the root system, and hence the requirement for respiratory substrate, and production of regulatory hormones, may be the same. In trickle irrigation experiments, or where plants are growing in very rocky soil with only a few cracks for root penetration, root distribution can be very asymmetric. Yet if the metabolic needs of the shoot are met, the plant will grow well.

Competing for water and nutrients

The main functional problem for competing root systems is competition for scarce water and nutrients. Nitrate, for example, is taken up by most plants far in excess of the immediate growth requirements when it is freely available in the soil solution. The plant simply reduces the excess nitrate to the level of NH_3 and stores it in the form of free amino acids until these are required for growth. If a plant's roots were programmed to take up only enough NO_3^- to meet the immediate requirements for growth, much of the available nitrogen would be lost through denitrification and leaching. Moreover, competing plants in the same vicinity which took up NO_3^- in excess of their immediate needs would have an advantage over a plant taking up NO_3^- in moderation because the internal reserves of nitrogen may be required for later season growth when the soil reserves are depleted. The plant attempting to depend upon externally stored nitrogen, taking up only enough to meet its immediate requirement for growth, will ultimately lose competitively because its neighbours will have accumulated extra nitrogen during the time it was freely available in the soil and can continue growth during periods of shortfall in the pool of nitrogen in the soil solution. When such factors as leaching and denitrification can interrupt the constant flow of nutrients, the optimal survival strategy is to take up as much NO_3^- as might be available and hold it internally, beyond the reach of competitors, until it is required for growth.

Because phosphorus and potassium are stored in the soil in large, buffered pools, their availability in the soil solution is much more constant than that of the soil nitrogen supply. Plants therefore have less of a reward for hoarding large amounts of these elements internally, and so have evolved mechanisms for taking up these cations only in amounts related to their immediate needs. If large quantities of NO_3^- anions are being absorbed by the root system, then comparable amounts of cations such as K^+ or Ca^{++} must be absorbed in order to maintain electrical neutrality.

At present we have scarcely begun to consider these issues in agroforestry although, clearly, they greatly affect the way in which disparate mixtures of species will get along together.

Roots and other aspects of species association and selection

Beyond the problem of competition for space and scarce resources, some plants may excrete phytotoxic compounds around their roots. Such plants, of course, are not good candidates for mixed cropping systems. They can generally be identified in field studies because of the absence of competing plants in the vicinity of a well-established individual. The identity of phytotoxic compounds excreted by root systems is not generally known, but most are probably species (or even cultivar) specific, and of low molecular weight for ease of diffusion within the soil (see Brunig and Sander, this volume).

Population studies at high planting rates are, in effect competition studies. Here, plants are directly competing with others of the same species, age, and background. Genetic differences between individuals, or a small advantage obtained for any reason, will enable some competitors to crowd out the others. In nature, the reward in such competition trials is given to the survivors: that is to those plants which are able to live long enough to produce seed. Under agricultural conditions, however, it is frequently not survival, but production of some particular plant component such as cotton fibre, sugar in storage organs, or flavour of a fruit which determines ultimate survival and the ability of an individual to reproduce.

Man selects individual plants which grow in such a way that his needs are met, and he intervenes to assure the survival of those selected individuals. Over long periods of time, domesticated crops adapted to the needs of man have evolved in this way (see Pickersgill, this volume). Root system performance, however, has generally been overlooked or at least not explicitly characterized in the past, but, in selecting for mixed cropping including agroforestry systems, a conscious effort is required to take this into account. Otherwise the basis of our selection of plants for particular agroforestry designs, and the arrangement and management of them, will necessarily be incomplete.

ROOTING CHARACTERISTICS AND PROBLEMS IN PARTICULAR ECOZONES

Arid zones

The gross morphology, biochemistry and micro-anatomy of roots of xerophytic plants are not markedly different from those of plants adapted to other regions. The principal adaptation of xerophytes involves the ratio of roots to metabolically active shoots, and the strategies which the plant evolves in order to reduce transpiration losses. Such a strategy might be called 'conservatism', or one of developing a very large root system with respect to the anticipated size of the shoot and its water requirement. In this way, survival of the plant is more likely, although total biomass production in above-ground organs may be substantially less than in plants adapted to more favourable water regimes.

Again, some arid zone species possess large underground storage organs, containing sufficient food reserves and meristematic tissue in a somewhat sheltered environment, and these insure an ability to make rapid regrowth when rainfall does occur. Meanwhile such a plant is able to survive long periods of

waiting between sporadic rainfall events, or rainy seasons.

Other adaptive strategies involving the root systems are also observed. If a permanent water table or other stable underground water supply can be located, species which develop roots capable of reaching this will be able to continue growth through periods of dry weather at a time when surrounding herbaceous plants with roots confined to the surface soil are dormant. Tree crops, having several years to extend roots deeply into the soil, are particularly useful for this purpose. They can then be intercropped with short-lived herbaceous crops, which grow from seed, tubers, or rhizomes, during seasons when rainfall is sufficient to support the growth of these.

Timing, or the phenology of root growth (see also Huxley, p.517, this volume) is especially important in arid regions. Plants must establish their root systems early so as to insure that water is available for completion of their life cycles. If the water supply is extremely transient, as is the case in desert areas, a 'bloom' of plants will appear briefly after each rain. Plants adapted to this growth habit will have very limited root systems. Shoot growth will proceed rapidly to the next phase which may be seed maturity, or a return to some intermediate dormant form which insures survival until the next rainfall event. Such plants are particularly susceptible to overgrazing during dry periods.

Many soils in the drier regions of the world have a high salt content. This provides an additional handicap for plants growing in these areas because of the greater amount of metabolic energy which must be expended in accumulating the high internal salt levels needed to maintain turgor against a strong osmotic gradient. The low water content, and therefore low heat capacity, of desert soils combined with generally clear nighttime skies, produce much larger fluctuations in soil temperature than those found in humid regions. Temperature extremes in the surface soil place an additional stress on root systems, which adapted species have to overcome.

Savannas

Areas on the American, Asian, and African continents designated as 'savannas' are characterized by infertile, acid soils. Temperature is generally favourable for plant growth throughout much of the year, and water is seldom limiting. But the presence of copious water supplies over geologic time has resulted in severe weathering of the clay minerals in these soils. Often there is substantial leaching and formation of highly developed acid or compacted subsoil layers which effectively inhibit root penetration to deeper layers of the soil profile. These soils are generally level, so that erosion is not a major problem, although some sheet and wind erosion may occur, and flooding can be a problem in certain instances.

In advanced stages of weathering, clay minerals break down to form kaolinite and other 1:1 lattice clays. With these clays there is no significant shrinkage or swelling as the soil goes through successive wetting and drying cycles. The absence of shrinkage permits formation of a stable soil physical structure, so that the clay forms a kind of 'glue', cementing larger sand particles into a rigid, stable mass. Even though mechanical

analysis may show only a few per cent clay (perhaps 5 to 10 per cent in these highly weathered soils), this amount of kaolinitic clay can cement a sandy soil matrix into a body with very high mechanical strength, which resists root penetration. There may be some plasticity when water content is high, serving as a lubricant for movement of the soil particles past one another; as these soils dry, however, they become extremely hard (Taylor and Ratliff, 1969; Taylor *et al.*, 1972). The problem is further compounded by mechanical tillage operations and by compression from vehicle or animal traffic on the soil surface.

Beyond the problems of high soil strength reducing root penetration, advanced weathering under warm, high moisture conditions produces a highly leached, acidic soil. At pH values below 5.0, trivalent Al^{+++} ions from the native mineral components of the soil matrix become soluble in concentrations which can be toxic to growing roots. Typical symptoms of aluminium toxicity include multi-nucleated cells and retarded cell division. Gross tissue examination shows a yellowing and dying of the growing tips (Huck, 1972). Matsumoto and Morimura (1980) have shown that aluminium ion alters the physical properties of DNA, which probably accounts for the difficulty in cell division. Toxicity from other commonly occurring multivalent ions has also been observed at low soil pH.

Correction of the soil acidity problem can be remedied on temperate soils by incorporating limestone, which both raises soil pH and increases the availability of Ca^{++} in the soil solution (Adams and Lund, 1966; Lund, 1970). This remedy is not so suitable for many tropical soils, however, apart from the cost. An alternative approach to preventing root growth problems is to change the plant itself so that its roots are able to grow in the unmodified soil. Foy *et al.*, (1980) have demonstrated possibilities for genetic adaptation to soils with low pH and high Al^{+++} concentration.[1]

Although the time requirement for development of new varieties is significant, and there may be a sizeable expenditure for labour, this approach offers a long-term solution to the problem at a much lower cost than chemical amendment of the soil itself. Especially for low input agroforestry land use systems. However, progeny testing must involve evaluation of root growth; a practice seldom seen in conventional plant breeding programmes.

Low cost solutions to the problem of high soil strength encountered on soils with highly weathered clay minerals have also been demonstrated. Deep tillage, or mechanical disruption of compacted soil layers generally produces good root growth for a few weeks or months until subsidence or additional machinery traffic have recompacted the soil to its original condition. Because the mechanical strength of compacted soils is a function of water content (as well as bulk density, particle size, and other factors) it is often possible to get rapidly growing taproots or strongly penetrating grass roots through a compacted soil horizon before the water has been removed and mechanical

---

1. And see the current programme at CIAT for breeding leucaena cultivars tolerant of acid soils (Hutton, E.M., ICRAF Newsletter No.6, December 1981). (*Ed.*)

resistance to root penetration established. Once roots have penetrated the soil, the same kaolinitic clays which tend to cement lateritic soils into a solid mass will now tend to retain the large pore structure established by the pioneering roots. As later roots attempt to explore the drying soil, they are able to follow old root channels which have now become a part of the soil matrix. In agroforestry we should, therefore, try to use mixtures of species with appropriate root growth characteristics. Minimum tillage and the use of woody mulch also offer a possible solution. However, in both cases a great deal more research is needed.

In some cases, compaction can restrict oxygen diffusion through the air-filled pore spaces of the soil. This situation, most often encountered on dense, level soils with poor internal drainage, is likely to cause damage at high temperatures when the biological oxygen demand is at its highest. When soil oxygen is limiting, root growth and the metabolic salt uptake processes are severely curtailed. On tropical, hydromorphic soils drying out is often accompanied by severe cracking and soil displacement. Many species of trees and shrubs are adversely affected by the consequent disturbance or actual fracturing of the roots. Drainage, and the selection of species which will tolerate such conditions are potential solutions to this problem.

Tropical uplands

In many tropical upland soils rapid weathering, and high levels of leaching and runoff result in very limited storage of mineral nutrients in the soil. The predominant phase of the nutrient cycling is storage in above-ground biomass, with new growth being dependent upon a continual release, or mineralization, from the death and decay of organic remains on the soil surface. While this system works well under climax forest vegetation, it is upset by attempts to clear the land and grow annual or herbaceous crops in monoculture. Unless a continuing renewal of mineral nutrients can be supplied from artificial fertilizers, it is almost imperative that some form of multicropping or mixed species cultivation such as agroforestry be employed to insure continuous ground cover. This will help ensure a release of nutrients to growing root systems and counter serious soil erosion problems which are usually also a part of tropical upland land use.

Where previous erosion has reduced available topsoil, the surface of the land may be little more than steep slopes covered by a very thin soil layer, and with large numbers of stones near the surface that make cultivation difficult. Both cover crops and trees or shrubs can play a part in building up biomass and re-establish a more fertile topsoil zone. There can be difficulties in establishing tree seedlings, however, in these circumstances. Once again this calls for a knowledge of species that are not only well adapted to the aerial environment but, also, have rooting characteristics that will maximize their chances of survival.

CONCLUSIONS

Because of the obvious difficulties involved, our knowledge of

the behaviour of roots lags far behind that of other plant organs. Where the species we are concerned with are to be grown in monoculture, the result of such lack of information is a serious impediment to a critical choice of cultivar and to its most effective management. Where species *mixtures* are involved — particularly in agroforestry where these are of species of widely differing habit and phenology — our lack of knowledge about roots and root behaviour becomes much more serious. Without some knowledge of root adaptive characteristics for particular sites of possible root complementarity or competitive attributes either in space or time, and of the behaviour of root systems in relation to that of the aerial parts, effective crop mixtures can only be assembled by trial and error and tested on an *ad hoc* basis.

One hopes that, at the present time, and with our rapidly growing ability to model crop situations, we can do better than this. If it is to be so, however, it will necessitate a concerted effort to establish, however crudely in the first place, a minimum level of information about the roots and root behaviour of the species we intend to use in any particular agroforestry situation.

PLATES illustrating this paper can be found elsewhere in the book.

REFERENCES

Adams, F. and Lund, Z.F. (1966). Effect of chemical activity of soil solution aluminum on cotton root penetration of acid subsoils. *Soil Science* 101, 193-198.

Baker, D.N., Lambert, J.R., Phene, C.J. and McKinion, J.M. (1976). GOSSYM: A simulator of cotton crop dynamics. *In* "Computers Applied to the Management of Large-Scale Agricultural Enterprises". Proc. US-USSR Seminar, Moscow, Riga and Kishinev. pp.100-133.

Brouwer, R. and Wit, C.T. de (1968). A simulation model of plant growth with special attention to root growth and its consequences. *In* "Root Growth" (W.J. Whittington, ed.), pp.224-244. Butterworths, London.

Browning, V.D., Taylor, H.M., Huck, M.G. and Klepper, B. (1975). Water relations of cotton: a rhizotron study. *Alabama Agr. Exp. Sta. Bull.* No.467. 20 pp.

Epstein, E. (1973). Roots. *Sci. Am.* 228, 48-58.

Esau, K. (1972). "Plant Anatomy". John Wiley & Sons, New York.

Ferguson, I.B. and Clarkson, D.T. (1975). Ion transport and endodermal suberization in the roots of *Zea mays*. *New Phytol.* 75, 69-79.

Foy, C.D., Jones, J.E. and Webb, H.W. (1980). Adaptation of cotton genotypes to an acid, aluminum toxic soil. *Agron. J.* 72, 833-839.

Harris, G.A. (1967). Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecol. Monogr.* 37, 89-111.

Huck, M.G. (1972). Impairment of sucrose utilization for cell wall formation in the roots of aluminum-damaged cotton seedlings. *Plant & Cell Physiol.* 13, 7-14.

Huck, M.G. (1977). Root distribution and water uptake patterns. *In* "The Belowground Ecosystem: A Synthesis of Plant-Associated Processes" (J.K. Marshall, ed.), pp.215-226. Colorado State University Range Science Dept. Series No.26, Fort Collins, Colorado, USA.

Huxley, P.A. and Turk, A. (1967). A new root observation laboratory for coffee. *Kenya Coffee* 32, 156-159.

Kawata, S. and Lai, K. (1968). On the correlation between the endodermis differentiation and the water absorption in the crown roots of rice plants. *Proc. Crop Sci. Soc. Japan* 37, 631-639.

Lambert, J.R., Baker, D.N. and Phene, C.J. (1976). Dynamic simulation of soil under growing row crops. Rhizos. *In* "Computers Applied to the Management of Large-Scale Agricultural Enterprises". Proc. US-USSR Seminar, Moscow, Riga, Kishinev.

Lund, Z.F. (1970). The effect of calcium and its relation to several cations in soybean root growth. *Soil Sci. Soc. Amer. Proc.* 34, 456-459.

Matsumoto, H. and Morimura, S. (1980). Repressed template activity of chromatin of pea roots treated by aluminium. *Plant & Cell Physiol.* 21, 951-959.

Pearson, R.W. and Lund, Z.F. (1968). Direct observation of cotton root growth under field conditions. *Agron. J.* 60, 442-443.

Pearson, R.W., Childs, J. and Lund, Z.F. (1973). Uniformity of limestone mixing in acid subsoil as a factor in cotton root penetration. *Soil Sci. Soc. Amer. Proc.* 37, 727-732.

Rogers, W.S. (1968). The East Malling root observation laboratories. *In* "Root Growth" (W.J. Whittington, ed.), pp.361-376. Butterworths, London.

Rogers, W.S. and Head, G.C. (1963). *In* "Report of the East Malling Research Station for 1962".

Russell, R.S. (1977). "Plant Root Systems: Their Function and Interaction with the Soil". McGraw-Hill, Maidenhead, UK.

Taylor, H.M. (1969). The rhizotron at Auburn, Alabama — a plant root observation laboratory. *Ala. Agr. Exp. Stn Circular* No.171. 9 pp.

Taylor, H.M. and Ratliff, L.F. (1969). Root elongation rates of cotton and peanuts as a function of soil strength and soil water content. *Soil Sci.* 108, 113-119.

Taylor, H.M., Huck, M.G. and Klepper, B. (1972). Root development in relation to soil physical conditions. *In* "Optimizing the Soil Physical Environment Toward Greater Crop Yields" (D. Hillel, ed.), pp.57-78. Academic Press, New York.

Willatt, S.T., Struss, R.G. and Taylor, H.M. (1978). *In situ* root studies using neutron radiography. *Agron. J.* 70, 581-586.

Willey, R.W. and Rao, M.R. (1981). A systematic design to examine effects of plant population and spatial arrangement in intercropping, illustrated by an experiment on chickpea/safflower. *Expl Agric.* 17, 63-73.

DISCUSSION

LOOMIS - In crop modelling it is not sufficient to know only root length. We also need to know how carbon is partitioned and

we need a measure of root activity, in terms of both water and nutrient uptake.

HUCK - I agree that root length is not the only measurement required to describe the activity of a root system, particularly in crop modelling situations when one must account for the partitioning of carbon into dry matter of specific organs. If you make realistic assumptions about root diameter, tissue water content, and chemical composition of root tissue in each category of roots considered by your model, however, you can generate an estimate of total root length which can be verified experimentally.

From a functional viewpoint, I believe that root length is the most important consideration, because at the elementary level, flows of water and minerals can be represented in polar co-ordinates moving toward a line-sink of variable length. The critical factor is the distance through the soil.

If you measure root weight, you get an enormous contribution from the major connecting tissues, and the roots engaged in active absorption weigh very little in proportion to their activity. Besides, they are often lost in excavation of the soil, although they can be estimated in root observation laboratories with glass windows such as those described. Root surface area would be an even better measurement than root length, but is even more difficult to measure experimentally, as both length and diameter must be known, and root hairs are generally neglected.

LOOMIS - What regulates root nitrogen uptake activity? Is it simply the rate of suberization?

HUCK - I do not know what regulates the rate of suberization, but Clarkson at the Letcombe Laboratory (UK) has some elegant experimental data on root uptake of specific ions by solution-grown roots as a function of distance from the tip.

KOZLOWSKI - Kramer showed that 90 per cent of the water could be taken up by the suberized roots of trees.

JACKSON - Old, suberized fruit tree roots certainly do take up a surprising amount of water, and some nutrients.

OLDEMAN - Is not the soil environment behind a glass plate very unlike the normal environment?

HUCK - This is a very common question. It is like the 'normal' root environment in some cases, but not in others. In Alabama we generally use a sandy soil with kaolinitic clays to reduce shrinkage and subsequent breakage of the glass. If the soil you wish to study has a tendency to shrink and swell with changes in moisture content (Montmorillonitic or 2:1 lattice clays) you will either have glass breakage or the clay will form a crack next to the glass. When this happens, the roots will prefer to grow in the cracks rather than through a resistive soil medium, and the results will be distorted. Some people have substituted Perspex or Plexiglass for glass so that it will bend as the clay changes shape with wetting and drying. Because of its oily, non-wetting surface, however, there is also a plane of weakness

along the plastic - soil interface and, again, the appearance is somewhat unlike the 'normal' environment. We have done a number of comparisons between the length and number of roots estimated at the glass window, and those found by excavating core samples from the soil volume behind it. With our sandy soils the results have almost always been within the statistical error estimates predicted by counts at the window. You must remember that the glass surface is a relatively small sample of the total soil volume and therefore the confidence limits improve at higher rooting density because the number of observations will be larger.

KOZLOWSKI - A previous paper of yours showed diurnal root shrinkage of about 50 per cent. Does this occur on all roots? Does it leave vapour gaps which could interfere with water transport?

HUCK - While shrinkage may occur on all roots, it is most noticeable on young, unsuberized roots where the cell walls have not accumulated the mechanical rigidity to counter large changes in internal water potential. By optical measurements, which is the only method we have used in the soil, we can detect changes of 2 to 5 per cent or more, and thus only the smallest roots with thin cell walls are seen to shrink. With mechanical L.V.D.T.s on stems of varying age, and electronic amplification, we have been able to detect diameter changes as small as one part in 10^4 on stems, and thus know that even the main stems on woody plants, like cotton and trees, shrink under water stress. Succulent tissues of the shoot have a much larger shrinkage coefficient than woody tissues, and I imagine the same is true of roots -- but we do not have a way to measure root shrinkage with the same precision as that used for stem and leaf tissues.

Time lapse cinematography under high magnification clearly shows vapour gaps during periods of high water stress, but it probably does not occur on all roots at the same time. Liquid films between soil and root are retained much longer if the soil is relatively wet, so roots in a moist soil are more effective during critical periods than those in dry soil where hydraulic conductivity can be limiting. At Aberystwyth (UK) it was shown that vibrating pots would restore turgor after plants had wilted. This is further evidence of the existence of a vapour gap which was restored by compacting the soil around the fine roots.

HUXLEY - Working with arabica coffee we observed shrinkage in a root laboratory in Kenya. This was catastrophic for root hairs. Presumably, after shrinkage water vapour transfer could occur, but no nutrient transfer. We also found that the coffee roots grew in local patches at any one time.

HUCK - We also observed that root growth was apparently concentrated in certain regions of the soil profile at any particular time. With each successive wetting and drying cycle the conditions favouring optimal root growth change and the system is very dynamic and takes advantage of this.

KOZLOWSKI - Are there differences in root longevity between grasses, herbs and trees?

HUCK - Yes. We have little experience with trees, but grass

roots tend to live 2 to 3 times longer than those of cotton, tomato, groundnuts or soya beans. For the purpose of a simulation model of carbon balance, however, the rate of formation of new root tissues is comparable. The result of longer root life at a comparable growth rate is that the number of roots observed at any particular time will be much greater with a grass than with a dicotyledenous plant. Of course, the number of young roots observed on a given day is only a small fraction of the total production during a complete season's growth.

TIESZEN - Did you measure gas exchange?

HUCK - We have measured oxygen concentration using polarographic electrodes at several depths in the soil. By flushing the profile with N_2/O_2 mixtures and noting the changes in concentration gradient we were able to infer the biological oxygen demand of the root - micro-organism complex.

LEYTON - We find in heavy clay soils in England that feeder roots of less than 0.5 mm diameter can live for many years.

HUCK - The mean life expectancy of our soya bean roots shown in the Plate referred to on p.529 is of the order of about 5 to 7 days during our summer growing conditions. If the soil is flooded, or cooled, the roots last much longer. We have observed maize roots intact over winter, but they rot quickly when the soil warms and die in the spring. As I mentioned earlier, I have no experience with trees.

CONNOR - I can confirm that old roots do provide channels for water penetration.

LOOMIS - Did you look at ethylene production in relation to root spatial patterns?

HUCK - No. It is a difficult task and the chance of contaminating the sample is enourmous. We have tried, but found ethylene everywhere we turned — from polyethylene in the lab. vessels to breakdown of butadiene in the rubber stoppers used in the sampling flasks. The soil levels required for physiological activity are so low that these background levels present a real analytical problem.

EFFECTS OF CULTURAL MANAGEMENT OF TEA (*CAMELLIA SINENSIS* (L.) O. KUNTZE) ON BIOMASS ACCUMULATION AND YIELD

M.J.S. MAGAMBO
Tea Research Foundation, Kericho, Kenya.

ABSTRACT. Tea is an example of a woody perennial that is intensely manipulated in order to produce a particular plant part: the young leafy twig ('two leaves and a bud'). Investigations of the changes in dry matter accumulation and distribution with time have shown how the harvest index is changed by frequent plucking and to what extent management changes the proportions of woody parts. The lesson to be learnt from this type of research could readily be applied to the new woody, multipurpose, perennial species now being considered for use in agroforestry, and help determine the management needed to optimize the proportions of wood (for fuel) or leaves (for fodder) that are required.

INTRODUCTION

It is conventionally believed that, in order to get large yields, tea bushes must have large woody frames, which provide as large a surface area as possible. For this reason, the bushes are manipulated in such a way that they cover the ground in the shortest possible time with a large woody frame and bush surface area. The methods of producing such bushes fall into three main categories: pruning (coppicing), tipping and pegging. There are slight modifications of these methods when applied to seedling tea, although only the techniques as applied to clonal plants, produced from vegetative propagation, are described below. The general principles underlying such manipulation of a woody perennial structure are relevant to the ways that other species, useful in agroforestry, might need to be managed.

THE GENERAL TRAINING AND MANAGEMENT OF TEA

Pruning during the formative period

As soon as the plants are 30 cm tall, they are 'decentred' by

cutting the main shoot down to a height of 15 cm from the ground in order to encourage as large a number as possible of new lateral branches, which are then allowed to develop. When this has occurred the plants are pruned down to a height of 20 to 28 cm, the majority of the branches being 1 cm in diameter at that height. Later, the bushes are pruned again, at a height of 40 cm; the majority of the branches are, similarly, 1 cm diameter. Finally, when the bushes reach a height of 60 cm all shoots, when they have formed two leaves and a bud, are removed above that level to establish a flat plucking surface ('tipping-in'). Once a flat surface is formed, all the subsequent terminal shoots of two leaves and a bud which grow above the flat surface, are removed at regular intervals (normal plucking), and these provide the economic yields. Normal plucking is done once every ten days to three weeks, depending on the weather.

In the 'tipping-in' method the plants are decentred as described above. Then the apical shoots of two leaves and a bud on the developing lateral branches are removed for two rounds at each of the following heights: 20, 30 and 40 cm. Finally, the bushes are tipped-in several times at a height of 51 cm to form a flat plucking surface, followed by normal plucking.

Another way of forming the basic branching structure required is the 'pegging' method. With this, the new lateral branches which develop after decentring are bent at an angle of approximately 45° and pegged when they reach a height of 60 cm. At the time of pegging, the terminal shoots of two leaves and a bud on each branch are removed to encourage more branching. Then the bushes are tipped-in over several rounds at 50 cm height, followed by normal plucking.

Pruning of established tea

Whether with seedling or clonal tea bushes, this serves two main purposes: first, to stimulate new growth, since the economic yields often tend to decrease quantitatively with time; second, to keep the bushes at a height convenient for manual labour during normal plucking operations, since the flat plucking surface rises about 8 cm a year. Normally, pruning is simply an operation to cut down the bush to a certain level (straight 'cut-across' pruning). The period between one pruning and the next (the pruning cycle) varies between three and four years in East Africa. The actual time at which to prune at the end of a pruning cycle partly depends on weather conditions. During the first pruning cycle the bushes are normally pruned at a height of 40 to 50 cm. The pruning level is raised about 5 cm during subsequent pruning cycles. After a number of pruning cycles the pruning level is lowered again to about 45 cm to start off a new series of pruning cycles.

DRY MATTER PRODUCTION AND DISTRIBUTION IN FREE-GROWN OR PRUNED TEA PLANTS

Some experiments carried out at Kericho have provided information about dry matter production and partitioning by tea bushes, both free-growing and under commercial management, which throws some light on the way a woody perennial responds to pruning. It is briefly outlined below.

Experimental results

Preliminary data from these investigations showed the large extent by which the proportion of the woody tissue increased as compared with leaf mass as commercially managed bushes grow older (Table 1). When the bushes are pruned at various levels as described above, approximately 50 to 75 per cent of the frame, mainly old woody branches, is left on the bushes. As the tea bushes increased in size, the proportion of the economic yield (harvest index) decreased from 20 to 8 percent over 8 years (Table 2). Harvest index is inversely proportional to total dry matter accumulation. Other investigators have also estimated low harvest indices for mature tea (Jain, 1977; Laycock and Othieno, 1978; Tanton, 1979). It has also been observed that most of the pluckings are concentrated in the centre and very few are found at the periphery of the bush surface (Figure 1). Also, the smaller the bush, the higher the shoot density along the entire plucking surface (Barua and Dutta, 1971; Barua, 1973). So that, with tea, large bushes do not necessarily give large yields.

Table 1. Percentage of absolute net dry matter allocated to various parts of commercial tea bushes of different age groups in the field (means of four bushes).

Age group yrs	Leaves %	Frame %	Roots %
1	48	35	17
2	34	44	22
8	23	41	36
15	9	67	24

Table 2. Harvest indices and net annual dry matter increments (kg plant^{-1}) of tea bushes of different age groups (means of four bushes).

	in the field		in the nursery
	8 yrs	2 yrs	1 yr
Harvest index (%)	8	12	20
Dry matter increment (kg plant^{-1})	1.57	0.81	0.23

When dry matter accumulation in commercial tea bushes was compared with free-growing, unplucked counterparts it was found that plucking reduced overall dry matter accumulation (Table 3). But dry matter accumulation in young bushes appeared to be more affected by plucking than in old bushes. Although plucking reduced overall dry matter accumulation, it enhanced the development of new shoots (Figure 2).

IMPLICATIONS FOR TEA GROWING

The results obtained from these investigations suggest that the low harvest index of mature tea bushes is partly due to large amounts of wood (Magambo and Cannell, 1981). This then raises

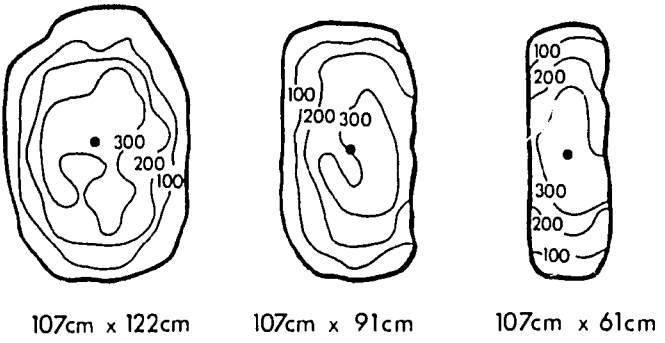


Fig. 1. Distribution of pluckable shoots on the plucking surface of bushes of clone 7/14 at different spacings over a period of 12 months. Prescribed numbers on contour lines refer to number of shoots per unit grid square — 15 cm × 15 cm. • indicates the physical centre of the bush. The thick lines are the boundaries of the plucking surface. Scale: approximately 0.0014 of actual size.

Table 7. Annual dry matter increments (kg plant^{-1}) according to parts, in plucked and unplucked tea bushes of different age groups (means of four bushes).

Age group	Treatment	Pluckings	Leaves	Frame	Roots	Total
1 yr	Plucked	0.042	0.034**	0.082**	0.070**	0.228**
	Unplucked	-	0.158**	0.280**	0.250**	0.688**
2 yrs	Plucked	0.096	0.222**	0.316**	0.173**	0.807**
	Unplucked	-	0.513**	0.628**	0.300**	1.441**
8 yrs	Plucked	0.133	0.361	0.684*	0.393	1.571*
	Unplucked	-	0.669	1.245*	0.522	2.436*

Treatment differences significant at P = 0.05(*) and 0.01(**), respectively.

some doubts about the present cultural management of tea which advocates large woody bushes. In terms of maximum land utilization the present management appears to be rather inefficient. For example, of the net biomass produced per unit area per year by mature tea bushes, only a small portion (about 8 per cent) is harvested as the economic yield and over 40 per cent goes into wood formation, which is poorly utilized at the moment. When the bushes are pruned, the prunings are left in the field to rot. This may have the advantage of protecting the pruned bushes from sun scorch soon after pruning, or as mulch for soil conservation and weed control. However, according to Monkhouse and Lenox (1976), the woody prunings left in the field add very little to soil nutrients, and are not particularly important where fertilizers are being used. Total prunings (leaves and branches) can be as much as 17 t ha^{-1} of dry matter (Magambo, unpublished), of which 11 t ha^{-1} (70 per cent) are branches. These branches,

therefore, could be utilized as fuelwood instead of being wasted.

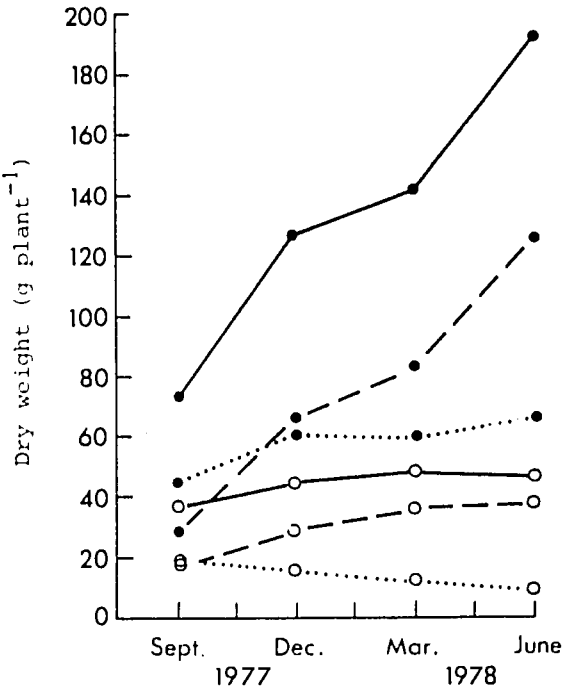


Fig. 5. Dry weight (including pluckings) of terminal shoots of two leaves and a bud on plucked and unplucked 8-year-old bushes of clone 6/8 at each sampling date. ● Plucked. o Unplucked. ——— All shoots. — — — Flushing shoots only. ..... Dormant shoots only.

The amount of wood could be reduced in order to increase the harvest index and economic yields of tea bushes, partly by increasing plant population per unit area. Rahman and Phukan (1976) showed that closer spacings reduced the number of branches per tea plant and progressively reduced the collar diameter (see also Cannell, p.489 this volume). Although there is a ceiling beyond which plant population does not increase yield appreciably (Holliday, 1960; Laycock, 1961; Eden, 1965), the highest plant population used in East Africa at the moment may be below that point. According to the Tea Research Institute of East Africa (1969) the highest plant population is about 13,822 plants ha^{-1}, at 0.91 × 0.91 m triangular planting. Yet, Eden (1965) reported that plant populations could be increased up to 20,000 plants ha^{-1} before tea yields level off. The low plant density adopted in East Africa has been partly dictated by costs and management problems, but the cultural operations in high density planting may not necessarily be more expensive or more difficult. For example, Laycock as quoted by Eden (1965) showed that a plant density of 7200 bushes ha^{-1} took three times as long to prune as one with a population of 18,000 bushes ha^{-1}. It could be said that it would be difficult for pluckers to walk through closely spaced bushes when plucking. But bushes at close spacings would

have fewer branches and such branches might not be as rigid as those formed on bushes at the wide spacings commonly used in East Africa. Alternatively, at closer spacings, the bushes might be planted in bands or strips, each consisting of a few rows of plants, so that the plucker can move along the sides of the band when plucking without moving inside. The space between the bands could also be made wide enough to be utilized by planting other suitable crops. Some reasons for and other approaches to changing the system of growing tea have been suggested by Huxley (1975). Clearly, our present knowledge of the physiology of the tea bush allows us to predict more precisely what the outcome of speculation about possible changes in plant management will be.

IMPLICATIONS FOP AGROFORESTRY

Although we do not as yet know, in detail, the responses to pruning or lopping of the many species of trees and shrubs which have been recognized as potentially valuable fodder plants (Von Maydell, 1980), or sources of fuelwood (National Academy of Sciences, 1980), the results of these detailed investigations with tea give very clear indications of the trends in the partitioning and total accumulation of dry matter that are likely to occur. Furthermore, these experiments carried out on tea, which involved a detailed evaluation of dry matter distribution under both free-growing and managed situations, indicate the type of study which is now urgently needed for new, woody agroforestry species.

A PLATE illustrating this paper can be found elsewhere in the book.

REFERENCES

Barua, D.N. (1973). Distribution of shoots on the plucking surface of a tea bush and its relationship to spacing. Part II. *Two and A Bud* 20, 1-10.

Barua, D.N. and Dutta, K.N. (1971). Distribution of shoots on the plucking surface of a tea bush and its relationship to spacing. Part I. *Two and A Bud* 18, 8-11.

Eden, T. (1965). "Tea". 2nd Edition. Longmans, Green and Co., New York.

Holliday, R. (1960). Plant population and crop yield. *Nature* 186, 22-24.

Huxley, P.A. (1975). Tea growing — or is it time for a new look at the system? *Tea in E. Africa* 15, 13-16.

Jain, N.K. (1977). Perspective: technological gaps in tea research. *Two and A Bud* 24, 1-5.

Laycock, D.H. (1961). Yields and spacing in tea. *J. Trop. Agric. (Trinidad)* 38, 195-204.

Laycock, D.H. and Othieno, C.O. (1978). Thoughts on annual dry matter production by tea. *Tea in E. Africa* 18, 2-4.

Magambo, M.J.S. and Cannell, M.G.R. (1981). Dry matter production and partitioning in relation to yields of tea. *J. Expl Agric.* 17, 33-38.

Maydell, H.-J. von (1980). Effect of goat husbandry on forest

and range ecosystems. *Plant Res. & Dev.* 12, 98-108.
Monkhouse, A.J. and Lenox, R.G. (1976). The effect of pruning trash mulch on mature tea, 1969-1975. *Tea in E. Africa* 16, 11-21.
National Academy of Sciences (1980). "Firewood Crops: Shrub and Tree Species for Energy Production". National Academy of Sciences, Washington D.C., USA.
Rahman, F. and Phukan, B.C. (1976). Planting and spacing. *In* "Annual Report for 1975/76". Tocklai Experimental Station, Assam. pp.14-15.
Tanton, T.W. (1979). Some factors limiting yields of tea (*Camellia sinensis* L.). *J. Expl Agric.* 15, 187-191.
Tea Research Institute of East Africa. (1969). "Tea Growers Handbook". Tea Boards of Kenya, Tanganyika and Uganda, Nairobi, Kenya.

DISCUSSION

HUCK - Your observed decreases in proportions of leaf probably occur because of simultaneous increases in growth of wood.

MAGAMBO - Since wood is not utilized, the objective could be to avoid generating wood as far as possible without also reducing leaf yield.

JACKSON - The most important cost in tea production is cost of plucking. What height of bush is best for plucking, and is this affected by changes in cultural practice?

MAGAMBO - Usual plucking height is 1 to 1.5 m. Growing tea at closer spacings or in closely planted strips will not affect plucking height but it could provide space for intercropping.

JACKSON - With regard to intercrops in tea; the important consideration is not yield of biomass but economic yield. Since tea is worth around US$1600 ha^{-1} (1981), it must be doubtful whether the value of the intercrop would justify the loss in yield of tea.

MAGAMBO - Close spacing may allow intercropping without necessarily reducing the numbers of tea plants per hectare. Since yield, at least in part, is related to plant density it might be possible to maintain tea yields despite intercropping. This needs to be tested.

HUXLEY - One general problem is nutrient removal. After tea has been pruned, one knows how much nutrient has been removed and must be replaced from other sources. Clearfelling of plantation forests is an analogous but more extreme situation in which all above-ground growth is taken off, often without provision for exported nutrients to be replaced and with a consequent decline in soil fertility.

MAGAMBO - At Kericho woody prunings of tea have been found to add only small amounts of nutrients to the soil.

KIRA - In forage crops leaf production is directly proportional to amount of grazing. Does plucking produce corresponding

increases in leaf biomass and hence yield of tea?

MAGAMBO - Overall yield of leaves is greater from unplucked bushes, but growers are concerned with yield of young shoots, not overall leaf yield.

LOOMIS - Rate of leaf production, rather than overall leaf yield, is therefore the significant factor. Is the total seasonal leaf yield greater with plucking or without?

MAGAMBO - Overall yield is greater without plucking. But rate of leaf production is greater with plucking; that is plucked plants had more young shoots than unplucked plants.

LEYTON - How far is quality determined by cultivar and how far by environment?

MAGAMBO - Both contribute, but environment is very important. For example, high quality teas are associated with low growth rates at high altitudes like Kericho.

THE ROLE OF CONTROLLED ENVIRONMENTS IN AGROFORESTRY RESEARCH

*T.T. KOZLOWSKI and †P.A. HUXLEY
*The Biotron, University of Wisconsin-Madison, Madison, Wisconsin, USA.
†International Council for Research in Agroforestry, Nairobi, Kenya.

ABSTRACT. Types of elaborate to relatively simple controlled environment facilities are described and some general considerations in using controlled environments are discussed, including some special difficulties with woody perennial plants. Controlled environment studies should be linked to field work and a range of specific areas of research on multipurpose tree species is outlined. Controlled environments can be used to good advantage to grow uniform plants and to explore genetic variation at the seedling stage; to investigate responses of seedlings and young plants to environmental stresses; to investigate adaptability where seedling - mature stage correlations can be established; to explore allelopathic relationships; to help optimize seed germination and plant propagation techniques; for root growth studies, especially those relating to nursery management and planting out; and in the study of plant pests and diseases.

Controlled environment facilities of one kind or another can provide a cost-effective way of obtaining needed information about multipurpose tree species, especially if used in conjunction with field experiments, and by linking these with a network of appropriate facilities according to the specific problems under investigation.

INTRODUCTION

Agroforestry is the term given to sustainable land use systems that involve more or less intimate and interacting associations of agricultural/horticultural crops and woody perennials (trees, shrubs, palms, vines, bamboos), all on the same unit of land. The present scope of interest in such land use systems has

exposed our serious lack of knowledge about them. We have not yet adequately described existing systems, or learned enough about their potential transferability to other similar ecozones. Agroforestry must develop as more than just a descriptive exercise and many of the problems now emerging will be solved only by a combination of appropriate experimental approaches adapted to studying the range of plant component species, as well as the temporal and spatial complexities found in agroforestry systems.

One such approach which has more than proved itself in supporting agricultural research, is the use of controlled environments to examine plant growth and development. This can be done under conditions of environmental stability, of specifically defined environmental differences or, sometimes, sequential types of controlled 'environments' can be applied to a wide range of experimental climatic manipulations which possess varying degrees of control precision.

Phytotron or biotron

Usually this is a complex of similar, controlled units, or batches of units, in which statistically replicated experiments can be conducted under controlled conditions. Environmental control covers radiation (light intensity, light quality and daylength); temperature (day and night, but often without separate control for soil temperature as opposed to air temperature); humidity (often less precisely regulated than the other climatic variables); carbon dioxide concentration of the aerial environment; mineral nutrition (through choice of planting media and/or solid or nutrient solution application); wind; physical rooting conditions (through choice of planting media, watering regime and, sometimes, temperature and control of CO_2 and oxygen concentrations in the root zone); and the facility for applying growth regulating compounds, if required.

Growth chambers or growth rooms

These are the equivalent of single units of controlled environment, with similar control facilities to those mentioned above. In some cases growth chambers are available that use available incoming short-wave solar radiation, thus providing natural light quality, and also natural light flux densities which most artificially lighted growth chamber facilities cannot do. For work on seed germination, or conventional or micropropagation, rather small, controlled environment structures are quite suitable.

Rhizotrons

These are units specifically constructed to enable plant roots and root systems to be examined, usually under some limited form of environmental control or manipulation (that is control of the soil or rooting media used, watering, mineral nutrition and some control of soil temperature). They have been used to study both root form and function and usually consist of one or more sets of subterranean multicomponent facilities (see Huck, this volume). A simpler arrangement may be useful such as a glass-lined pit, or box with glass walls.

Growing rooms

These are enclosed spaces provided with supplementary lighting and watering facilities in which container-grown plants can usually be grown faster in the seedling stage than would otherwise be the case. In temperate regions several sectors of the horticultural industry use growing rooms to produce vigorous seedlings out of season, under low light conditions, in readiness for planting out at the start of more favourable periods. Supplementary CO_2 is sometimes used to further stimulate growth.

Controlled environment glasshouses or plastic houses are cheap and simple structures, with much less precisely regulated control of temperature and humidity. Light, particularly day-length, can be manipulated if plants are on trolleys which are wheeled into adjacent light-tight, temperature controlled dark rooms. This can be done automatically. Even relatively simple, automated glasshouses in which cooling/heating facilities are provided can be useful to provide 'standard' environments for some kinds of experiments. In the tropics, shade houses often fulfil a similar function, but temperature control is more difficult because of the relatively much greater heat load that must be dissipated.

Field operated cuvettes

Plant or crop physiologists use these to study particular plant processes, for example, carbon fixation and respiration, under otherwise field climates. They consist of relatively small, transparent, gas-tight structures, with ancillary temperature control and monitoring equipment, which can enclose leaves, leafy branches, whole plants or, sometimes, small communities of plants.

Modification of the field environment

This is the crudest form of control, but it can be a useful and cost-effective method. This approach is especially valuable for initial studies of relatively unexplored species. It can take many forms, depending on the objectives of the experiments: shading; control of available water (both by irrigating and by diverting rain with movable covers); shelter; and soil covers to modify topsoil temperatures, are some of the more common techniques.

INVESTIGATING RESPONSES TO ENVIRONMENT

Controlled environment facilities have been developed because there are many problems in evaluating, in the field, the effects on plant growth and development of individual environment factors, or the interactions among them. Light, temperature, humidity, and other factors are so interdependent that a change in one alters the others. It is also virtually impossible in the field to reproduce very closely the environment of any one day on subsequent days (Rook, 1968; Kramer *et al.*, 1972; Kramer, 1978). For such reasons use of sophisticated environment controlled research facilities, such as phytotrons, has accelerated greatly in recent years. The many environmental combinations that are available in such facilities make it possible to study accurately and rapidly

the action and interaction of environmental factors. Phytotrons can be used to dissect or construct a given environment. Growth responses of plants over a wide range of environments can be studied concurrently. Interactions of two or more factors can be evaluated while other factors are kept relatively constant. A major advantage of environment controlled research facilities is that they decrease variability and increase reproducibility of data. Furthermore, such facilities can simulate both diurnal and seasonal changes in climates for widely separated locations.

Phytotrons have sometimes been criticized because of the costs of building and maintaining them. However, they should be judged on the basis of the much better information they provide than can possibly be obtained in the field, glasshouse, or even from small groups of controlled environment chambers (Hellmers, 1969). Controlled environment research often costs less than field research because the smaller number of plants necessary for samples reduces the cost of laboratory analysis. Comparisons of costs of phytotrons and field research often have been woefully misleading because they did not mention the high costs of maintaining and managing experimental areas, costs of field travel, cost of damage to field experiments by weather, insects, and disease (thereby requiring repeating experiments), and the cost of delays in waiting for specific weather conditions (Rook, 1968; Kramer *et al.*, 1972). In any event there is no need to build expensive controlled environment facilities in tropical areas. Such facilities are already established in many countries (Table 1) and arrangements can readily be made to conduct research on tropical plants in such facilities.

GENERAL CONSIDERATIONS IN USE OF CONTROLLED ENVIRONMENTS

Where a high level of control is possible a choice exists as to whether experimental plants are subjected to 'standard' or 'simulated' climatic conditions. 'Standard' climates can be any combination of levels of climatic variables that the experiment requires and the equipment can provide. 'Simulated' light intensity and quality are not easily reproduced artificially. In addition humidity is a somewhat difficult and expensive variable to control precisely. Furthermore diurnal changes in climate, and occurrence of climatic 'noise' (intermittent cloudiness, wind, and temperature and CO_2 fluctuations) are difficult to reproduce exactly under artificial conditions. If the experiment is designed to help relate plant growth or development to field situations then a 'near-simulated' environment is likely to provide the most useful information.

Most plants grown in any form of controlled environment are relatively much more stress-free than those grown outdoors. However, by applying particular environmental stress factors (heat, drought, waterlogging, chilling), either alone or in combination, the effects of these can be critically studied in controlled environment facilities in a way that is not possible outdoors.

In controlled environment facilities using artificial light the daily photosynthetically active radiation (PAR-400-700 nm) can, with modern equipment, equate to that received in many tropical locations, although not to the maximum received in semi-arid regions (for example, usually up to 8 to 12 MJ $m^{-2}day^{-1}$

Table 1. Locations of some major controlled environment facilities available for research on plant growth. There are numerous other smaller controlled environment facilities throughout the world, well capable of carrying out the kind of research work, relevant to agroforestry, that is discussed in this paper.

Name of facility	Location
Phytotron	Division of Plant Industry, CSIRO, PO Box 1600, Canberra, AUSTRALIA
Phytotron	Research Station, Agriculture Canada, Lethbridge, Alverta T1J 4B1, CANADA
Phytotron	91190 Gif-sur-Yvette, FRANCE
Phytotron	Agricultural Research Institute, Martonvasar, 2462 HUNGARY
Phytotron	Government Forest Experiment Station, Tsukuba, Ibaraki, 305 JAPAN
Biotron Institute	Kyushu University, Fukuoka, JAPAN
Controlled Environment Laboratory	DSIR, Palmerston North, NEW ZEALAND
Phytotron	Duke University, Durham, North Carolina, USA
Phytotron	North Caroline State University, Raleigh, North Carolina, USA
Biotron	2115 Observatory Drive, University of Wisconsin, Madison, Wisconsin, USA

compared with around 10 to 18 MJ $m^{-2}day^{-1}$ in semiarid regions. However, 8 to 12 MJ $m^{-2}day^{-1}$ is usually achieved in growth cabinets or rooms, only by using a 'square' climate — that is by providing the full, available energy flux during the entire day.

Pest control is sometimes a problem, inasmuch as the level of phytotoxicity of some normal pesticide formulations is unacceptable when applied to stress-free (unhardened) plants. Biological control offers a useful alternative, particularly for pests such as red spiders, mealy bugs, and aphids which can be extremely troublesome under controlled environment conditions using high humidity levels.

Generally speaking the costs of working at temperatures below ambient are greater than where applied temperature standards or differentials are above it. This can be especially a problem in hot climates where experiments requiring lower temperatures may have to be postponed to the cool season, if there is one. Otherwise the resources of another laboratory in a temperate region must be sought.

SOME DISADVANTAGES WITH WOODY PERENNIAL PLANTS

Agroforestry systems can include a wide range of plant components, one of which, by definition, is a woody perennial plant. No special problems will arise where the plant component to be studied is a herbaceous species. However, controlled environment facilities have several disadvantageous features where experiments with large woody perennials are concerned.

Space is usually limited, even in walk-in growth rooms, and this limits both the number of experimental plants and the length of time they can be maintained in the facility. Plants can be respaced after sequential harvests, but the cost of building very large facilities to carry out experiments with adult trees may well be prohibitive. Hence with woody plants, only relatively young seedlings or small saplings can be investigated.

All controlled environment facilities have climatic gradients of one kind or another. With smaller, easily handled plant species the easiest way to overcome these is to periodically move all the experimental plants within a growth room or chamber. With larger seedlings or small trees this is less easily done without damaging the plants.

The cost of an experiment using a controlled environment facility is increased in proportion to the length of time it continues. Experiments with woody perennials are, therefore, relatively more costly than those with annual plants. Breakdowns in equipment are also more likely the longer an experiment continues.

Some of the information required about multipurpose tree species concerns the effect of environmental factors on phenology and, more particularly, on the reproductive stages. These are difficult to study in controlled environment facilities because of the size and cost restrictions mentioned above.

The behaviour of a woody perennial in any one season is often highly dependent on what occurred in a previous one. Most controlled environment facilities cannot maintain woody plants under controlled conditions for such a long period of time.

Despite these disadvantages a number of types of experiments can be of immediate value to support studies of multipurpose tree species.

LINKING CONTROLLED ENVIRONMENT STUDIES WITH FIELD WORK

The kind and degree of control of particular climatic factors that is necessary, as well as the degree of control over nutrition and the rooting environment, very much depend on the kind of experiment being undertaken. For example, a study of day-length responses is of little value unless both day temperatures and night temperatures are also controlled, because the interactions between these are often of considerable importance. Then again, with nitrogen fixation tests, it may well serve just to standardize the environment using relatively crude environmental control. At the same time, facilities for sterilized conditions are essential to prevent crossinfection of *Rhizobium* strains.

The need for separate environmental controls over plant roots and tops may well be important (for example, see Cooper, 1973), as for instance in studying early growth patterns of multipurpose tree species in support of nursery techniques and

planting-out practices. Many other examples could be given.

There are relatively few sophisticated phytotron facilities available (see Table 1), but growth room/growth cabinets are more widespread, and the simpler forms of controlled environment equipment to modify and monitor changes in field environments are now commonplace. With the co-operation of the more advanced facilities there exists the possibility of establishing networks of research activity which are mutually supportive, and range from field tests to highly specific problem solving studies of more detailed plant - environment responses.

At this stage in the study of woody species which have promise for agroforestry systems, controlled environment facilities will be used primarily in conjunction with field experiments to solve problems, or provide information about essentially practical issues. These will be related to questions about biosystematics and seed source identification, juvenile - mature stage correlations, environmental adaptability of species and provenances, appropriate propagation methods, responses of juvenile plants to environmental stress factors (particularly in relation to planting-out techniques), allelopathic relationships in agroforestry plant mixtures, root studies, and *Rhizobium* and mycorrhizal investigations (in relation to field programmes on nitrogen fixation and plant nutrition, and inasmuch as these concern establishment and growth on particular sites). All such investigations can be made more fruitful by using controlled environment studies of an appropriate kind to support the necessary field experiments, as a considerable amount of work with agricultural crop species has already shown.

EXAMPLES OF USE OF CONTROLLED ENVIRONMENTS

The following are some specific examples of the types of experiments that have already established controlled environments as valuable research tools.

Growth of uniform plants

Controlled environments are now considered indispensable for producing uniform plants for biochemical studies such as those of Alofe *et al.*, (1973), Jeffs and Scharver (1976) and Sun *et al.*, (1978), something that cannot be satisfactorily accomplished in the field or even the glasshouse. With controlled environments experiments can be repeated under identical conditions, regardless of season or weather, and the work of various investigators can be reliably compared.

With the exception of a few genera (for example, *Leucaena*, *Prosopis*, *Casuarina*, and the Australian *Acacia* spp.) the genetic variation available for many multipurpose tree species has, as yet, been only sparsely explored. Much remains to be done in identifying both clinal and non-clinal within-species genetic variation. Because of the magnitude of the task, most of this work is being done by simple field tests, but inevitably there will be a case for using controlled environment facilities to explore the biosystematic relationships of the less tractable groups (for example, within-species variation in the *Prosopis alba / chilensis / flexuosa* complex).

In cases that warrant it the current confusion arising

through international exchange of multipurpose tree germplasm of dubious origin may also need attention; specifically to establish accurate seed source identification under completely uniform growing conditions.

Apart from selecting species and genotypes able to withstand particular site-imposed environmental stresses (see below) there is an urgent need to investigate the general adaptability range of multipurpose tree species to particular ecozones. There is also need to gain some knowledge of the genotype × environment (G × E) interactions involved, in order to be able to predict the performance of any species or provenance more precisely when it is moved into a similar, but altered, environmental situation. Again, a good deal of this work will be done through normal field elimination trials sited throughout the environmental range considered suitable. However, to the extent to which early seedling or juvenile stage growth is related to later performance, it will be possible to ascertain general climatic adaptability in terms of temperature ranges and daylength responses much more rapidly if controlled environment facilities are available. This may be particularly important for multipurpose tree species whose normal range covers a wide variation in latitude and/or altitude (for example, *Acacia tortilis*, *Azadirachta indica*, *Parkinsonia aculeata*, *Pithecellobium dulce*, and so on).

Exposure of plants to stress at different stages of development

An important advantage of using controlled environments is that plants can be subjected to stress at any stage of growth. This usually is not possible in the field where the desired stress only rarely coincides with the plant growth stage under study. Controlled environments have been found indispensable in studying the physiological role of cotyledons of woody plants in seedling development. For example, exposure of *Pinus resinosa* seedlings in the cotyledon stage to low temperature, low light intensity, or air pollution inhibited initiation and growth of primary needles as well as dry weight increment of seedlings (Kozlowski and Borger, 1971; Constantinidou *et al.*, 1976). Marked variations among species in the physiological role of cotyledons of woody angiosperms to seedling development were demonstrated under controlled environmental conditions (Marshall and Kozlowski, 1974a, b, 1976, 1977).

Many of the multipurpose tree species now being considered for use in agroforestry systems, or in some form of social or community forestry, will be needed for sites that are less than completely favourable; that is they may be subjected to soils which are saline/alkaline, or acid, which have impeded drainage, or are extremely sandy or unstable. There may be permanent or intermittent exposure to high winds, salt spray, high advective energy loads, prolonged drought periods, chilling or frosts. All environmental variables that can be very precisely simulated in appropriate, controlled environment facilities which are well suited for cost-effective germplasm screening programmes. Even crude environmental modification can be a useful technique to investigate the effects of plant stresses (Summerfield *et al.*, 1976).

Juvenile - mature stage correlations may have to be established using seedlings, or juvenile stages, to develop tests for

the appropriate plant characters which are found to be correlated with the capacity to overcome such particular environmental disadvantages. Large numbers of seedlings can be screened in controlled environments, using an appropriate test method to select suitable stress-resistant germplasm. For such work a relatively low level of environmental control is suitable for the actual screening processes, although the initial experimental work to establish the technique may require more elaborate controls.

The agricultural crop plant components in agroforestry systems, which have usually been selected for sole cropping, may need further attention from plant breeders. Similarly they too will need screening for such factors as shade tolerance, drought tolerance, and so on. Much of this work can be hastened by the use of controlled environment facilities.

Effects of environmental factors on physiological processes and growth

Controlled environments can provide insight into the influence of radiation, temperature, humidity, wind, and the composition of the atmosphere, as well as such edaphic factors as soil temperature, water supply, aeration, mineral supply and pH, on physiological processes and the growth of plants (Tibbitts and Kozlowski, 1979). Research in controlled environments can also produce excellent data on effects of interactions of environmental factors. Examples are the interactions of light intensity and temperature, light intensity and CO_2, and air humidity and mineral supply on stomatal aperture (Meidner and Mansfield, 1968; Davies and Kozlowski, 1974; Pereira and Kozlowski, 1976; Pallardy and Kozlowski, 1979), and photoperiod and temperature on physiological mechanisms of development which lead to flowering (Blondon *et al.*, 1977). Whole programmes of experiments have been carried out to explore the responses of a crop, in this case cowpea (*Vigna unguiculata*), to climatic variables and changes in nitrogen nutrition in relation to field practices (see Huxley and Summerfield, 1976a and many subsequent papers by various authors).

Controlled environment facilities can be used to select climatic regions in which to field test new species and varieties or to assist in the selection of plants for use in specific climatic regimes. Went (1957) wanted to find plants capable of growing rapidly on the mountains of Southern California, so that they could provide quick cover for watershed protection following large forest fires. A series of temperature conditions in a phytotron included field averages and extremes. Two species, from over 30 species suggested and tested, were selected. The entire study was completed and the results successfully applied in the field within a year.

Allelopathy

Seed germination and plant growth are inhibited by a variety of naturally occurring compounds that are released to the soil from roots and aerial tissues of neighbouring plants (Kramer and Kozlowski, 1979; Norby and Kozlowski, 1980). Allelopathic compounds may be released by volatilization, leaching from living

or dead tissues, exudation from roots, and decay of plant tissues. Allelopathic compounds are important because they influence plant succession, dominance, vegetation dynamics, structure of plant communities, and crop yield (Rice 1974, 1979; and see Brunig and Sander, this volume).

A large body of evidence shows that allelopathic compounds are produced by many tropical plants. For example, Abdul-Wahab and El-Naib (1972) found that water extracts of the leaves and culms of *Imperata cylindrica* contained scopolin, scopoletin, chlorogenic acid, and isochlorogenic acid, all known phytotoxins. Eussen and Soerjani (1970) also demonstrated an allelopathic effect of *Imperata* because leaves placed on the surface of the soil were incorporated into soil that inhibited growth of a test species. Chou and Young (1975) showed that aqueous extracts of 12 species of subtropical grasses inhibited seed germination and radicle growth of test plants.

Parpiev (1971) investigated the relationships between shrubs and small trees in the middle Asia deserts and the herbaceous vegetation under the shrubs and trees. Extracts of genetically and ecologically similar species of shrubs and small trees were favourable to germination of the seeds, but extracts of genetically and ecologically distinct species inhibited germination. Thus patterning was strongly influenced by allelopathy. Parpiev's results emphasized a very important point, namely that toxic interactions are generally much more likely to occur, and to be more striking, if species have only relatively recently been brought in contact with each other. This is probably the chief reason why introduced weeds and trees exhibit such striking allelopathic effects at times (for example, *Eucalyptus* spp. in California are pioneer weeds in old-field successions). Species that have evolved together for thousands of years in natural climax ecosystems are unlikely to retain strong allelopathic interactions.

Agroforestry research must be particularly concerned with allelopathy because allelochems have been shown to block nitrogen fixation by inhibiting nodule production and reducing haemoglobin content of nodules (Rice, 1979).

Plants of Faboideae and Mimosoideae generally nodulate under proper conditions, as do the majority of the legumes which do not belong to the Caesalpinioideae. Rao *et al.*, (1973) tested extracts of non-nodulating *Cassia fistula* and *C. occidentalis* (Caesalpinioideae) and non-nodulating *Leucaena leucocephala* (Mimosoideae) against *Rhizobium* strains from six genera and species of legumes. All strains of *Rhizobium* were inhibited by extracts of the non-nodulating species. Pieces of roots of the non-nodulating species also inhibited *Rhizobium*.

The evidence from many geographical areas and vegetation types indicates that inhibition of nitrification by vegetation is a widespread phenomenon. In South Africa soils taken from the *Trachypogon plumosus* grassland climax community showed a consistent lag in production of nitrate (Stiven, 1952). Meiklejohn (1962) reported that the lack of available nitrogen in Ghana grassland soils was due mainly to absence of bacteria able to oxidize nitrite to nitrate. Meiklejohn (1968) also found that soils under native grass in Rhodesia contained very few nitrifiers, but that the same soils, when cleared and planted with

crops, contained many more nitrifiers. Soils under improved grass pasture and under two legumes contained about 100 times as many nitrifiers as soils under native grass.

The mechanisms of action of allelochems are diverse and include:

- inhibition of cell division and elongation;
- inhibition of gibberellin - or indoleacetic acid induced growth;
- reduction of mineral uptake;
- retardation of photosynthesis;
- inhibition or stimulation of respiration;
- inhibition or stimulation of stomatal opening;
- inhibition of protein synthesis and changes in lipid and organic acid metabolism; and
- inhibition of haemoglobin synthesis (Rice, 1974).

It is quite clear that controlled environment facilities will be very useful in quantifying allelopathic effects on growth, mechanisms of action of allelochems, and isolation and identification of allelopathic chemicals.

Environmental effects on plant propagation

A very wide range of multipurpose tree species is currently being introduced, but relatively few of these species have been critically investigated with regard to their optimum requirements for seed germination. Furthermore, because many of them are outbreeding species, germplasm is highly heterozygous and the possibility for immediate distribution of superior genotypes exists only if vegetative or micropropagation techniques are used. So far little work has been done on this for the species concerned. Although some genera such as *Albizia*, *Erythrina*, *Glyricidia* are propagated vegetatively with ease, others (*Acacia*, *Leucaena*, and some *Prosopis* spp.) are not.

Seed germination and vegetative and micropropagation techniques all require, to a greater or lesser extent, some form of environmental control. Experiments to determine the optimum conditions under which practical field or laboratory production should be carried out are best done using an appropriate, controlled environment research facility. In some cases there is opportunity to manipulate the plant in order to obtain suitable material for propagation, and this can be done for tropical species even in temperate regions.

During the last decade there has been a surge of interest in producing 'containerized' forest nursery stock in semicontrolled greenhouses rather than in conventional forest nurseries (Owston and Kozlowski, 1981). In some regions containerized seedlings, using control of temperature, photoperiod, water and mineral supply, can be produced in ten weeks to a year. In arid or semiarid regions, planting of containerized seedlings is usually more reliable than direct sowing (Weber *et al.*, 1977). However, little is known about the specific environmental regimes needed to produce the best planting stock for many sites. Much more work is needed to establish optimum economic conditions for raising containerized seedlings of multipurpose tree species. Although much of this work can be done in the field, the use of fairly simple controlled environment facilities can provide more

precise, extrapolated results.

Studies of Rhizobium and mycorrhizas

Many of the trees showing promise for agroforestry are not only multipurpose but fast growing and nitrogen fixing (refer to Nitrogen Fixing Tree Association, PO Box 680, Waimanalo, Hawaii, 96795, USA). They include not only those in the Papilionaceae and Mimosoideae, but also such genera as *Casuarina* and *Alnus*. Furthermore, we now appreciate that endotrophic mycorrhizal associations are both commonplace and important in improving the nutrient extracting capacity of many plant species. The positive interactions which occur when plants are simultaneously hosting both rhizobial and mycorrhizal associations are relatively new and exciting areas to explore (Daft and El-Giahmi, 1976).

A great deal of preliminary work is still needed with multipurpose tree species to record the occurrence of nodules in the field, to test them for their nitrogen fixing capacity, and to examine roots for the occurrence of mycorrhizas (Keya, 1979; Redhead, 1979). Such work must be closely followed by planned programmes of research to evaluate nitrogen fixation quantitatively, using young plants in containers, and to examine strain-host relationships. Rather precise environmental control is required and programmes have already been initiated in various laboratories in support of field trials and investigations. There is scope for considerable expansion of such research if benefits from field inoculation are to be achieved similar to those which have been made with leguminous agricultural crop species and, for mycorrhizas, with certain species of forest and fruit trees.

Root studies

One of the most neglected areas of research still remains the study of plant roots and root systems. Largely because of the difficulties involved in studying living materials in soil, especially *in situ*. However, there has been considerable progress in methodology in recent years. Once again a combination of approaches using both field investigations and more detailed studies under controlled conditions (rhizotrons) has been very effective in obtaining results (Head, 1973; Huck and Taylor, 1981; and see Huck, this volume). One of the most urgent and more practical areas for research concerns the examination of rooting in nursery and planting-out situations for so far unexamined species of multipurpose trees. This could quickly result in guidelines for their more efficient field management.

Studies of plant pests and diseases

In the field or glass- or plastic house it is often impossible to separate the effects of fungal pathogens and environmental factors on plants. Each pathogen, and often each stage of pathogen with a complex life cycle, has specific environmental requirements. Plant pathogens are particularly sensitive to soil water supply (Griffin, 1978), air humidity (Yarwood, 1978), temperature (Helgeson *et al.*, 1972), and light intensity and quality (Yarwood, 1959). Wind commonly prevents formation of dew, which plays a vital role in the infection process, and it causes

raindrops or dew to dry off faster than in quiet air. For such reasons controlled environment facilities are now considered essential in conducting research on plant diseases. Controlled environments provide optimum conditions for studies of effects of disease on physiological processes and the growth of higher plants, as well as for virus assays, insect vector multiplication, root infection studies, and successive completion of disease cycles. Controlled environments also are essential for detailed studies of effects of climatic factors on host-parasite relations (Dimock, 1967).

Comparatively little is known about the diseases and pests of many multipurpose tree species, except where they have been specifically studied because of a pest-associated character (for example, *Azadirachta indica*, because of the insecticidal properties of its sap (Schmutterer *et al.*, 1981)). Although studies must begin in the field to inventory the occurrence of pests and diseases, and to establish their aetiology and epidemiology, there is considerable scope for establishing, early on, screening programmes for resistance using all the advantages that controlled environmental research can offer.

CONCLUSIONS

Information about growth and development of a wide range of multipurpose tree species is urgently needed. It would be foolish not to utilize controlled environment facilities, of one kind or another, to help provide this information as rapidly as possible. In many cases, and as long as the experimental work is closely related to problem-oriented field programmes, to do so can be cost-saving. Controlled environment facilities can then be used to investigate relevant plant responses to environment or to eliminate, or at least greatly reduce, the normal range of environmental variation which can obscure responses to other factors which are the specific objective of the investigation.

There is a whole range of agroforestry investigations, with multipurpose tree species in particular, for which one form or another of controlled environment facility will be helpful. At the lower end, crude forms of control or modification are easily and relatively cheaply established, and this should be encouraged at a national level. The more elaborate facilities, such as phytotrons and rhizotrons, are limited in number but, for more detailed work, some form of international support for research networks which include these powerful facilities, could be of considerable value.

In all cases, controlling the environment whether at a simple or sophisticated level, provides just such a facility. If the experimental objectives are clear and the experiments well-designed and planned to take advantage of the environmental control available, the costs involved will be low relative to the information that can be obtained. Otherwise investment in such research may well be misplaced.

Controlled environments should be used judiciously to answer critical questions that cannot be readily answered in the field alone. However, experienced investigators use controlled environments with due regard to some of their limitations. For example, responses of field grown and chamber grown plants to

environmental stresses are not always identical. Van Volkenburg and Davies (1977) found that cotton and soya bean leaves of field grown plants were thicker than leaves of plants grown in growth chambers at 30°C and 26°C, day and night temperatures, respectively. Davies (1977) also found that stomata of chamber grown cotton and soya bean plants were more sensitive to low light intensity than were field grown plants. The morphological differences brought about by changing light quality through the use of different kinds of lamps, may not even be the same for different cultivars of the same species (Huxley and Summerfield, 1976b) and, overall, plant morphology may well differ from that of field grown plants.

Another problem is that the responses of a species to stress in the competitive situation of a plant community may differ from results predicted on the basis of responses determined without plant competition. For example, growth of some species in a plant community in the field may be increased, despite allelopathy stress, because they may gain a competitive advantage as a result of greater impacts on other species with which they interact in the successional process. Growth of certain other species may be reduced by allelopathy stress more than expected because of reduced competitive potential.

For a discussion of guidelines for use of controlled environments the reader is referred to the book by Tibbitts and Kozlowski (1979). Despite some limitations of controlled environments they can be a valuable research tool in agroforestry, especially when field experiments are used in conjunction with research conducted in controlled environments.

REFERENCES

Abdul-Wahab, A.S. and Al-Naib, F.A.G. (1972). Inhibitional effects of *Imperata cylindrica* (L.). *P.B. Bull. Iraq Nat. Hist. Mus.* 5, 17-24.

Alofe, C.O., Schrader, L.E. and Smith, R.R. (1973). Influence of high day and variable night temperatures on nitrate reductase activity of young corn (*Zea mays* L.) plants. *Crop Sci.* 13, 625-629.

Blondon, F., Jacques, M., Jacques, R. and Mousseau, M. (1977). The combined action of light and temperature on development. Some examples analyzed in a phytotron. *In* "Environmental Effects on Crop Physiology"(J.J. Lansberg and C.V. Cutting, eds), pp.309-320. Academic Press, London and New York.

Chou, C.H. and Young, C.C. (1975). Phytotoxic substances in twelve subtropical grasses. *J. Chem. Ecol.* 1, 183-193.

Constantinidou, H.A., Kozlowski, T.T. and Jensen, K. (1976). Effects of sulphur dioxide on *Pinus resinosa* seedlings in the cotyledon stage. *J. Environ. Qual.* 5, 141-144.

Cooper, A.J. (1973). Root temperature and plant growth: a review. *Comm. Agric. Bur. Hort. Rev.* No.4, Farnham Royal, UK.

Daft, M.J. and El-Giahmi, A.A. (1976). Studies on nodulated and mycorrhizal peanuts. *Ann. appl. Biol.* 83, 273-276.

Davies, W.J. (1977). Stomatal responses to water stress and light in plants grown in controlled environments and in the field. *Crop Sci.* 17, 735-740.

Davies, W.J. and Kozlowski, T.T. (1974). Stomatal responses of five woody angiosperms to light intensity and humidity. *Can. J. Bot.* 52, 1525-1534.

Dimock, A.W. (1967). Controlled environments in relation to plant disease research. *Ann. Rev. Phytopath.* 5, 265-289.

Eussen, J.H.H. and Soerjani, M. (1978). Allelopathic activity of alang-alang (*Imperata cylindrica* (L.) Beauv.), and isolation of growth regulating substances from leaves. *In* "Studies on the Tropical Weed *Imperata cylindrica* (L.) Beauv. var. *major*" (J.H.H. Eussen, ed.). Paper No.6. Drukkerij Elinkwijk BV, Utrecht.

Griffin, D.M. (1978). Effect of soil moisture on survival and spread of pathogens. *In* "Water Deficits and Plant Growth" (T.T. Kozlowski, ed.), Vol.V, pp.175-197. Academic Press, New York.

Head, G.C. (1973). Shedding of roots. *In* "Shedding of Plant Parts" (T.T. Kozlowski, ed.), pp.237-293. Academic Press, New York.

Helgeson, J.P., Kemp, J.D., Haberlack, G.T. and Maxwell, D.P. (1972). A tissue culture system for studying disease resistance. The Black Shank disease in tobacco callus cultures. *Phytopathology* 62, 1439-1443.

Hellmers, H. (1969). Phytotrons: tools for plant physiological research. *What's New in Plant Physiology*. 6 pp.

Huck, M.G. and Taylor, H.M. (1981). The rhizotron as a tool for root research. *In* "Advances in Agroforestry" (N.C. Brady, ed.) pp.1-35. Academic Press, New York.

Huxley, P.A. and Summerfield, R.S. (1976a). Effects of daylight and day/night temperatures on growth and seed yield of cowpea cv. K2809 grown in controlled environments. *Ann. appl. Biol.* 83, 259-271.

Huxley, P.A. and Summerfield, R.S. (1976b). Photomorphogenetic effects of lamp type on growth of some species of tropical grain legumes in controlled environment growth cabinets. *Plant Science Letters* 6, 25-33.

Jeffs, P.W. and Scharver, J.D. (1976). Biosynthesis of ophiocarpine. Introduction of a stereoscopic label through transannular cyclization. *J. Am. Chem. Soc.* 98, 4301-4310.

Keya, S.O. (1979). The role of dinitrogen fixation in agroforestry. *In* "Soils Research and Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.243-270. ICRAF, Nairobi, Kenya.

Kozlowski, T.T. and Borger, G.A. (1971). Effect of temperature and light intensity early in ontogeny on growth of *Pinus resinosa* seedlings. *Can. J. For. Res.* 1, 57-65.

Kramer, P.J. (1978). The use of controlled environments in research. *HortScience* 13, 447-451.

Kramer, P.J. and Kozlowski, T.T. (1979). "Physiology of Woody Plants". Academic Press, New York.

Kramer, P.J., Slatyer, R.O. and Hellmers, H. (1972). Phytotrons and environmental physiology. *Nature and Resources* 8, 13-16.

Marshall, P.E. and Kozlowski, T.T. (1974a). The role of cotyledons in growth and development of woody angiosperms. *Can. J. Bot.* 52, 239-245.

Marshall, P.E. and Kozlowski, T.T. (1974b). Photosynthetic activity of cotyledons and foliage leaves of young angiosperm seedlings. *Can. J. Bot.* 52, 2023-2032.

Marshall, P.E. and Kozlowski, T.T. (1976). Importance of photosynthetic cotyledons for early growth of woody angiosperms. *Physiol. Plant.* 37, 336-340.

Marshall, P.E. and Kozlowski, T.T. (1977). Changes in structure and function of epigeous cotyledons of woody angiosperms during early seedling growth. *Can. J. Bot.* 55, 208-215.

Meidner, H. and Mansfield, T.A. (1968). "Physiology of Stomata". Academic Press, London and New York.

Meiklejohn, J. (1962). Microbiology of the nitrogen cycle in some Ghana soils. *Emp. J. expl Agr.* 30, 115-126.

Meiklejohn, J. (1968). Number of nitrifying bacteria in some Rhodesian soils under natural grass and improved pasture. *J. appl. Ecol.* 5, 291-300.

Norby, R.J. and Kozlowski, T.T. (1980). Allelopathic potential of ground cover species on *Pinus resinosa* seedlings. *Plant and Soil* 57, 363-374.

Owston, P.W. and Kozlowski, T.T. (1981). Growth and cold hardiness of container-grown Douglas fir, noble fir, and Sitka spruce seedlings in simulated greenhouse regimes. *Can. J. For. Res.* 11, 465-474.

Pallardy, S.G. and Kozlowski, T.T. (1979). Stomatal response of *Populus* clones to light intensity and vapor pressure deficit. *Plant Physiol.* 64, 112-114.

Parpiev, Y.P. (1971). Influence of excretions of seeds and fall of some tree shrubby species of middle Asia deserts on seed germination of subcrown plants. *In* "Physiological-Biochemical Basis of Plant Interactions in Phytocenoses" (A.M. Grodzinsky, ed.), Vol.2, pp.46-51. Naukova Dumka, Kiev, USSR. (In Russian)

Pereira, J.S. and Kozlowski, T.T. (1976). Influence of light intensity, temperature, and leaf area on stomatal aperture and water potential of forest trees. *Can. J. For. Res.* 7, 145-153.

Rao, V.R., Rao, N.S.S. and Mukerji, K.J. (1973). Inhibition of *Rhizobium in vitro* by non-nodulating legume roots and root extracts. *Plant and Soil* 39, 449-452.

Redhead, J.F. (1979). Soil mycorrhizas in relation to soil fertility and productivity. *In* "Soils Research and Agroforestry" (H.O. Mongi and P.A. Huxley, eds), pp.175-204. ICRAF, Nairobi, Kenya.

Rice, E.L. (1974). "Allelopathy". Academic Press, New York.

Rice, E.L. (1979). Allelopathy — an update. *Bot. Rev.* 45, 15-109.

Rook, D.A. (1968). Phytotronics in forestry. *N.Z. J. For.* 13, 90-97.

Schmutterer, H., Ascher, K.R.S. and Rembold, H. (Eds) (1981). "Natural Pesticides from the Neem Tree (*Azadirachta indica* A. Juss)". German Agency for Co-operation (GTZ), Eschbon.

Stiven, G. (1952). Production of antibiotic substances by the roots of a grass (*Trachypogon plumosus* (H.B.K.) Nees) and of *Pentanisia variabilis* (E. Mey.) Harv. (Rubiaceae). *Nature* 170, 712-713.

Summerfield, R.S., Huxley, P.A., Dart, P.J. and Hughes, A.P. (1976). Some effects of environmental stress on seed yield of cowpea (*Vigna unguiculata* (L.) Walp.) cv. Prima. *Plant and Soil* 44, 527-546.

Summerfield, R.J., Huxley, P.A. and Minchin, F.T. (1977). Plant

husbandry and management techniques for growing grain legumes under simulated tropical conditions in controlled environments. *Expl Agric.* 13, 81-92.

Sun, S.M., Mutschler, M.A., Bliss, F.A. and Hall, T.C. (1978). Protein synthesis and accumulation in bean cotyledons during growth. *Plant Physiol.* 61, 918-923.

Tibbitts, T.W. and Kozlowski, T.T. (Eds) (1979). "Controlled Environment Guidelines for Plant Research". Academic Press, New York.

Volkenburgh, E. van and Davies, W.J. (1977). Leaf anatomy and water relations of plants grown in controlled environments and in the field. *Crop Sci.* 17, 353-358.

Weber, F.R., Holman, F.J. and Palmer, V.C. (1977). "Reforestation in Arid Lands". *Action/Peace Corps Program and Training Manual, Series* No.5. VITA Publications Manual Series No.37E. VITA, Mount Rainier, Maryland, USA.

Went, F.E. (Ed.) (1957). "Experimental Control of Plant Growth". Chronica Botanica, Waltham, Massachusetts, USA.

Yarwood, C.E. (1959). Microclimate and infection. *In* "Plant Pathology 1908-1958" (C.S. Holten *et al.*, eds), pp.548-556. Univ. Wisconsin Press, Madison, Wisconsin, USA.

Yarwood, C.E. (1978). Water and the infection process. *In* "Water Deficits and Plant Growth" (T.T. Kozlowski, ed.), Vol.V, pp. 144-173. Academic Press, New York.

Meeting Organization
and
Reports of Working Groups

PARTICIPANTS

P. de T. ALVIM, Centro de Pesquisas do Cacao (CEPLAC), Km 26, Rodovia Ilheus-Itabuna, PO Box 7, Itabuna, BA, Brazil.

J.G. BENE, 2830 S.W. Marine Drive, Vancouver V6N 3X9, British Columbia, Canada.

C.B. BRISCOE, Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE), Turrialba, Costa Rica.

E.F. BRUNIG, University of Hamburg, Federal Research Centre for Forestry and Forest Products, Institute for World Forestry Science, 91 Leuschnerstrasse, PO Box 80 02 10, D-2050 Hamburg 80, West Germany.

G. BUDOWSKI, Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE), Turrialba, Costa Rica.

M.G.R. CANNELL, Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian EH26 0QB, Scotland, UK.

D.J. CONNOR, La Trobe University, School of Agriculture, Bundoora, Victoria 3083, Australia.

J. COOMBS, Winchcombe Cottage, Bucklebury Common, Reading, Berks. RG7 6SL, UK.

H. CROZE, United Nations Environment Programme (UNEP), Global Environment Monitoring Service, PO Box 30552, Nairobi, Kenya.

C.W. GAITHO, Forest Research Station, PO Box 74, Kikuyu, Kenya.

A. GETAHUN, International Institute for Tropical Agriculture (IITA), P.M.B. 5320, Ibadan, Nigeria.

W. GODFREY-SAM-AGGREY, University of Swaziland, Faculty of Agriculture, P.O. Luyengo, Swaziland.

M. GWYNNE, United Nations Environment Programme (UNEP), Global Environment Monitoring Service, PO Box 30552, Nairobi, Kenya.

W. HETSCH, Tirdep Soil Erosion Control/Agroforestry Project W. Usumbaras (SECAP), PO Box 72, Lushoto, Tanzania.

M.G. HUCK, United States Department of Agriculture (USDA), Auburn University, Department of Agronomy and Soils, 235 Funchess Hall, Alabama, AL 36849, USA.

P.A. HUXLEY, International Council for Research in Agroforestry (ICRAF), PO Box 30677, Nairobi, Kenya.

J.E. JACKSON, East Malling Research Station, Department of Pomology, Maidstone, Kent ME19 6BJ, UK.

M. KINYA, Ministry of Energy, PO Box 30582, Nairobi, Kenya.

T. KIRA, Lake Biwa Research Institute, Uchide-Hama, Otsu, Shiga 520, Japan.

T.T. KOZLOWSKI, University of Wisconsin-Madison, The Biotron, 2115 Observatory Drive, Madison, Wisconsin, WI 53706, USA.

H.F. LAMPREY, United Nations Educational, Scientific and Cultural Organisation (UNESCO), Regional Office for Science and Technology for Africa, PO Box 30592, Nairobi, Kenya.

T. LEDIG, United States Department of Agriculture (USDA), Forest Service, Pacific Southwest Forest and Range Experiment Station, 1960 Addison Street, PO Box 245, Berkeley, California, CA 94701, USA.

L. LEYTON, University of Oxford, Department of Forestry, Commonwealth Forestry Institute, South Parks Road, Oxford OX1 3RB, UK.

R.S. LOOMIS, University of California, College of Agricultural and Environmental Sciences, Department of Agronomy and Range Science, Agricultural Experiment Station, Davis, California, CA 95616, USA.

M.J.S. MAGAMBO, Tea Research Foundation of Kenya, PO Box 91, Kericho, Kenya.

H.-J. von MAYDELL, Federal Research Centre for Forestry and Forest Products, Institute for World Forestry Science, 91 Leuschnerstrasse, 2050 Hamburg 80, West Germany.

G. MICHON, Institut de Botanique, Laboratoire de Botanique, 5 Rue Auguste-Broussonet, 34000 Montpellier, France.

P.K.R. NAIR, International Council for Research in Agroforestry (ICRAF), PO Box 30677, Nairobi, Kenya.

B. NDUNGURU, University of Dar es Salaam, Faculty of Agriculture, Forestry and Veterinary Science, Department of Crop Science, PO Box 643, Morogoro, Tanzania.

D. NGUGI, University of Nairobi, Faculty of Agriculture, PO Box 30197, Nairobi, Kenya.

J. ODERA, Kenya Agricultural Research Institute (KARI), PO Box 30148, Nairobi, Kenya.

B.N. OKIGBO, International Institute for Tropical Agriculture (IITA), P.M.B. 5320, Ibadan, Nigeria.

R.A.A. OLDEMAN, Agricultural University, Department of Silviculture, 64 Generaal Foulkesweg, PO Box 342, 6700 AH Wageningen, The Netherlands.

D. OSIRU, Makerere University, Faculty of Agriculture, PO Box 7062, Kampala, Uganda.

F. OWINO, University of Nairobi, Forestry Department, Kabete Campus, PO Box 30197, Nairobi, Kenya.

B. PEDERSEN, Royal Veterinary and Agricultural University, Department of Plant Physiology and Anatomy, 40 Thorvaldsenseveji, DK 1871 Copenhagen V, Denmark.

B. PICKERSGILL, University of Reading, Department of Plant Sciences, Whiteknights Park, Shinfield Road, Reading, Berks. RG6 2AS, UK.

K.O. RACHIE, The Rockefeller Foundation, 1133 Avenue of the Americas, New York, NY 10036, USA.

J.B. RAINTREE, International Council for Research in Agroforestry (ICRAF), PO Box 30677, Nairobi, Kenya.

H.A. STEPPLER, International Council for Research in Agroforestry (ICRAF), PO Box 30677, Nairobi, Kenya.

L.L. TIESZEN, Augustana College, Department of Biology, 29 & Summit, Sioux Falls, South Dakota, SD 57197, USA.

F. TORRES, International Council for Research in Agroforestry (ICRAF), PO Box 30677, Nairobi, Kenya.

TRAN VAN NAO, Food and Agriculture Organisation of the United Nations (FAO), Forestry Department, Via delle Terme di Caracalla, Rome 00100, Italy.

CONTRIBUTORS ONLY

D.O. HALL, University of London, King's College, 68 Half Moon Lane, London SE24 9JF, UK.

A. KUMURA, University of Tokyo, Faculty of Agriculture, Department of Agronomy, Tokyo 113, Japan.

J.A. MAGHEMBE, University of Dar es Salaam, Faculty of Agriculture, Forestry and Veterinary Science, Division of Forestry, PO Box 643, Morogoro, Tanzania.

J.F. REDHEAD, University of Dar es Salaam, Faculty of Agriculture, Forestry and Veterinary Science, Division of Forestry, PO Box 643, Morogoro, Tanzania.

N. SANDER, University of Hamburg, Federal Research Centre for Forestry and Forest Products, Institute for World Forestry Science, 91 Leuschnerstrasse, PO Box 80 02 10, D-2050 Hamburg 80, West Germany.

C.E. WHITMAN, University of California, College of Agricultural and Environmental Sciences, Department of Agronomy and Range Science, Agricultural Experiment Station, Davis, California, CA 95616, USA.

MEETING ORGANIZATION

SESSION CHAIRMEN

E.F. Brunig
G. Budowski
T. Kira
L. Leyton
B. Ndunguru
D. Ngugi
B.N. Okigbo
R.A.A. Oldeman
F. Owino
L.L. Tieszen

RAPPORTEURS

K.O. Rachie, Co-ordinator

M.G.R. Cannell
M.G. Huck
J.E. Jackson
P.K.R. Nair
B. Ndunguru
B. Pickersgill
J.B. Raintree
F. Torres

CHAIRMEN OF WORKING GROUPS

H.A. Steppler, Co-ordinator

P. de T. Alvim
M.G.R. Cannell
T.T. Kozlowski
R.A.A. Oldeman
B. Pickersgill

MEETING ORGANIZER

P.A. Huxley

SECRETARIES

C. Kanyeki
B. Kibe

REPORT OF WORKING GROUP 1

THE ANALYSIS OF PLANT-TO-PLANT INTERACTIONS IN AGROFORESTRY

P. de T. Alvim, Chairman
J. Coombs
W. Hetsch
M.G. Huck
R.S. Loomis
B. Pedersen

BACKGROUND AND FRAMEWORK

The productive activities of plant communities must always be viewed and interpreted on an area basis. The reason is that the controlling factors of plant growth (light, water, nutrients and space) are all dependent in some way on land area. When the occupation of land increases, the interactions among adjacent plants increase at the same time. We may say that competition for scarce resources occurs when the potential resource use of several plants cohabiting in time and space exceeds the resource supply. The growth of one or more of the individual plants is then reduced to less than its potential. The term 'interference' is usually preferred to competition since the influence of neighbouring plants is usually indirect through modifications of nutrient supply or the microclimate, rather than direct.

In monospecific communities with all individuals of the same size, spacing and age, interference is more or less the same for all individuals, and all plants respond the same. In mixed communities the interference may be unequal at one extreme or the other. It may be that each species finds interference from unlike species more severe than from individuals of its own kind. In agroforestry, for instance, shading by the overstorey crops invariably interferes with photosynthesis of understorey species. At the other extreme, some species may find less interference. That occurs when the competing species use resources somewhat differently. Since all plants use the same resources (for example, the essential nutrients are all the same), the 'different use' depends mainly upon the plants acquiring the resources at a somewhat different time or from a different space.

The possible range of such interactions can be expanded beyond resource use to include modifications in the spread of pests and diseases, and the possibility that a surviving species will expand in its growth and thus compensate for a species that fails. With agroforestry, the dimensions expand further. Particularly important aspects are the degree to which the overstorey modifies the microclimate (especially light intensity), checks the understorey growth to match nutrient supply, cycles nutrients from deep soil layers, and so forth.

Our concern for proper management and improvement of agroforestry cannot be achieved unless we have a clear understanding of how such systems work. And such understanding depends upon our knowing about the nature and extent of the plant-to-plant interactions. The alternative is to approach the system empirically and with only a slow and uncertain chance for progress;

one gains a perspective on this by considering the ramifications of introducing a new maize cultivar in a maize - bean agroforestry complex. Empirically, this could entail a re-examination, among other things, of the appropriate bean cultivars, of space relations, and of the types and density of the interactive trees. Progress in improvement, as well as in day-to-day management, requires improved understanding and some simpler means for evaluating the mechanisms and results of interference. We present here guidelines for obtaining that better understanding.

GUIDELINES

These involve several levels of sophistication and detail.

Survey

Methods need to be evolved for the characterization of sites where different agroforestry schemes are operating. This will include descriptions of geographical, climatic, topographic, phenological and plant characteristics. It will also include a qualitative judgment and preliminary estimate of the main interactions.

The aim of this preliminary characterization is to define the smallest recognizable unit or area in which the tree - field crop interaction occurs. We termed this an *agro-unit*. To identify the agro-unit requires an accurate map of species and their distribution in space and time. For instance, linear measurements, photographs, identification of the species and other simple observations, made and plotted on graph paper. This map is then inspected for repeating identical units. If no pattern emerges a unit of importance must be selected on a judgment basis, or units must be centred around a tree, or trees, and extended to the limits of tree interactions with field crops.

Monitoring

More detailed analytical listing is then carried out to establish the state of various parameters within the unit; with emphasis on water, light and nutrients. Further measurements are taken to determine biomass production and harvest index. From these data a judgment is made to identify limiting factors.

Perturbation tests

The conditions observed through monitoring can be tested by putting perturbation into the systems, for example by adding water, fertilizer, or by removing part of the plants, or their canopy, in order to see what happens.

Experimental studies

Controlled experiments within research stations, or demonstration farms, can be used to show what improvements in management can be made if limiting factors, identified above, are overcome.

This overall programme provides basic quantitative definitions of the controlling factors and processes at the tree - herb interface.

REPORT OF WORKING GROUP 2

ECOLOGICAL CONSIDERATIONS

T.T. Kozlowski, Chairman
E.F. Brunig
D.J. Connor
J.E. Jackson
T. Kira
H. Lamprey
L. Leyton
L.L. Tieszen

The group had in mind agroforestry land use involving high-inputs, low-inputs, sustainable farms and gardens, and silvo-pastoral systems. Also agroforestry as a means of land rehabilitation and conservation.

SOME QUESTIONS FOR CONSIDERATION

Although agroforestry practices are commonplace in the tropics and subtropics, there is only scanty information about their functions and overall place in land development. Answers are needed for the following.

- What is the role of agroforestry, in the systems context, in energy, water, and nutrient partitioning and utilization?
- What is the role of agroforestry in food production and in economic return?
- How can agroforestry associations provide a buffer against physical, biological, and social disruption?
- How can ICRAF most effectively contribute to the development and utilization of analytical and predictive methods appropriate to agroforestry?
- How can information concerning ecosystem status and functioning be disseminated, demonstrated, and applied?

RESEARCH NEEDS BY PRIORITY

The answers to at least some of these questions will be obtained through the following lines of investigation.

- Development of guidelines for site assessment as a basis for the choice of species. These should be based on site characteristics: geology, existing plants, amount, and annual and seasonal distribution of rainfall, potential evapotranspiration (E_T), soil physical and chemical characteristics, topography, and temperature.
- Development of an information system that will identify tree species suited to a particular site and, as far as possible, selection of species combinations for agroforestry systems suited to that site.
- Quantitative studies of specific agroforestry systems in terms of water and nutrient cycles and budgets, as well as energy utilization, productivity, and yield. A key objective

should be to determine their efficacy as sustainable land use systems.

- Development of simulation models of agroforestry systems at varying levels of complexity. The objectives being:
  - to study the interactions of processes, and the responses of systems to cultural practices and environmental changes;
  - to predict the effects of such changes;
  - to experimentally validate these predictions.
- Studies of physiological processes. For example, the growth responses and phenological characteristics of important species in relation to environmental and biological factors, as needed to provide information for systems analysis.

PROVISION OF MANUALS

Information about agroforestry is widely scattered and there are few guidelines as to how our existing knowledge of experimental design and management can be adapted to solve the problems arising from the greater range of components, and the more complex space/time factors, that are commonplace in agroforestry systems. There is an urgent need for research manuals that include the following topics, and existing manuals could be surveyed, in the first place, as a source of content.

- Measurement techniques for environmental, plant and edaphic factors.
- Applicable statistical designs.
- Systems analysis.
- Data manipulation.
- Principles of studying energy, nutrient, and water flow in agroforestry systems.
- Lists of equipment and suppliers.
- Techniques for ecological surveys.
- Tabular presentations of nutrient and energy content and economic yield from agroforestry systems.

Manuals would ideally be used for, and developed along with, training courses for research workers in agroforestry.

THE ROLE OF ICRAF

This was seen as follows.

- To co-ordinate and disseminate information on agroforestry systems.
- To demonstrate agroforestry systems in the field.
- To conduct research to develop methodologies for evaluating agroforestry systems.
- To stimulate and arrange funding for research in agroforestry by other institutions and organizations, and to encourage co-ordination and co-operation among projects. Also to facilitate the integration and synthesis of results.
- To promote training for research and extension work in agroforestry.

REPORT OF WORKING GROUP 3

PLANT TYPES FOR AGROFORESTRY

M.G.R. Cannell } Chairpersons
B. Pickersgill
J.G. Bene
C. Briscoe
T. Ledig
G. Michon
D. Osiru
K.O. Rachie

KEY ISSUES

Identifying a role for agroforestry

It is first necessary to identify where there is a role for agroforestry; considering the semiarid and the humid tropics separately. A need will exist whenever the following situations occur

- The land use or farming system is perceived to be non-self-sustaining because of:
  - depletion of soil nutrients (especially N and P);
  - soil degradation due to absence of soil cover at certain times;
  - inadequate fuel and food supplies.
- Trees might lessen the risk of hardship because of crop failure (because of the inherently well-buffered ecosystem in agroforestry), and wherever trees will allow farmers to accumulate capital or cash.
- Trees will help to spread productive activities throughout the year, by staggering the harvests, providing products in dry seasons, or spreading the labour load.

Deciding what tree species should be grown.

There are several relevant factors.

- To determine what environmental resources are limiting (usually N, P and/or water), and what products the trees should provide.
- To decide if there is a need to establish trees quickly to arrest soil degradation and sustain food crop production as an emergency measure. If so, fast-growing, easily-propagated soil restorers could be introduced before multipurpose trees. (However, multipurpose trees may be preferred to minimize risks and increase the harvest index.)
- To choose species from the locality, if possible, or from analogous sites elsewhere, and from slightly more favourable environments. (Genetic diversity should be maintained rather than selection for single adaptable genotypes.)

Deciding what understorey crop / tree crop combinations should be used

For this it is necessary to undertake the following.

- First, to study the socio-economic context.
- Then, to promote dissemination of genetically diverse herbaceous crops (not just sole-crop cultivars) for farmers themselves to integrate into complex site-specific agroforestry systems.

RESEARCH NEEDS

Research needs to be promoted in the following areas.

- The selection of 'soil improvers'. That is, trees that will fix or absorb large amounts of N and P and will return them to the soil via leaf fall or lopping. Research should concentrate on the amounts of N and P that can be transferred to the soil per year in this way.
- Socio-economic studies on farming systems in 'fragile ecosystems' in the semiarid and humid tropics. Including assessments of constraints, impacts and human aspects, with projections of the socio-economic consequences of introducing tree species into various types of tropical land use.
- The screening of trees for their complementarity with a range of locally acceptable herbaceous crops, by planting beneath existing trees where this is possible.
- The evaluation of
  - exotic (non-native) species,
  - palms,
  - underexploited crop plants for use in agroforestry systems.
- Observations on the phenology of potentially valuable trees, including investigations on the manipulation of tree phenophases.
- Studies on the responses of trees to coppicing and lopping (timing, frequency, severity, and so on).
- The screening of trees for undesirable traits such as allelopathy, poisonous foliage, weediness, and so on.

TOPICS FOR MANUALS ON AGROFORESTRY

Loose-leaf reference manuals should be produced and regularly updated on the following.

- Species of value, or potential value, in agroforestry. Topics covered should, where possible, include obvious features such as the relative value of the species when cultivated for a particular purpose, plus methods of propagation, sources of planting material, Hallé-Oldeman architectural models, phenology, microbial associations, allelopathy and other undesirable attributes, as well as performance in given environments.
- Agroforestry crop associations. Topics covered should, where possible, include the performance of the components, the management system, the nitrogen budget, climate and soil, the ecological and socio-economic content. Known failures should be included.

THE ROLE OF ICRAF

With regard to plant types of use in agroforestry, ICRAF should emphasize the following activities.

- The promotion and co-ordination of the establishment of species collections and seed banks at various national centres, each dealing with specific species in their domain. ICRAF itself should take the lead in Kenya, by establishing a small gene bank of locally useful species.
- The explanation of ways to facilitate the transfer of genetic resources across national boundaries. This might be done by
  - promoting discussion on criteria for the movement of plant material,
  - convening a meeting of interested parties, such as quarantine officers, and
  - encouraging work on methods of transporting material other than by seeds or cuttings, that is by meristem or tissue culture.
- The co-ordination of international networks of species and provenance trials, perhaps beginning with tree legumes that conserve the soil and improve its nutrient status. Work on (other) multipurpose trees, particular tree-crop associations and management practices, might follow later.
- Pooling of information from various countries on methods of disseminating seeds or seedlings, and cuttings, to farmers at regional and local levels. For example, by using schools, local organized groups, and the provision of incentives, and so on.

REPORT OF WORKING GROUP 4

PLANT MANAGEMENT CONSIDERATIONS IN AGROFORESTRY[1]

R.A.A. Oldeman, Chairman
G. Budowski
M. Kinya
M.J.S. Magambo
P.K.R. Nair
B. Ndunguru
B.N. Okigbo
J.B. Raintree
F. Torres
Tran van Nao

BACKGROUND AND FRAMEWORK

The proper management of plants in agroforestry depends entirely on a sufficient knowledge of the following.

- The interactions between the species.
- The available resource spaces ('niches') for every species within the agroforestry ecosystem, as well as the ecosystem processes determining this space (for example, the nutrient budget and water balance).
- The biological profiles of possible plant species.
- What pathogens and pests may be present, and their behaviour in these systems.
- Socio-economic factors, especially those having a direct bearing on the landuser's problem and his decision making processes.

Other working groups have considered some aspects of the first three points, but management considerations should also include the following.

- Criteria to compare agroforestry systems with other land use systems including assessment and performance evaluations. Sole crop production data for each of the woody and other crop components should also be available, as standards or checks.
- An awareness that management is a dynamic not a standard recipe, and it requires continuous refinement based on experience, information and changing objectives.

OBJECTIVES

No management plan can be conceived without first defining objectives. For agroforestry and other land uses these are essentially, and in optimal combination, the following.

- Production goals.
- Sustainability requirements.
- Efficiency of resource use.
- The acceptability (adoptability) of the system.

---

1. Aspects of integration of this subject within systems is considered also in this Working Group's recommendations.

Implied in the broader aims, more specific items can be listed as follows.

- Effects on adjacent land.
- Farm or community benefits.
- Ecological soundness.
- Socio-economic desirability (for example, product and service diversity, low risk, and desirable labour utilization patterns).
- Regional complementarity.
- Balance between short- and long-term objectives and effects, including nature conservation.

Agroforestry (as with other forms of land use) is conditioned by location. Location can be differentiated at several levels.

- As climatic zones (humid to dry, low to high altitude).
- As soil regions.
- As toposequences (small-scale gradients linked to topography).

Each location has its own management objectives.

RESEARCH NEEDS

The strategy

Investigations on agroforestry plant management should follow the same steps as that in other aspects of agroforestry research.

- The systematic cataloguing of plant management practices within existing land use systems.
- A qualitative and quantitative performance assessment of management aspects relevant to agroforestry. Especially as to their overall flexibility in terms of the objectives.
- The identification of appropriate research areas relevant to agroforestry.
- The design of appropriate plant management practices by refinement of existing practices, or the development of new ones.
- Testing the improved practices.
- Validation.
- Transfer to land users.
- Evaluation.

This is a cyclic process of constant feedback from evaluation, with consequent refinement. Three entries give access to this strategy.

- Constraint analysis.
- Analysis of possibilities (new or alternative).
- Analysis of local or transferable success stories.

Research topics

These are only indicative examples of broad areas of research.

- The management of canopy types, including light management for higher and lower canopy strata.
- The spatial and temporal arrangement of plants.
- Growth and development cycles in management situations.
- Input management, particularly with regard to low level of inputs.
- The management of biomass production; efficiency per unit amount of growth factor.
- Nutrient management, including di-nitrogen fixation.
- Soil conservation management.
- Studies of response, or reactions, to stress factors.
- Performance related to water balance (excesses or deficits).
- Soil management (for example, tillage) in relation to plant management.

All these areas of research have to be covered at different integration levels; field - farm, or family - community, or village (the largest unit where everyone knows everyone) - region - nation. The village market, with outputs to the local population (subsistence) and the outside population (plus-revenue for locals), is at the crux of the system.

These levels have to fit, also, when agroforestry management is introduced. Ancillary or supporting requirements of each level have to be considered.

Guidelines for planning research

The plant components, and their efficient management, are but one set of factors to be considered within any particular agroforestry land use systems.

The following guidelines need to be borne in mind when planning any specific agroforestry research projects. No priorities are indicated as any number, or all, may be relevant in particular situations.

- In as much as it is possible, plant management practices should not compete, but be compatible with other land use practices.
- Plant management should be socially acceptable and adapted to land tenure patterns.
- The efficiency of the system as a whole will depend on:
  - types of components (for example, the versatility of plant components);
  - number of components, as a determinant of labour requirements: the higher the number, the more complex the system;
  - arrangement pattern of components, especially in relation to water availability.
- A long list of recommended or selected plant types should be the basis for devising management systems containing a maximum number of low risk species of potential use that do well at low levels of inputs.
- Plant management should aim at efficient resource utilization both of externally applied and native resources, and take into account the possible growth of resources.
- Systems as a whole should be compatible with the values,

customs, problem-perception and decision-making structures and capabilities of local landusers.

- Where species with conservation properties (anti-soil erosion, potentials for di-nitrogen fixation) are to be used, preference should be given to those species which also yield products (the landusers conservation perception may often be absent).

- Plants and plant management should aim at supporting self-regulating ecosystems with optimal resource use, and low-cost reliable techniques for countering adverse conditions, where possible. Favourable aspects of such systems are:

  - complementary sharing of above- and below-ground resources by plants;
  - sequential planting and harvesting to yield products during lean seasons;
  - the use of versatile plants (for example, palms, legumes, bamboos, certain tuber crops, climbers).

- Research into existing agroforestry land use systems with regard to the management of plants should be done especially with regard to the following situations:

  - reclamation of degraded lands;
  - agroforestry systems (such as forest gardens) which have been proven a success under local conditions;
  - water harvesting systems and oases in dry regions;
  - agroforestry systems using perennial crop species; and management systems where the harvest is spread over a long period (for example, sequential lopping, or fruit harvesting).

- In plant management studies labour should be as regularly measured as other factors, so that labour requirements may be quantified.

- Land users should have as wide a choice of species as possible for any particular end uses / ecozones.

Some further generalizations can be stated thus.

- Agroforestry should not be considered as a panacea to cure all evils of land management, nor is it of uniform applicability. Its merits or demerits have to be rigorously compared with alternative forms of land use.

- Emphasis in devising practical schemes of plant management in agroforestry will often be on the smallholder.

- The economic appraisal of the outcome of any particular ways of associating or managing plants should be made using economic methodologies suited to the analysis of long-term multiple output land use systems, if these are available. Where they are not plant researchers and economists need to work closely together.

THE ROLE OF ICRAF

ICRAF has an essential part to play in developing our knowledge and expertise in relation to plant management aspects of

agroforestry in the following ways.

- By continuing, forcefully, to develop a methodology to describe and evaluate agroforestry systems, and to promote the identification and description of existing systems with other agencies. Only in this way will the technical aspects of plant management be related, holistically, with all the other parts of the agroforestry land use system.
- To classify agroforestry systems, and help to develop an understanding of the plant functions and interactions within them.
- To initiate and prepare a plant management manual for selected agroforestry systems.
- To promote complementary work among regional and national agencies on all these aspects, be it on a geographical or a functional basis.

INDEX OF PLANT NAMES

abaca, see *Musa textilis*
Abies 353
A. veitchii 356
Acacia 105, 112, 197, 200, 260, 310, 318, 409, 477, 514, 557, 561
A. albida 72, 119, 120, 121, 123, 259, 275, 276, 318, 408, 514
A. ancura 380
A. harpophylla 405
A. muricata 105
A. nilotica 120
A. reficiens 133
A. senegal 119, 120, 133
A. tortilis 133, 514, 558
Acer saccharum 432, 434, 438
Acioa barteri 35, 276
Aconitum japonicum 357
Actinomycetes 312
Adansonia digitata 32
Aerva lanata 338
African breadfruit, see *Treculia*
African mango, see *Irvingia*
African pear 30, see also *Dacryodes*
Agave 198, 200
alabhang, see *Dicanthium aristatum*
Albizia 20, 105, 189, 260, 561
Alchornea cordifolia 35
alder, see *Alnus acuminata*
alfalfa, see *Medicago sativa*
algaroba, see *Prosopis*
almond 465
Alnus 147, 276, 562
A. acuminata 53, 58, 61, 62, 312
A. jorullensis, see *Alnus acuminata*
A. rubra 438
Aloe 133
Alternanthera peploides 338
alyce clover, see *Alysicarpus vaginalis*
Alysicarpus vaginalis 93
Amaranthus 340
A. hybridus 338
A. lividus 338
Amazon peach palm, see *Bactris gasipaes*
Amorphophallus campanulatus 89, 91, see also elephant foot yam
Anabaena 150
Ananas comosus 88, see also pineapple
Andropogon scoparius 443
animal millet, see *Brachiaria*
Annona 139
A. senegalensis 190
Anthocephalus chinensis 64
Anthonotha macrophylla 35
apple 313, 366, 370, 371, 372, 373, 457, 460, 463, 465, 468, 49.
Arachis glabrata 106, 311
A. hypogaea 89, 119, 312
Areca catechu 88
areca nut, see *Areca catechu*
arek 18
arrowroot, see *Maranta arundinacea*
Artocarpus altilis 88, 111, see also jackfruit
aspen 460, see also *Populus*
Aspergillus 141
Atriplex halimus 338
Auricularia polytricha 73
avocado 315, 463
Axonopus compressus 93
A. scoparius 53
Azadirachta indica 133, 558, 563
Azotobacter 150, 151
azuki beans 360

Bactris gasipaes 111, 114, see also pejibaye
Balanites 260
bambara groundnuts, see *Voandzeia subterranea*
bamboo 18, 190, 388, 389, 390
banana 14, 18, 19, 20, 28, 30, 73, 82, 87, 94, 187, 190, 394, 470, 473, 478, 481, 493

see also *Musa* and plantain
baobab 410, see also *Adansonia*
Baphia nitida 35
barley 311, 357, 480, 497, see also *Hordeum vulgare*
batiki blue grass, see *Ischaemum asistatum*
beans 18, 28, 188, 478, see also under types and species
beans, climbing 109
beech, see *Fagus grandifolia*
beet 313, 495
Beijerinckia 150
Bermuda grass, see *Cynodon dactylon*
Betula 45, 147
black cherry, see *Prunus serotina*
black cottonwood 440, see also *Populus trichocarpa*
black fonio, see *Digitaria iburua*
black gram 90, see also *Vigna mungo*
black pepper, see *Piper nigrum*
Boehmeria nivea 90
Boerhavia diffusa 338
bonavist bean, see *Lablab niger niger*
Brachiaria 340
B. brizantha 93
B. decumbens 66, 93
B. humidicola 66, 93
B. miliiformis 93
B. mutica 93
B. ruziziensis 93
Brachychiton 410
Brassica intergrifolia 338
brazil nut 65, 69
breadfruit 30, 113, see also *Artocarpus altilis*
Brosimum 260
B. alicastrum 112, 514
bruchids 318
buffalo grass, see *Stenotaphrum secundatum*
Butyrospermum paradoxum 27, 35, 36, 120, see also shea butter nut
Byrsonima 190

cabbage 373
cacao 18, 21, 28, 47, 49, 50, 80, 81, 82, 86, 87, 94, 96, 97, 101, 104, 189, 192, 277, 310, 312, 315, 391, 392, 465, 474, 481, 505, see also *Theobroma cacao*
cacao pod rot, see *Monilia roreri*
cadam, see *Anthocephalus chinensis*
Cajanus 318
C. cajan 49, 89, 106, 112, 119, 128, 276, see also pigeon pea
Calliandra 105
calopo, see *Calopogonium mucunoides*
Calopogonium mucunoides 92
Camellia sinensis, see tea
Campnosperma brevipetiolatum 316
Canavalia ensiformis 119
Canarana erecta, see *Echinochloa pyramidalis*
Canna edulis 76
Capsicum 315, see also sweet pepper
C. annuum 88, 89, 198
cardamon, see *Elettaria cardamomum*
Caribbean pine 176, see also *Pinus caribaea*
Carica papaya 88, 133
carob, see *Ceratonia siliqua*
carrot 495
Caryocar 112
cashew 80, 81, 82, 463, 465
cassava 14, 18, 19, 21, 28, 30, 32, 48, 49, 65, 69, 82, 87, 90, 94, 110, 139, 313, 371, 410, 456, 474, 478, 480, 494, 495, see also *Manihot esculenta* and manioc
Cassia 105, 260
C. fistula 560
C. occidentalis 560
Castanea 112
Castanopsis 356
Casuarina 562, 557
C. equisetifolia 316
Cedrela odorata 53
cedro, see *Cedrela odorata*
centro, see *Centrosema pubescens*
Centrolobium 105
Centrosema pubescens 92, 93
Ceratonia 260
C. siliqua 156, 514
Cercropia 313, 349
Chenopodium quinoa 314
cherry 313, 315

chestnut, see *Castanea*
chickpea, see *Cicer arietinum*
chillies, see *Capsicum annuum*
chillipepper 315, see also *Capsicum annuum*
Chinese cabbage 360
Chinese potato 90, see also *Coleus parviflorus*
Chrysanthemum 456
C. morifolium 432
Cicer arietinum 119
Cinnamomum zeylanicum 88
cinnamon 87, see also *Cinnamomum zeylanicum*
citrus 18, 30, 35, 47, 61, 372, 394, 463, 465, 466, 470, see also *Citrus sinensis* and orange
Citrus sinensis 48
Clathrotropis 105
Clostridium 150
C. thermocellum 142
clove 14, 16, 19, 21, 87, see also *Syzygium aromaticum*
coconut 18, 19, 28, 30, 69 79 - 99, 101, 275, 309, 310, 316, 371, 463, 465, 473
cocoyam 28, 30, 474, see also *Colocasia esculenta* and taro
Coffea arabica 48, 82, 506
C. canephora 82, 88
coffee 18, 19, 21, 28, 47, 49, 50, 61, 80, 81, 82, 104, 176, 189, 192, 267, 277, 312, 394, 457, 463, 465, 473, 474, 481, 491, 492, 493, 516, see also *Coffea arabica* and *C. canephora*
Coleus parviflorus 91
Colocasia 89, 193
C. esculenta 90, 190, see also cocoyam
coloniao, see *Panicum maximum* cv colonial
Congo grass, see *Brachiaria ruziziensis*
conifer 381
Corchorus 90
C. olitorius 338
Cordeauxia 260
Cordia alliodora 44, 45, 47, 49, 51, 52, 61
Cordyline 18
cori grass, see *Brachiaria miliiformis*
Coriandrum sativum 88
corn 65, 66, see also maize
cotton 28, 32, 392, 394, 406, 456, 507, 508, 509, 531, 532, 542, see also *Gossypium*
cotton, perennial 313
cottonwood, see *Populus deltoides*
cow tree 113, see also *Brosimum alicastrum*
cowpea 28, 30, 32, 126, 127, 456, 468, 472, 495, 496, 497, 509, 510, 511, 512, see also *Vigna unguiculata*
Crossopteryx febrifuga 190
Crotalaria brevidens 338
Cryptomeria japonica 352, 353, 354, 471
cucumber 18, 82, see also *Cucumis sativum*
Cucumis sativum 44
Cucurbita maxima 44
cucurbits 311, 456
cupuacu 69
Curcuma longa 76, 88, 91, see also turmeric
Cyclobalanopsis 356
Cynodon dactylon 93
C. plectostachyus 49
Cyperus esculentus 190
cypress 44

dacheen, see *Colocasia esculenta*
Dacryodes edulis 36
Dactylis glomerata 435
Dactyloeladus 232, 234
Dahlbergia 105
dandelion, see *Taraxacum officinale*
Danthonia 411
date palm 190
deglupta 65, see also *Eucalyptus deglupta*
Desmodium 105
D. canum 93
D. heterophyllum 93
D. intortum 93
D. trifolium 93
Dialium 105
D. guineense 35, 36
Dicanthium aristatum 93
Digitaria exillis 340
D. iburua 340
Dioscorea 76, 89, 192, 198
D. alata 91
D. esculenta 91
Dipterocarpus 349
Douglas fir 433

durian 18, 19, see also *Durio zibethinus*
Durio zibethinus 193

Echinochloa pyramidalis 66
Elaeis guineensis, see oil palm
elephant foot yam 90, see also *Amorphophallus campanulatus*
elephant yam 94
Elettaria cardamomum 76
Eleusine coracana 89, 340, see also millet
Enterolobium 105
Eragrostis curvula 128
E. tef 128, 340
Erythrina 60, 61, 105, 192, 561
E. poeppigiana 49, 51, 55, see also poró
Eucalyptus 120, 128, 147, 176, 189, 260, 318, 350, 363, 380, 393, 409, 410, 457, 514, 560
E. camaldulensis 61, 120, 121, 123
E. citriodora 311
E. deglupta 44, 45, 46, 61, 64,
E. globulus 176
eucalyptus hybrid, Turrialba 45
E. melliodora 121, 122
E. microtheca 312
E. ovata 438
E. sideroxylon 439
E. socialis 388
E. urophylla 64
E. viminalis 438, 439
Euphorbia 346
European cherry 464
European larch, see *Larix decidua*

Fagus crenata 356
F. grandifolia 438
Festuca arundinaceae 442
Ficus benjamina 514
field beans, see *Phaseolus vulgaris* and beans
figs, Smyrna 315
finger millet 340, see also *Eleusine coracana*
fir 354, see also *Abies veitchii*
Flemingia 105
fonio millet, see *Digitaria exillis*
frangipani, see *Plumeria*
French bean 373, see also *Phaseolus vulgaris* and beans
Funtumia 33

genipapo 69
ginger 87, 90, 190, see also *Zingiber officinale*
Gleditsia triacanthos 105
Gliricidia 105, 260, 561
G. maculata, see *G. sepium*
G. sepium 35, 74, 106, 276
Glochidion 349
Glycine javanica, see *G. wightii*
G. max 89, 119, 312, 388, 435
G. wightii 93, see also soyabean
Gmelina 128
G. arborea 44, 47, 64, 236
Gomphrena globosa 338
Gonystylus 232, 234
G. bancanus 233
Gossypium 88
G. hirsutum 388, see also cotton
gram 394, see also *Vigna*
grape 465, see also vine
greater yam 94
green gram, see *Vigna radiata*
green panic, see *Panicum maximum* var. *trichoglume*
Grevillea robusta 514
groundnut 28, 32, 82, 127, 259, 275, 315, 318, 394, 468, 496, 497, 542, see also *Arachis hypogaea*
Guatemala grass, see *Tripsacum laxum*
guava 18, see also *Psidium guajava*
Guinea grass, see *Panicum maximum*
gum arabic, see *Acacia senegal*
Gynandropsis gynandra 338

Haematoxylum 105
Hausa potato, see *Plectranthus* and *Solenospermum*
hazelnut 465
hetero, see *Desmodium heterophyllum*
Hevea brasiliensis 316, 453, see also rubber
Hibiscus 90
Hildegardia barteri 506
honey locust, see *Gleditsia triacanthos*

Hordeum vulgare 433, see also barley
Hymanea 105
Hyparrhenia rufa 66
Hypsipyla grandella 53

Imperata cylindrica 61, 480, 560
Inga 60, 105, 260, 312, 318
ipil-ipil, see *Leucaena leucocephala*
Ipomoea batatas 48, 89, 91, see also sweet potato
Irvingia gabonensis 35
I. gabonensis var. *excelsa* 36
Ischaemum asiatatum 93
Italian ryegrass 357, see also *Lolium temulentum*

Jacaranda copaia 64
jackfruit 18, 19, 69, see also *Artocarpus artilis*
jambo cacao 69
jaragua, see *Hyparrhenia rufa*
Jessenia polycarpa 112
jojoba, see *Simmondsia chinensis*
Juglans 61, see also walnut
jute, see *Corchorus*

Kaimi clover, see *Desmodium intortum*
kenaf, see *Hibiscus*
Kikuyu grass, see *Pennisetum clandestinum*
Kochia scoparia 338
koronivia grass, see *Brachiaria humidicola*
kudzu, see *Pueraria phaseoloides*

Lablab niger 119
Landolphia 33
Larix decidua 437
Larrea divaricata 388
laurel 50, 53, see also *Cordia alliodora*
Lemna minor 360
lentil 311
leucaena, see *Leucaena* and *L. leucocephala*
Leucaena 151, 260, 310, 312, 314, 557, 561, see also *L. leucocephala*
L. leucocephala 36, 37, 39, 93, 105, 106 - 111, 120 - 123, 128, 276, 282 - 286, 515, 560
lima bean, see *Phaseolus lunatus*
limba, see *Terminalia superba*
Liriodendron 457
little bluestem, see *Andropogon scoparius*
loblolly pine, see *Pinus taeda*
locust bean 32, see *Parkia clappertoniana*
lodgepole pine 440, see also *Pinus contorta*
Lolium 411, 480
L. perenne 432, 436
L. temulentum 433
Lonchocarpus 105
lucerne 381, see also *Medicago sativa* and alfalfa
Lupinus mutabilis 314
Lycopersicon esculentum 315, see also tomato
Lysiloma 105
Lythrum salicaria 437

Macaranga 480
M. hypoleuca 349
Macroptilium atropurpureum 93, 128
mahogany 315
maize 28, 30, 32, 45 - 49, 82, 90, 106, 107, 108, 120 - 123, 126, 127, 139, 142, 144, 176, 188, 217, 261, 267, 276, 303, 315, 316, 323, 339, 340, 348, 357, 360, 371, 392, 394, 470, 472, 474, 477, 478, 480, 498, 499, 507, 509, 510, see also corn and *Zea mays*
Mallotus paniculatus 349
mandarin 73
Mangifera indica 88, see also mango
Manglieta glauca 76
mango 18, 19, 35, 371, 392, 463, 465, see also *Mangifera indica*
mangosteen 18
mangrove 26
Manihot esculenta 89, 90, 91, 435, see also cassava and manioc
M. utilissima 44, 190
manioc 66, see also cassava

and *Manihot esculenta*
Maranta arundinacea 90
Medicago sativa 212 - 216, 219, 220, see also lucerne
Melia azedarach 133
melina 65, see also *Gmelina arborea*
Melinis minutiflora 61, 66, 93
mesquite, see *Prosopis*
millet 28, 32, 126, 259, 275, 318, 339, 340, 394, 408, 477, see also under individual species
Mimosa pudica 93
Miscanthus sacchariflorus 357
M. sinensis 357
molasses grass, see *Melinis minutiflora*
Monilia roreri 51
Morinda officinalis 76
mugga, see *Eucalyptus sideroxylon*
Muhlenbergia 326
mung bean 48, see also *Vigna radiata*
Musa 88, see also banana
M. textilis 88
Musanga 313, 480
M. cercropioides 349
mushrooms, see *Auricularia polytricha*

n'jugo beans 126, 127
napier grass, see *Pennisetum purpureum*
Napolleona 35
Neoscortechinia 232, 234
Norway spruce 440, see also *Picea abies*
nutmeg 315

oak 354, 395, see also *Quercus rubra*
oats 276
oil bean 30, see also *Pentaclethra macrophylla*
oil palm 26, 27, 28, 30, 80, 81, 315, 316, 371, 380, 391, 392, 463, 473, 492, 493
onion 495
Opuntia 200
O. ficus-indica 198
orange 73, 460, 463, see also *Citrus sinensis*
orchard grass 440, see also *Dactylis glomerata*
Oribygnia 112
Ormosia 105
Orthosiphon stamineus 18
Oryza sativa 64, 89, see also rice

paddy, see rice
palisade grass, see *Brachiaria brizantha*
palm, sugar 18
palms 470, 473, 481, see also species and common names
pangola grass (*Digitaria decumbens*) 93
Panicum 333
P. maximum 91, 93, 333, 388
P. maximum cv. colonial 66
P. maximum var. *trichoglume* 66
papaya 14, 18, 35, 73, see also *Carica papaya* and pawpaw
para grass, see *Brachiaria mutica*
pará-pará 65, see also *Jacaranda copaia*
Parkia 20, 27, 35, 36, 105, 260
P. clappertoniana 120, 275
Parkinsonia 135
P. aculeata 133, 558
parsnip 495
Paspalum 340
P. commersonii 93
P. conjugatum 93
pawpaw 315, see also *Carica papaya* and papaya
pea 468, see also *Pisum sativum*
peach 457, 460, 466, see also *Prunus persica*
peanut 90, 371, see also groundnut and *Arachis hypogaea*
peanut, perennial, see *Arachis glabra*
pecan 465
pejibaye 113, see also *Bactris gasipaes*
Peltogyne 105
Pennisetum 340
P. clandestinum 53
P. purpureum 53, 66, 91, 93, 348, see also napier grass
Pentaclethra macrophylla 27, 35

pepper 21, 74, 82, 86, 94, 315 see also *Piper nigrum*
phaseolus beans 49, 65, 69, 75, 110, 120, 121, 127, 217, see also beans, field beans and *Phaseolus vulgaris*
Phaseolus 318
P. lunatus 119
P. vulgaris 44, 45, 47, 48, 108, 118, 122, 123
Phragmites 337
P. communis 357
Picea abies 437
P. sitchensis 439
pigeon pea 32, see also *Cajanus cajan*
Piliostigma thonningii 150
pin cherry, see *Prunus pennsylvanica*
pine 44, 354, 390, see also *Pinus*
pineapple 87, 90, 94, 96, 190, 384, 467, see also *Ananas comosus*
Pinus 128, 313, see also pine
P. caribaea 316
P. caribaea var. *hondurensis* 64, 65, 69
P. contorta 431, 439, 440
P. densiflora 352
P. kesiya 316
P. oocarpa 316
P. radiata 407, 429, 462, 471
P. resinosa 558
P. rigida 429, 442
P. sylvestris 430, 471
P. taeda 436
Piper betel 18
Piper nigrum 88
Piscidia 105
Pisum sativum 473
pitch pine, see *Pinus rigida*
Pithecellobium 105
P. dulce 558
Pittosporum resiniferum 112
plantain 48, 49, 82, 113, see also banana and *Musa*
Plectranthus 28
Plumeria 18
Poa 480
poplar 395, 462, see also *Populus*
Populus 147, 459
P. deltoides 436
P. tremuloides 438
P. trichocarpa 439
poró 50, see also *Erythrina poeppigiana*
Portulaca quadrifida 338
potato 309, 373, 377, 378, 381, 406, 467, 468, 470, 474, 494, 495, see also *Solanum tuberosum*
potato, Irish 28
Prosopis 35, 105, 112, 156, 260, 318, 514, 557, 561
P. alba 557
P. chilensis 75, 133, 557
P. cineraria 276, 459, 461
P. flexuosa 557
P. juliflora 75, 135
P. limensis 75
Prunus pennsylvanica 438
P. persica 430, see also peach
P. serotina 441
Pseudotsuga menziesii 432
Psidium guajava 189, see also guava
Psophocarpus tetragonolobus 119
Pterocarpus 105
Pueraria phaseoloides 92
pumpkin 127

Quercus rubra 433, see also oak
quicuio amazonica 66, see also *Brachiaria humidicola*

radish 360, 495
rambuttan 18
ramie, see *Boehmeria nivea*
ramon 113, see also *Brosimum alicastrum*
raspberry, see *Rubus hispidus*
red alder, see *Alnus rubra*
rhizobium, see *Rhizobium*
Rhizobium 150, 151, 312, 556, 557, 560, 562
Rhodes grass (*Chloris gayana*) 93
ribbon gum, see *Eucalyptus viminalis*
rice 14, 21, 27, 28, 69, 72, 73, 106, 188, 282 - 286, 348, 357, 371, 391, 392, 394, 473, 497, see also *Oryza sativa*
robusta coffee 391, see also coffee
rubber 28, 80 - 83, 309, 311, 315, 371, 392, see also

Hevea brasiliensis
Rubus hispidus 443
ryegrass, see *Lolium perenne*

Sabinea 105
Saccharum officinarum 88, see also sugar cane
sago palm 190
salak 18
Salix 147
Salvadora persica 133
Samanea 105
Schinus molle 514
scrobic, see *Paspalum commersonii*
sensitive plant, see *Mimosa pudica*
sesame 28, 477, see also *Sesamum indicum*
Sesamum indicum 88
Sesbania 260
S. aculeata 72, 73
S. bispinosa, see *S. aculeata*
S. cannabina, see *S. aculeata*
S. grandiflora 73, 77, 105
Setaria 333, 345
S. anceps 66
shea butter nut 32, see also *Butyrospermum paradoxum*
Shorea 349
S. albida 232, 233, 234
S. leprulosa 349, 350
signal grass, see *Brachiaria decumbens*
Simmondsia chinensis 112, 507
siratro, see *Macroptilium atropurpureum*
Sitka spruce 440, see also *Picea sitchensis*
Solanum nigrum 338
S. tuberosum 495, see also potato
Solenospermum 28
Solidago altissima 357
sorghum 28, 30, 121, 122, 126, 127, 259, 275, 339, 340, 392, 394, 395, 408, 477, 498, 499, see also *Sorghum bicolor* *S. sudanense*
Sorghum bicolor 388
S. sudanense 433, see also sorghum
sour paspalum, see *Paspalum conjugatum*
soursop 73
soya, perennial, see *Glycine wightii*
soyabean, soybean 28, 82, 90, 357, 360, 371, 373, 394, 406, 480, 496, 497, 510, 532, 542, see also *Glycine max* *G. wightii*
Spartina 326
Sphenostylis stenocarpa 119
spinach 18
Spirilum lipoferum 150
Spirodela oligorrhiza 360
Sporotrichum 141
Stenotaphrum secondatum 93
Stipa 411
strawberry 370, 371, 372, 373
stylo, see *Stylosanthes guianensis*
Stylysanthes guianensis 92, 93
Sudan grass 360
sugar beet 252, 253, 373, 406
sugar cane 28, 49, 127, 139, 142, 143, 144, 323, 339, 340, 348, 394, 480, see also *Saccharum officinarum*
sunflower 90, 311, 315, 348, 470
swamp gum, see *Eucalyptus ovata*
sweet chestnut 460
sweet pepper, see *Capsicum*
sweet potato 28, 82, 87, 94, 394, 474, see also *Ipomoea batatas*
sword bean, see *Cananvalia ensiformis*
Syzygium aromaticum 88, see also clove

tall fescue, see *Festuca arundinacea*
Tamarindus 105
Tamarix 135, 198, 200, 318
tapereba 69
Taraxacum officinale 443
taro 18, 21, see also *Colocasia* and cocoyam
tea 28, 74, 80, 104, 277, 311, 315, 373, 380, 388, 389, 390, 459, 460, 473, 516, 543 - 550
teak 44, 315
tef, see *Eragrostis tef*
Tephrosia candida 106, 276
Terminalia ivorensis 44, 47, 48, 61
T. superba 74
Themeda 411

Theobroma cacao 48, 52, 74, 88, see also cacao
Thuja occidentalis 441
tobacco 28, 32, 117, 394, 406, 473
tomato 18, 315, 456, 543 see also *Lycopersicon esculentum*
Trachypogon plumosus 560
Treculia africana 27, 36
trembling aspen, see *Populus tremuloides*
Trianthema ceratocepala 338
Tribulus terrestris 338
Trichoderma 141
Trifolium 411
T. repens 437
T. subterraneum 407
Trigonella foenum-graecum 88
Tripsacum laxum 91
Triticum aestivum 442, see also wheat
Tsuga 353
T. heterophylla 433
turmeric 87, 90, see also *Curcuma longa*
turnip 495

Uapaca kirkiana 120
urophylla, see *Eucalyptus urophylla*
Uvaria 35

Vanilla 315
velvet tamarind, see *Dialium*
Vicia faba 314
Vigna 312, see also gram
V. aureus 119
V. mungo 89, 119
V. radiata 89, see also mung bean
V. unguiculata 48, 89, 92, 119, 338, 559, see also cowpea
vine 373, 463
Vitex doniana 35
Voandzeia subterranea 119

walnut 463, 465, 480, see also *Juglans*
wheat 251, 252, 256, 311, 317, 406, 413, 470, 473, 480, 497, 498, see also *Triticum aestivum*
white cedar, see *Thuja occidentalis*
wild rubber, see *Funtumia* and *Landolphia*
willow 460, see also *Salix*
winged bean, see *Psophocarpus tetrogonolobus*

Xanthosoma 89

yam 27, 28, 30, 87, 90, 467, 478, see also *Dioscorea*
yam bean, see *Sphenostylus stenocarpa*

Zea mays 44, 388, see also corn and maize
Zingiber officinale 76, 88, 91, see also ginger
Ziziphus 260

SUBJECT INDEX

Acanthaceae 324
acceptability 582
adaptability 316, 418, 428, 514, 579
  to stress 403
  (*see also* phenotypic plasticity)
adaptation 316, 439
adoptability 280
aerial reconnaissance 292, 294
age
  classes 174
  of forest stands 352
  mosaic 174
ageing 517
agricultural crops, choice of 259
agroforest 173
  architecture 173
  design
    alternatives 189
    analog methods 182
    cultural practices 188
    studying variability 185
    transformation 184
  for humid tropics 185
agroforestry
  and allelopathy 559 (*see also* allelopathy)
  and alternative land use 585
  classification 161, 586
  definition of 3, 257, 299, 301, 309, 401, 551
  enterprise 280
  local successes 585
  and location 583
  and mixed cropping 470
  need for new cultivars 487
  and other land use systems 582
  and plant breeding 321
  and plant growth distribution 443
  and plant management 582
  research techniques 425
  role of 579
  and root competition 532
  and scale 3
  and the smallholder 585
  and sole cropping 470
  and stress
    light 405
    nutrient 413
    water 408
  systems 577
    co-adaptation in 317
    and ICRAF 299, 586
    quantitative studies of 577
    time dimensions 165
    and water 395
  and training 578
  and water shortage 412
agro-unit 576 (*see also* proto-agroforestry unit)
Aizoaceae 324
alachlor, herbicide 108
alcohol production, and solar power 156
alfalfa
  regrowth after cutting 212
  sink limitation 220
  water stress 219
algae 141
alkaloids 314
allelopathy 61, 231, 235, 534, 559, 580
  and drought 235
alley cropping 37, 106, 268, 282
allometric relationship 429, 454, 459, 467, 517
alternative row cropping 166
aluminium toxicity, and roots 536
Amaranthaceae 324
Amazonia 197, 226, 227, 228, 230, 236, 240, 316 (*see also* separate countries)
anaerobic digestion 140
analysis
  of management possibilities 583
  of transferable successes 583
Andes 314
Angola 294

animals 14, 28, 36, 39, 40, 57, 61, 75, 81, 82, 91, 125, 129, 135, 164, 192, 194, 197, 200, 314, 318, 339
  and agroforestry 65
  and deforestation 138
  in forest gardens 22
  grazing under coconuts 92
  (*see also* browse, fodder, forage, grazing, livestock and silvopastoral systems)
annual dry matter increment 442
annuals, and seeding 311
antibiotic substances 227
antibiotics 231
antimetabolites 314
antitranspirants 392, 399
apical dominance 516
apiculture 71, 75, 76 (*see also* bees)
apomixis 317
aquatic plants 141
architecture, pioneer phase 190
  (*see also* dry matter distribution and plant architecture)
area, defining for classifications 166
arid zone resource management 129
ASCL, simulation language 253
Asteraceae 324
Australia 142, 196, 373, 405, 409, 411, 413, 498

bagasse 143
Bangladesh 295
basic needs approach 301
beekeeping, *see* apiculture
bees 465
  and crop yields 318
beeswax, *see* apiculture
behavioural strategies, *see* phenology
Belize 293, 316
bending, *see* tree spreading
Benin 291, 294 (*see also* West Africa)
bentazon, herbicide 108
Bhutan 295
biennial bearing 12, 311 (*see also* irregular bearing)
biennials 313
bioeconomics 271
biological control 555
biological profiles, of species 582
biomass 221, 227, 326, 352, 417, 491, 492
  and agroforestry 148
  and animal manure 148
  annual production v. oil use 145
  and cassava 144
  conversion systems 139
  of *Erythrina* 55
  integrated systems 152
  management of 584
  and maize 144
  optimization 265
  partitioning, in alfalfa 213
  production 137
  raw materials 139
  and scale 148
  and soil depletion 149
  and sugar cane 143
  of tea 546
biostasis 189
biosystematics 557
biotrons 552
birds 314 (*see also* pests)
Bolivia 293
Boriginaceae 324
Borneo 227, 228, 236, 241
Bos indicus 66
Bos taurus 66
Botswana 125
branched complexes, and scale 174
branching 313, 470, 472, 491
Brazil 63, 80, 138, 139, 142, 147, 225, 293
breeding systems 314 (*see also* inbreeding and outbreeding)
browse 35, 112, 197
  shrubs 197
  (*see also* animals and silvopastoral systems)
Brunei 295
Bubulus arnee f. *bubalis* 66
Budowski's rule 195
Burma 192, 295
Burundi 294
bush fallow 33
by-products 141

C_3 and C_4 systems, a comparison 329
C_3 photosynthetic system characteristics 327
C_3 plants
  and canopy efficiency 348

C_3 plants (*cont.*)
photosynthetic rates 373
(*see also* photosynthetic systems)
C_4 exploitation, realities of 340
C_4 photosynthetic system characteristics 327
C_4 plants
and canopy efficiency 348
and growing season 336
and nutrient content 338
photosynthetic rates 373
(*see also* photosynthetic systems)
C_4 system subtypes 331
cacao pod rot 51
cacao and shade 51
cacti 198
Calvin cycle 327
Cameroon 292, 294 (*see also* West Africa)
Canada 146, 147, 372
canopy 241
aerodynamic roughness 241
aerodynamics 227
area modification 410
arrangement 374
C_3 and C_4 405
and C_3 grasses 327
of coconut 86, 96
and dry matter production 347
duration 116
excessive density 366
geometry, and light stress 405
and heat fluxes 227
management 407
mixture 355
multistoreyed-discontinuous 367
and photosynthesis 368
and photosynthetic performance 347
and photosynthetic systems 336, 348
reduction, and water saving 413
reflectance 227
roughness 227
sclerophyllous 227
structure 318, 350
types 584
water percolation 224
(*see also* leaf canopy and plant canopy)
Capparaceae 324
carbon
economy 507
-nitrogen ratios 232
turnover, and roots 530
Caribbean 88
Caryophyllaceae 324
Cau Hai Research Experiment Station, N. Vietnam 76
cause - effect
assessment 212
pathways, analysis of 210
relationships 209
cell division 176
cellulose 150
Central African Republic 294
Central America 192, 394
Central Plantation Crops Research Institute, India 91, 95, 97
Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE) 43
Centro Internacional de Agricultura Tropical (CIAT) 106, 276, 536
Centro Internacional de Mejoramiento de Maiz y Trigo (CIMMYT) 303
Centrospermae 324
phylogeny 325
chablis 20, 177, 181
and thunderstorms 185
characteristics of trees 3, 258, 260
charcoal 135 (*see also* fuelwood)
Chenopodiaceae 324, 325
cherelle wilt 465
China 80, 148, 149
chromosome numbers 315
classification
generating compatibility 162
types of 162
of woody vegetation 293
(*see also* agroforestry classification)
climate classification 385
climatic matching 507
and cotton 509
and cowpea 510
and maize 509
climatic noise 554
climax
species 313
vegetation 174
climbers 585
clones 311, 315

clones and G × E studies 311
CO_2 concentration, in canopies 350
co-adaptation 310
Coconut Research Station, Sri Lanka 92
coconuts
  for agroforestry 83
  button abortion 465
  dwarf varieties of 101
  and intensive land use 83
coffee
  fruit drop 465
  and shade 50
co-habitation 405
co-incident crop sequences 166
collectivities 176
Colombia 80, 82, 106, 281, 293
combustion 139
commensalism 474
competition 273, 274, 575
  and distribution 404
  for nutrients 417
  (*see also* interference)
competitiveness 11, 268
complementarity 274, 580
complementary sharing 585
complementary use of resources 404
components of yield 492
compound farms, West Africa 29
concomitant crop sequences 166
Congo 294
Congo Brazzaville 74
conservation 31, 75
  land users perception of 585
constraint analysis 583
continuous succession 166
controlled environments 510, 551
  artificial light 551
  disadvantages 556
  general considerations 554
  and plant morphology 564
  stress-free plants 554
convergent evolution 405
coppicing 104, 108, 165, 194, 198, 313, 407, 413, 460, 480, 516, 580 (*see also* tree spreading)
Corner's rule 195
Costa Rica 43, 293
crop
  geometry 166
  habit, and sole cropping 472
  mixtures
    manipulating 474
    some principles 470
  plant, the ideal 310
  rotation 117, 240
  season, water availibility 392
  sequence 165
  water
    consumption 386
    requirements 391
    use 379
  - tree mixtures, and light 365
cropping, alternative row 166
cropping period 165
cropping systems 272 (*see also* farming systems)
crops
  for cash in West Africa 28
  and complementarity 97
  of the forest/savanna 28
  of the Guinean savanna 28
  of the humid tropics 28
  subsistence in W. Africa 28
  of the Sudan/Sahel savanna 28
  of the tropical highlands 28
  underexploited species 580
crown 242
  geometry 206
  structure 189
CSMP, simulation language 253
Cuba 293
cultivar selection 507
current annual increment 489
cuvettes 553
cyanogenic glycosides 314
cycle of technology development 300
Cyperaceae 324, 326

daylength 510
day temperature 510
deblossoming 465
deciduousness 47, 227, 275, 351, 405, 507
definition, of agroforestry 257, 299, 301, 309, 401, 551
deforestation 41, 292, 294
density
  conversion factor 359
  stress 468, 470 (*see also* plant population)
desert encroachment 129
  causation 131
  problems of 132
desertification 130

design 207, 238, 241, 271, 299, 301, 476
  for cropping 36
  and phenology 512
  specifications 280
  using linear programming 283
determinate crops, and light stress 408
development
  cycles 584
  phases 512
developmental patterns 429
diagnosis 269, 280, 298, 299
diagnostic methodology 304
dichogamy 315
differential stresses, in communities 402
dinitrogen fixation 54, 61, 106, 118, 214, 240, 403, 415, 518
  by free-living organisms 518
  inhibition 560
  (*see also* nodulation)
dioecy 315
diseases 7, 11, 51, 310, 313, 318, 321, 478, 575
  research 562
  seed borne 6
  and seeds 6
  (*see also* pathogens)
distribution, and physiological potentials 404
disturbed habitats 313
diuron, herbicide 108
DNBP, herbicide 108
domestication 310, 312, 321
Dominican Republic 293
dormancy
  breaking 514
  of shoots 514
  of vine buds 516
drainage 380
  and roots 537
drought 240
  adaptation 425
  resistance 392
dry matter
  distribution 427
    and ecovariants 439
    and habitat 442
    and management 456
    and natural selection 443
    and nutrient levels 436
    and overcrowding 454
    and photoperiod 433
    and pruning 459
    and soil structure 436
    and soil water status 435
    summary 444
    in tea 544
    and temperature 433
  increment 442
  partitioning and light 432
  production, and pruning 457
  (*see also* pruning)
dwarf habit 313
dwarfing rootstocks 442

early cropping 313
East Africa 80, 82, 93, 118, 326, 340, 386, 497, 544, 547, 548
East African Agricultural and Forestry Organisation (EAAFRO) 383, 388, 390
East African Herbarium 328
East Indies 93
ecological
  assessment, of a dry region 132
  considerations 577
  investment strategy 196
  monitoring 291
  niche 179, 313 (*see also* niche)
  stability 19
  stress 195 (*see also* stress and plant stress)
  successions 196
economic analyses 264
economics 577, 585
  budgeting techniques 280
  limiting production factors 280
  monetary equivalents 280
  price ratios 279
  and returns to land 272
  returns to various factors 281
ecosystem
  buffering 579
  and cyclic change 174
  dynamics 225
  light climate 370
  preforest stages 177
  processes 582
  self-regulating agroforestry 585
  (*see also* fragile ecosystems)
ecotone 182
eco-unit 176
  death of 179
  dynamics 181

eco-unit (*see also* agro-unit)
ectomycorrhiza, *see* mycorrhiza
Ecuador 198, 293
edible flowers 73
El Salvador 293
Empire Cotton Growing Corporation (ECGC) 509
endogenous rhythms 505
energy plantations 72, 138, 146
enrichment planting 71
entrainment 506
environment monitoring system 291
environmental
  cues 505
  factors, plant response 553
  influences on dry matter distribution 432
  stimuli 430
  stress 512 (*see also* stresses)
    and phenology 505
epiphytes 225
epitrophy 457
Equatorial Guinea, *see* Guinea
erosion 403
establishment 104, 312
  phase 405
ethanol
  for fuel 138
  production, energy required for 156
  from sugar cane 157
Ethiopia 80, 82, 294
ethylene, and roots 542
etiolation 407
Euphorbiaceae 324
evaporation
  from catchment areas 383
  direct measurement 384
  empirical estimates 381
  from mean air temperatures 384
  from net radiation 383
  oasis effect 384
  potential 381
  from soil 380, 413
evergreen forests, and productivity 351
evergreenness 227, 351, 507
evergreens 409
evolution 309
exogenous rhythms 505
extinction coefficient 367

Fabaceae 339
factor identification 218
fallow 35, 105, 117, 480
  systems 35
FAO forestry field projects 71 (*see also* UN Food and Agriculture Organisation)
Far East 138
farming systems
  cacao - forest trees 74
  designing improvements 209
  rice - *Sesbania* 72
  sole cropping 169
  spices/medicinal plants 76
  in West Africa 25
  (*see also* cropping systems)
farm size
  in Costa Rica 53
  in West Africa 27, 34
fast growth, *see* growth rates
Federal Republic of Germany 129
feed profile, *see* animals
feeder roots 530 (*see also* roots)
fences, thorn 130
fermentation 140
fertilizer 8, 44, 45, 53, 68, 73, 87, 111, 196, 200, 276, 277, 283, 284, 411, 436, 516, 517
Fick's law 210
Fiji 89, 93, 142, 147
Finland 147
fire 197
  and phenology 505
fish culture 71
fitness, of genetic systems 314
flexibility, of genetic systems 314
floral initiation 463, 465
floristic
  composition, and peat 233
  structure 225
flower
  abscission 512
  development 511, 513
  initiation 510
flowering
  strategies 317
  wood 506
fodder 121, 125, 133, 198
  species 71, 73
food
  production, and village-forest-gardens 21
  profile 114
forage 106

forest
  bamboo 388
  boreal 351
  broadleaved 293, 350
  coniferous 351
  dipterocarp 228
  Douglas fir 410
  drought deciduous 352
  ecosystem, modification of 20
  and fuelwood 33
  gardens 585 (*see also* village-forest-gardens)
  'kerangas' 236
  Malaysian marsh 185
  man-made 20
  Mediterranean sclerophyll 353
  montane 133
  mountain evergreen 388
  net production 354
  peatswamp 228, 231
  reserves, in Nigeria 33
  sections through 228
  temperate 222
  temperate deciduous 351
  'tierra firme' 228
  tropical equatorial 222
  (*see also* tropical forest)
fragile ecosystems 580
France 147
French Guiana 179, 202, 293
fruit
  bud formation and shade 372
  bud production 463
  crops 313
  development 511, 513
    period 465
  quality, and shade 372
  ripening 466
  set 465
  shedding 465
  trees 18, 27, 28, 34, 39, 65, 69, 76, 189, 318, 473, 481
    and plant populations 491
fruiting 462
fuel
  from biomass 137
  plants 346
fuelwood 4, 30, 32, 34, 38, 57, 60, 73, 74, 104, 110, 117, 122, 125, 131, 133, 146, 189, 198, 260, 314, 318, 491
  consumption 117
  lots 4, 260
functional balances 210
fungi, *see* micro-organisms
G × E interaction 512
Gabon 176, 294
Gambia 117
gasification 139
gasohol, *see* power alcohol
geitonogamy 317
gene
  bank 581
  migration 317
genetic
  differentiation 317
  diversity 310, 321, 579
  erosion 310
  fitness 514
  flexibility 514
  recombination 314
  variability 314
genotype, and shoot:root ratio 438
germination, and light 312
germplasm 6, 261
  transfer of 581
Ghana 80, 82, 225, 294, 560
  (*see also* West Africa)
Global Environment Monitoring System (GEMS) 291
gossypol 314
graft compatibility 442
grain legumes 117
grape drop 465
grasses, C_3 and C_4 genera 325
gravimorphism 457
grazing
  lands 125
  studies, and systems analysis 210
  systems, *see* animals
  and tree spacing 69
gross primary production 354
ground cover crop 367
ground reconnaissance 292, 294
growing stock, *see* biomass
growing uniform plants 557
growth
  of aerial parts 513
  allocation 428 (*see also* dry matter distribution)
  chambers or rooms 552, 553
  control, exogenous/endogenous 505
  cycles 584
  dynamics 182
  flushing 515
  patterns 429
  phases, of coconut 86
  rates 227, 313
Guatemala 293

guidelines for research, *see* research guidelines
Guinea 294
Guinea-Bissau 294
Guinea savanna 275 (*see also* savanna)
Guyana 293

H-22234, herbicide 108
habitats
  and C_4 plants 326, 335
  disturbed 443
  nutrient-poor 313
  open 312, 326, 327
    and dry matter distribution 442
  open above / closed below 416
  and phenology 507
  saline 326
Haiti 293
hand pollination 465
harvest index 313, 579
  of tea 545
harvestibility 11
harvesting 12, 313
  periods 165
  problems 156
  sequential 585
heat units 509
heliophiles 181, 188
herbaceous
  communities, production 354
  crops, and genetic diversity 580
herbicides 108, 418
  for killing leucaena 109
heterozygosity 6
holistic analyses 210
home gardens 14, 73, 193
Honduras 293
honey, *see* apiculture and bees
hoplexols 189
hormonal control, and development 430
hormones 220, 465
  and phenological behaviour 505
  and roots 531
human impact 196
humic substances, effects on plants 231
humus 227
  formation 223
  and plant responses 231
  (*see also* humic substances)
hybrids 315
hypotheses, *see* models

ideotypes 261, 268, 304
inbred lines 315
inbreeding 311, 315
India 76, 80, 82, 83, 87, 88, 91, 93, 98, 276, 295, 314, 373, 386, 497
Indian Ocean Islands 315
Indonesia 13, 76, 80, 83, 93, 189, 192, 193, 198, 201, 202, 295
infraplexion 190
input management 584
insecticides 465
insects 77, 524
  as pollen vectors 315
Institute of Soil Biochemistry Brunswick, FRG 231
integrated forestry 63
integrated populations, *see* eco-unit
Integrated Project on Arid Lands, Kenya, *see* IPAL Project
integrative physiology 210
interactions, *see* plant interactions
interbreeding populations 317
intercropping 13, 27, 34, 45, 71, 82, 104, 106, 115, 117, 118, 165, 259, 273 278, 280, 310, 318, 319, 321, 355, 364, 366, 370, 443, 470, 474, 476, 515
  with C_3 and C_4 species 339
  with coconuts 83, 87
  and logging 50
  with maize and beans 217
  and management 95
    considerations 110
  and plant form 122
  and roots 528, 531
  and soil 236
  and stability 247
  in tea 549
  with trees 257
  and water 395
    limitations 110
  (*see also* mixed cropping)
interface, tree/herb 576
interference 473, 575 (*see also* competition)
intermediate succession 313
intermittent succession 166
International Amazon Rainforest Ecosystem Project 230, 240

International Biological Programme (IBP) 347
International Council for Research in Agroforestry (ICRAF) 37, 297, 426, 577, 578, 581, 585
  Charter 297
  programme of work, *see* Preface
  research strategy 299
  (*see also* Preface)
International Institute of Tropical Agriculture (IITA) 36, 37, 40, 105, 276, 303
International Livestock Centre for Africa (ILCA) 36
International Service for National Agricultural Research (ISNAR) 303
International Union for the Conservation of Nature and Natural Resources (IUCN) 291
intrapopulation variation 441
inulin crops 141
IPAL Project, Kenya (UNESCO) 129
  species planted 135
irradiance contour 368
irregular bearing 465 (*see also* biennial bearing)
irrigation 75, 83, 135, 196, 200, 392, 436, 516
isoresource condition 274
Israel 380, 514
Italy 372
Ivory Coast 80, 82, 179, 190, 197, 207, 294

Jamaica 93, 293
Japan 350, 356, 357
jardin créole 13 (*see also* village-forest-gardens)
June drop, of apple 465
juvenile
  -mature correlations 557
  period 462
  stage, and shade 474
juvenility 517

K-selection gradient 443
Kampuchea 295, 356
kampung 13
kebun 13
Kenya 82, 129, 142, 189, 217, 294, 299, 302, 326, 327, 337, 338, 345, 383, 385, 388, 389, 491, 541, 544, 550
Kranz anatomy, of leaf 327

labour 585
  requirements, and village-forest-gardens 21
land
  equivalent ratio 259, 264, 273, 475
  occupancy cycles 165
  succession 165
  use systems, *see* cropping systems and farming systems
Landsat imagery 292
landscape uses 37
Laos 295
Latin America, *see* separate countries
  and cacao 82
latitude, and growth 439
latitudinal races 439
leaching 403
leaf
  angle 366
  area
    density 350
    index 339, 350, 366, 367, 369, 491, 492
      of alfalfa 220
      seasonal change 371
  average and 'ideal' 363
  canopy, ageing 505 (*see also* canopy)
  changes of angle 378
  clusters 351
  conductances 337
  density 367
  erect foliage benefits 373
  fall 10
  flush 10
  movements 409
  photosynthetic response 366
  production
    and leaf removal 549
    rate, with plucking 550
  senescence 506
Letcombe Laboratory, UK 540
leucaena cropping sequences 109
ley systems 37
lianes 177, 179
Liberia 294
light
  climate 365

light (*cont.*)
distribution within trees 368
and dry matter distribution 432
extinction coefficient 351, 369
gradients 189
intensity, and economic yield 371
interception
of alfalfa 220
improvement of 370, 371
and morphological changes 433
profile 367
coconut 83
and leaf area density 350
quality, changes in 374
as a resource pool 402
stress, minimization 407
transmission 366 (*see also* light profile)
Liliaceae 324
limiting factor approach 210
linear programming 281, 487
Linuron, herbicide 108
liquifaction 139
litter 222, 227, 231, 242, 259, 317, 318, 413, 418
transfer 268
live fence posts 55
livestock 35, 36 (*see also* animals)
in West Africa 28
local customs 584
long-lived species 315
lopping 55, 122, 189, 190, 268, 418, 461, 516, 580
sequential 585
loss of crop lands, globally 294

Madagascar 82, 294
Malawi 294, 385
Malaysia 80, 82, 83, 88, 93, 147, 225, 226, 240, 295, 311, 349, 350, 356, 371, 487, 495
Mali 195
Man and the Biosphere Programme (MAB) 129, 238, 240
management 110, 265, 268, 269
boundary 169
and objectives 582
(*see also* plant management)
manipulating crop mixtures 474
manuals
for agroforestry 578
and crop associations 580
of plant management 586
and species information 580
(*see also* research manuals)
manure 79, 200 (*see also* fertilizers)
mast fruiting 311
mathematical models 201 (*see also* models)
mean annual increment 489
medicinal plants 21, 31, 36, 193
meristem culture 581 (*see also* propagation and tissue culture)
methanol 140, 146
methodology v. technology 302
metribuzin, herbicide 108
Mexico 293, 317, 406, 498
micro-forestry 4, 260
micro-organisms 227, 230, 240, 242, 312, 415, 418
periodic phenomena 518
phytotoxic compound 236
(*see also by name*)
microclimate, modification 575
micropropagation 561
microsite enrichment 261
microzonal system, *see* alternate row cropping
Middle East 326
mimosine 314
mineral nutrients, and C_3 and C_4 species 338
minerals, *see* nutrients
minimizing light stress 407
minor forest products 177
mixed agroforestry systems 164
mixed cropping 310 (*see also* intercropping)
mixing ratio 355
modelling, and sensitivity analysis 255
models 239, 255
agroforestry components/interactions 226
of agroforestry plant associations 249
agroforestry systems 237
of alfalfa growth/development 212
for biomass cycle 222
conceptual 210
of crop mixtures 474

models (*cont.*)
and endogenous rhythms 505
for growth distribution 428
and ICRAF's programme 305
and intercropping 256
of light climate, validation 377
of light interception 366
mathematical 201
and missing information 210
nitrogen cycling 224
PAPRAN 237
of pasture growth 253
of plant water use 411
process specification 253
and production with time 353
response surfaces 262
and root
activity 540
growth 531
length 539
and sensitivity analysis 255
for shoot/root growth 453
simple qualitative 210
simulation 249
languages 253
of wheat crop 251
(*see also* mathematical models and plant architectural models)
modifying the field environment 553
Molluginaceae 324
monitoring
activities 291
tropical forest cover 291
monocarpy 311
monoecy 315
Monte-Carlo method 366
Mozambique 80, 82, 294
mulch 8, 37, 104, 107, 109, 120, 259, 283
multiple
cropping 165
heading, *see* tree spreading
multiplication, of organisms 176
multipurpose trees 260, 478, 579, 581
and growth regulation 514
and litter 236
and phenology 504
planting stock 561
propagation 561
research 557
and seed dormancy 312
multistorey canopy 40, 86, 477
multistorey systems 13, 16, 20, 49, 73, 247, 274, 405
and light 366
mushroom production 73
mycorrhizas 151, 179, 227, 230, 313, 395, 403, 415, 518
nutrient exploration 416
and nutrient pools 416
research 562

nematodes 77
Nepal 295
net primary production 354
net production rate
and stand age 352
and tree density 353
New Guinea 316 (*see also* Papua New Guinea)
New Hebrides 93
New Zealand 142
Nicaragua 142, 293
niche 19, 371, 582 (*see also* ecological niche)
Nigeria 80, 82, 105, 275, 277, 278, 294, 498
compound farming in 30, 32
night temperature 510
nitrate reductase 150
nitrite reductase 150
nitrofen, herbicide 108
nitrogen
and C_4 grasses 334
fixation, *see* dinitrogen fixation
reduction of 215
nodulation 312
of alfalfa 214
phenology of 518
notching 460
nursery, *see* plant nursery
nutrients
availability, changes in 417
competition, and fruit drop 465
cycle, and systems 221
cycling 218, 227, 317
and systems analysis 210
deficiencies 217
and density stress 474
depletion zones 415
inputs 223
leaching, in canopy 220
management of 584
and precipitation 223
preserving mechanisms 227

nutrients (*cont*)
procuring mechanisms 227
recycling 106, 107, 110, 414, 417
regime 241
removal, and tea 549
as a resource pool 403
and shoot:root ratio 436
and throughfall 226
transfer 259
uptake 414
strategies 416
and zones of depletion 415
Nyctaginaceae 324

oases 198, 200, 585
occult precipitation 380
Oceania, *see* Pacific Islands
Office de la Recherche Scientifique et Technique Oûtre-Mer (ORSTOM) 189, 202
oil crops, for energy 156
onset
of flowering 313
of rest 505
open habitats, *see* habitats
optimum sowing date 509
Oregon State University 286
organic matter 221
and nutrient cycling 231
turnover 227
and water cycling 231
organs, complexes and scale 174
ornamentals 18
outbreeding 6, 258, 311, 315
overbearing 277
overgrazing 130
overlapping crop sequences 166
Overseas Development Ministry, UK (ODM) 277, 511
overstocking 130
overstorey, and C_4 plants 339

pachyphylly 231
Pacific Islands 82, 83, 88, 92, 93, 310
paddy rice systems 73
Padjadjaran University, Indonesia 20
Pakistan 295
palatability 9, 314
under shade 62
Panama 225, 226, 293
Papua New Guinea 225, 226, 295, 497
Paraguay 142, 293
parthenocarpy 463
pasture growth, model of 253
pathogens 582 (*see also* diseases)
peat 231
and plant responses 233
pegging, of tea 544
pekarangan, *see* home gardens
Penman equation 382
PEP carboxylase 327
perennials
food crops, new possibilities 111
legumes, characteristics required 104
seed crops 313
and seeding 311
perturbation, of systems 20
Peru 74, 289, 293, 309
pesticides 111
pests 7, 110, 310, 313, 314, 321, 336, 478, 555, 575, 582
cross infestation 318
management 258
and systems analysis 210
research 562
and seeds 6
phenological
complementarity 513, 515
records 514
strategies 505
phenology 10, 19, 253, 580
definition 504
and plant management 515
of seasonal crop plants 503
and stress 525
of tropical woody perennials 503
phenophases 513
and environmental cues 525
and management 516
phenotypic plasticity 440 (*see also* adaptability)
Philippines 80, 82, 83, 87, 88, 138, 142, 295, 316, 371
photocell system, for estimating F_{max} 370
photoperiod 439, 505, 506
photosynthesis
of alfalfa 216
and production 335
sink limitation 406
and yield 335
photosynthetic efficiency 330

photosynthetic (*cont.*)
rates 335
and fruiting 466
at high PAR 373
and species 348
systems 323
and agroforestry 335
anatomical 327
and canopy 336
CO_2 concentration 332
and crop growth rate 348
ecological distribution 326
and growing season 336
isotope discrimination 334
and light 337
light responses 331
nutrient requirement 333
physiology 331
taxonomy 324, 328
temperature responses 332
water requirements 333
and water stress 386
photosynthetically active radiation 354, 365, 371
physiological processes, and growth 559
phytohaemagglutinins 314
phytomass, *see* biomass
phytotron 552
pioneers 313, 480
species 313
photosynthetic rates 349
plant
architecture 182, 428
models 174, 188, 190
(*see also* architecture)
arrangement 584
and light interception 374
breeding 303, 310
canopy, efficiency of 347 (*see also* canopy and leaf canopy)
compatibility 106
components, and yield balance 476
density 355
and ecosystem interactions 487
(*see also* plant population)
-environment interactions 209, 218
handling 314 (*see also* plant management)
interactions 95, 120, 170, 259, 317, 355, 575, 582
interfaces 4, 268, 475
management 455, 582
and compatibility 584
(*see also* management, plant handling)
nursery, duration in 7
population 261, 313
and bananas 493
and branching 470
and cereals 497
and crop performance 466
economic optima 467
and environment 468
and forest trees 489
and fruit size 470
and grain legumes 495
and harvest index of tea 547
and herbaceous crops 493
plant diameter 470
and plant habit 468
and plant weight 467
and rooting 470
and shoot:root ratio 438
and storage root crops 495
and tillering 470
and tree crops 489
and yield 489
product optimization 265
propagation research 561
stress 401, 584 (*see also* ecological stress, resource deprivation and stress)
factors, summary 418
types 579
for management situations 584
water potential, and stress 255
water status 255
plantation crops
and agroforestry 79
and integrated land use 81
and research 81
and smallholders 81
planting
density, and mean annual increment (MAI) 490
material, to farmers 581
planting out
and plant size 8
and soil conservation 8
and soil requirements 8
plasticity 468
plucking surface, of tea 546
Poaceae 324, 326
poisonous plants 69
Poland 372

poles 73
pollarding 74, 194, 461, 516
  to control flowering of understorey 61
  time of 60
pollen vectors 465
pollination 463
  competition for pollinators 318
  foraging behaviour 317
  by insects 315
  and plant spacing 493
  by wind 315, 317
pollinators 524
Polygonaceae 324, 325
polyphenolics 227
Portulacaceae 324
potential productivity 366
power alcohol 142
power law, for self-thinning 468
precipitation, and nutrients 225
primary
  land unit 169
  production, and energy efficiency 354
processing, of crops 314
production
  ecology 209
  functions 284
  goals 582
  possibility curves 274
  rhythms 19
productivity 249, 261, 273
  data, and variability 363
  of mixed canopies 355
progeny testing, and root growth 536
propagation
  environmental requirements 7
  by seeds 7
  tissue culture 7
  vegetative 7, 316 (*see also* meristem culture, tissue culture, and vegetative propagation)
propagules, supply of 311
  (*see also* cuttings, seeds and tissue culture)
proto-agroforestry unit 162
  (*see also* agro-unit and eco-unit)
provenances, and latitude 439
pruning 268, 407, 456, 516
  branches 462
  delays flowering 517
  and irregular bearing 465
  and mulch 546
  practices 460
  roots 462
  of tea 543, 544
  (*see also* dry matter distribution)
Puerto Rico 226
pulpwood 73, 76
  plantations 491
pyrolysis 139
  small scale 156

R-selection gradient 443
rainfall 379
  interception 380
  (*see also* precipitation)
ramets, and self-thinning 468
rangeland monitoring 293
rapid assessment 304
ratooning 165
reciprocal yield relationships 467
reclamation 585
rectangularity, and plant spacing 468
reduction
  of carbon dioxide 324
  and conversion of biomass 140
reflection coefficient, vegetation 384
regeneration 176
regular bearing 465
reiterated complexes, and scale 174
reiteration 176, 457
rejuvenation 176
  unit 174
relative yield total 475
relay cropping 165, 166
replacement series 262
replanting
  land preparation 12
  problems 12, 466
replication, at the genetic level 176
reproductive
  allocation, of dry matter 442
  biology 314
  phase 10, 313
  yield, and light 406
research
  co-ordination of species trials 581

research (*cont.*)
  and development of site assessment 577
  on environmental interactions 559
  experimental studies 576
  guidelines 31, 38, 55, 58, 66, 73, 74, 76, 99, 111, 113, 123, 128, 132, 134, 153, 201, 210, 217, 241, 244, 250, 254, 269, 272, 295, 303, 317, 319, 340, 350, 353, 360, 369, 371, 374, 375, 386, 393, 395, 407, 411, 412, 413, 417, 443, 444, 466, 470, 477, 489, 504, 507, 512, 518, 531, 534, 536, 538, 548, 557, 575
  and manuals 578, 580 (*see also* manuals)
  monitoring 576
  and networks 581
  perturbation tests 576
  and physiological studies 578
  plant management strategy 583
  on selection of species 577
  and simulation models 578
  and 'soil improvers' 580
  and surveys 576
residues 141
resistance analogy, and water loss 210
resource(s)
  demands, and phenology 515
  deprivation, to density stress 473
    (*see also* environmental stress, plant stress and stress)
  and management 584
  pools 402
  sharing
    horizontally 475
    in time, *see* phenology
    vertically 477
respiration, of plant community 353
response functions 210
returns to land 41
rhizobium 150, 312, 415, 512
  research 562
  and root growth 152
rhizotrons 552
Rhodesia 560 (*see also* Zimbabwe)
Rice Research Station, Sierra Leone 283
ringbarking 109, 110
risk
  avoidance 364
  reduction 289
  spreading 477
Rockefeller Foundation 286
root(s) 101, 104, 194, 197, 198, 200, 207, 210, 216, 223, 227, 230, 231, 317, 400, 411, 439, 470, 477, 513
  activity 394
    and fruiting 466
  aerial 227
  cap 529
  coconut 85, 96
  competition 532
    for nutrients 533
    for water 533
  complementarity 531
  and controlled environments 556
  death/decay 530
  density
    and nutrient mobility 415
    in plant mixtures 415
  distribution, growth and activity 527
  and dry matter distribution 428
  extension 395
  growth 528
    plant co-ordination 530
    regionalized 541
  hairs 541
  length density 394
  longevity 529, 541
  meristem 529
  morphology, and provenances 441
  and nitrogen uptake 540
  and nutrient uptake 414
  observation laboratories 528
  penetration, and soil strength 536
  phenology 517
    in arid regions 535
  pruning 413, 460
  radial expansion 529
  relative profiles 403
  research 562
  -shoot alternation of growth 429, 517
  -shoot ratio
    and mycorrhizas 453
    and plant stress 439
    (*see also* shoot-root ratio)

root(s) (*cont.*)
shrinkage 541
and soil compaction 437
and soil cracks 540
soil occupancy 416
and soil pore structure 537
suberization 540
tip elongation 529
of trees and herbs 411
and vapour gap 541
volumes 189
and the water table 535
rooting
in arid zones 534
depth 394, 532
in savannas 535
in tropical uplands 537
rotational land use 163
rotations, and nutrients 417
row
cropping, and light interception 374
orientation 407, 468
ruderal vegetation 181
RuDP carboxylase 327
Rwanda 294

Sahel 289
and IPAL Project, Kenya 130
savanna, *see* savanna
salination 135
salinity 411
and C_4 species 337
and roots 535
salinization 318
saponins 314
Sarawak 231, 232, 234
savanna 197 (*see also* Guinean savanna)
sawlog production 471
scale 207, 247, 295, 584
of living systems 174
spatial 162
temporal 162
sclerophylly 231, 242, 405
Scrophulariaceae 324
seasonal growth trends 506
secondary succession 350
seed
banks 581
collection, sampling strategy 316
dispersal 317
dormancy 6, 258, 312, 321, 507
germination 312, 510, 561
and light 374
large v. small 312
maturation 511
predation of 314
predators, and irregular bearing 465
respiration rates 466
source identification 557
treatment 106, 312
viability 6, 312
seedlings 258
establishment, and rooting 537
protection 200
selection index 261
self-fertility 465
self-incompatibility 315
self-pollination 315
self-pruning 491
self-thinning 467
senescense, time of onset 12
sequential planting 585
serendipity 316
Seychelles 88
shade 47, 49, 55, 217, 275, 277, 303, 313, 318, 369, 372, 377, 432, 465, 473, 474
and flower initiation 463
and fruiting 491
mutual shade effects on fruiting 470
and productivity 405
tolerance, and C_4 plants 345
tolerant crops 173
trees 277
shading, and production costs 364
shelterbelts 72, 318, 393, 409, 481
shifting cultivation 33, 294, 310
shoot(s)
dormancies 10
and dry matter distribution 428
removal, and growth extension 516
-root growth 530
-root ratio 427, 470, 473
and age 429
and annual habit 438
and desert species 438
and genotype 438
and light 432
and maturity 454
in mixtures 453
and perennial habit 438
and perturbation 430

shoot-root ratio (*cont.*)
and plant population 438
and provenance 439
(*see also* root-shoot ratio)
Sierra Leone 282, 294, 495
silicon cells 369
silvopastoral
land use 132
systems 411, 474 (*see also* animals, browse, fodder, forage and grazing)
SIMCOMP, simulation language 253
simulated climates 554
simulation
languages 253
models 210, 578
sinks, young fruits as 465
site-specificity 261
size-frequency distribution 467
slash-and-burn 103
slow growth, *see* growth rates
smallholders 73, 81, 91, 103, 110, 117, 125, 193, 217, 260, 272, 277, 283, 289
smallholdings 27, 48, 72, 81
(*see also* village-forest-gardens)
social
acceptability 584
problems 289
socio-economic aims 272
socio-economics 579, 582
soil
and agroforestry design 187
carbon, residence time 223
catenas, and vegetation 227
compaction 197, 200
and roots 537
conservation 11, 83, 261, 265, 268, 313, 584
cracking, and roots 537
degradation
assessment 291
and tree species 579
environment status 262
erosion 105
evaporation 413
fertility 117, 261, 276
management 11, 584
organic matter 222, 223
oxygen 542
pH, and roots 536
stabilization 318
surface mat 223
surface temperature, high, 105
temperature, and germination 510
water storage 403
solar energy
efficiency 354
interception 366
utilization 354
solar radiation
and dry matter yield 365
and heat balance 510
intensity 371
and phenology 505
solar tracking, of leaves 345
Solomon Islands 316
Somalia 294
source-sink relationships 10
South Africa 326, 372, 487, 560
South America 192, 196, 200
(*see also* separate countries)
South Asia 72
South Pacific 93
Southeast Asia 195, 316, 480
spacing, and stem form 486
spatial configuration 475
spatial units 169
species
choice of 585
collections 581
diversity 228
and stability 246
spices 91, 193
spininess 314, 315
'square' climate 555
Sri Lanka 74, 76, 80, 82, 83, 87, 88, 92, 93, 295
stability, in systems 246
stages, of growth and development 513
staggered planting 478
stand
closure 471
density index 468
standard climates 554
starchy tree crops 111, 156
state-variable methods 210
state variables 251
static land use 163
stemflow 225, 379
stem suckering 189
stocking density 468, 489
stomata, midday closure 378
storage root crops 470, 472
stress
adaptability to 403
and interactions 426
for light 405

stress (*cont.*)
in natural and agricultural systems 425
for nutrients 413
plant responses to 403
and predicting adaptability 404
response to in controlled environment 558
and survival 404
tolerance 104
(*see also* environmental stress, plant stress and resource deprivation)
sub-crowns 189
succession 174, 184, 186
successional mosaic 174
suckers 460
sucrose inversion, and temperature measurement 510
Sudan 294, 498
savanna, *see* savanna
sugar crops 141
summer rainfall, and phenology 514
sun
elevation, and light interception 378
leaves 349
supplementarity 274
supraplexion 190
Surinam 202, 293
survival 241
sustainability 31, 115, 249, 261, 289, 477, 578, 579, 582
Swaziland 125
Sweden 147
sylvigenesis 179
systems
analysis 161, 209, 299, 487
computer implementation 252
subsystems 251
applications 305
efficiency 584
interactions 225
interactive linkages 243
synthesis 300

tannins 231 (*see also* polyphenolics)
Tanzania 80, 82, 88, 117, 118, 294, 472, 495
taungya 33, 44, 119, 192, 194, 310, 470, 471, 517
Tea Research Institute of East Africa 547
tea, management of 543
temperature
and C_4 plants 326
and growth 373
and phenology 505
and soil 115
temporal arrangement 584
temporal separation 515
terminology, for agroforestry classification 165
termites 200
Thailand 82, 138, 142, 295
thinning 44, 45, 353, 487, 491, 517
throughfall 225
tillage, reduced 83
tillering 472, 497
timber 491
time
-dependent factors, *see* phenology
of sowing 507
and soil temperature 509
trends 264
tipping, of tea 544
tissue culture 581 (*see also* propagation)
Togo 292, 294 (*see also* West Africa)
toposequences 188
total area 169
toxicity 314
traditional land use 13
training 153
translocation
of carbohydrates 428
of roots 433
transmission, of light 367
transpiration ratio 391 (*see also* water use efficiency)
tree(s)
age, and mean annual increment 491
arrangement 265
attributes for intercropping 120
benefits of 104
for biomass 141
and boundary marking 289
C_4 species 324
characteristics of 3, 258, 260
and choice of genotype 524
choice of species 260, 579
criteria for species 104

tree(s) (*cont.*)
- crop combinations 579
crop plantations 34
as energy crops 147
environmental requirements 10
flowering/fruiting times 10
for fodder 480
and fruiting 366
for fuelwood 480
of the future 194
geometry and light measurement 369
germplasm 6
and grass 66, 82
in Costa Rica 53
incipient domestication 310
intercropping with 105
maize 107
internal water capacity 410
as investment 289
juvenile phase 9
late successional 474
leaves, distribution of 350
and light interception 370
light requirements 372
manipulation of 455
mature phase 10
morphology 9
as nurse plant 49
and nutrient cycling 417
optimum number 261, 278
and outbreeding 315
of the past 194
in pastures 53
pioneers 174
place in landscape 4
and plant population 489
for planted fallow 480
planting out 8
planting trials 133
in Kenya 133
poisonous foliage 580
pollination in arid regions 525
as pollinators 465
of the present 194
and productivity 263
propagation 7
protection 9
for pulp 63
rate of growth 9
removal 12
replanting 12
research on indigenous species 40
role of 257
rooting characteristics 9
and roots 527
senescence 12
shape 456
in shifting cultivation 35
and soil improvement 262
and spacing 45, 46
spatial arrangements 487
to spread productive activity 579
spreading 460 (*see also* coppicing)
and stems 410
as support 37, 74
for climbers 109
for timber 44, 49, 63, 478
training 268
in tropical land use systems 104
and vegetative yield 456
and weediness 580
and xeromorphy 409
(*see also* fruit trees, multipurpose trees and woody perennials)
trenching experiments 416
trifluralin, herbicide 108
Trinidad 82, 277, 293
Mora forest 185
tripsin inhibitors 314
trophic chains 210
tropical forest, resources 291
tropical hardwoods, genetic variation 317
tuber crops 585
Turkey 314

Uganda 294, 394, 509
underexploited crop plants 580
underground storage organs 534
understorey
and C_3 plants 339
and light requirements 372
species, and light 406
Union of Socialist Soviet Republics (USSR) 146, 326
United Kingdom (UK) 370, 372, 382, 498, 499, 528
Department of Energy 146
Meteorological Office 382
United Nations
Educational, Scientific and Cultural Organisation (UNESCO) 129, 238, 291
Environment Programme (UNEP) 291

United Nations (*cont.*)
  Food and Agriculture Organisation (FAO) 71, 76, 80, 291
  World Health Organisation (WHO) 291
  World Meteorological Organisation (WMO) 291
United States of America (USA) 138, 139, 142, 147, 148, 212, 276, 315, 326, 331, 338, 356, 372, 413, 497, 499, 514, 528, 532
University of
  Durham 231, 233
  Nairobi 341
  Reading, Plant Environment Laboratory 511
Upper Volta 198
useful plants, protection of 36

validation, of models 210
variability, decrease in 310
vegetables 18, 338, 373
vegetation
  communities, and models 210
  dynamics 181
  geometric structure 225
vegetative propagation 20
  of *Erythrina* 55
  stumps 48
  (*see also* propagation)
Venezuela 223, 224, 226, 230, 293
vernolate, herbicide 108
vernalization 313
versatile plants, need for 585
vesicular-arbuscular mycorrhizas, *see* mycorrhizas
Vietnam 72, 76, 295
village-forest-gardens 13
  ecological stability 19
  man-made forest 20
  social aspects 21
  spatial organisation 16
  temporal organisation 18
  (*see also* forest gardens)
vine growing 516
virus-free stock 466
volatilization, of soil nitrogen 403

wastes 141
water
  balance 381
    and plant management 584
  catchments 133, 388, 390
  conservation 265, 268
  consumption 388
  cycle 221, 240
  harvesting 585
  management 116
  as a resource pool 402
  stress 110, 386, 465
    adaptation to 424
    avoidance 408
    and canopy considerations 409
    and co-habiting species 408
    overcoming 399
    and plant development 412
    toleration 408
  supply 241
    and forest structure 400
  use
    efficiency 210, 276, 389, 412
      and C_4 plants 333
    and cotton 509
    and soil 386
    and tea 388
watersheds 31
weeds 69, 106, 108, 120, 192, 194, 318, 326, 478, 480, 491
  control 11
wells, and settlements 130
West Africa 25, 177, 480
  and cacao 82
  climate 26
  compound farms and fields 29
  soils 26
  vegetation 26
  (*see also* separate countries)
West African Institute for Oil Palm Research (WAIFOR) 34
West Java 13
Western Samoa 93
wild populations 310
wildlife 135
William and Flora Hewlett Foundation 341
wilting 410
windbreaks, *see* shelterbelts
winter rainfall, and phenology 514
wood
  density 313
  for liquid fuels 146
  production 471

woodland management, in dry areas 132
woody perennials, elimination of 110
(*see also* trees)
woody plants, extending climatic range 516
World Bank (International Bank for Reconstruction and Development) 146

yield
- density relationships 467
diagram 358
stability 241

Zaire 192, 294, 380
Zambia 142, 294
Zimbabwe 142, 294 (*see also* Rhodesia)
Zingiberaceae 18
zonal agroforestry 476
systems 164, 268
zoo forestry 197
Zygophyllaceae 324

618

OTHER ICRAF BOOKS

1979 Mongi, H.O. and Huxley, P.A. (Eds). "Soils Research in Agroforestry". Proceedings of an Expert Consultation, Nairobi, 26-30 March 1979. ICRAF, Nairobi. 584 pp.

1980 Chandler, T. and Spurgeon, D. (Eds). "International Cooperation in Agroforestry". Proceedings of an International Conference, Nairobi, 16-21 July 1979. ICRAF, Nairobi. 469 pp.*

1980 Nair, P.K.R. "Agroforestry Species, A Crop Sheets Manual". ICRAF, Nairobi. 335 pp.

1981 Buck, L. (Ed.). "Proceedings of the Kenya National Seminar on Agroforestry". Nairobi, 12-22 November 1980. ICRAF, Nairobi University. 638 pp.*

1983 Hoekstra, D., Kuguru, F. and Ntiru, R C. (Eds). "Agroforestry for Small-Scale Farming Systems". Proceedings of a Workshop. Nairobi, 5-10 September 1982. ICRAF/BAT, Nairobi. 304 pp.

ICRAF PUBLICATIONS — A full list of reports, working papers, and so on is available on request from the Information and Documentation Section, ICRAF, PO Box 30677, Nairobi, Kenya.

* Out of print, but a list of contents and single photocopies of papers can be provided on request.