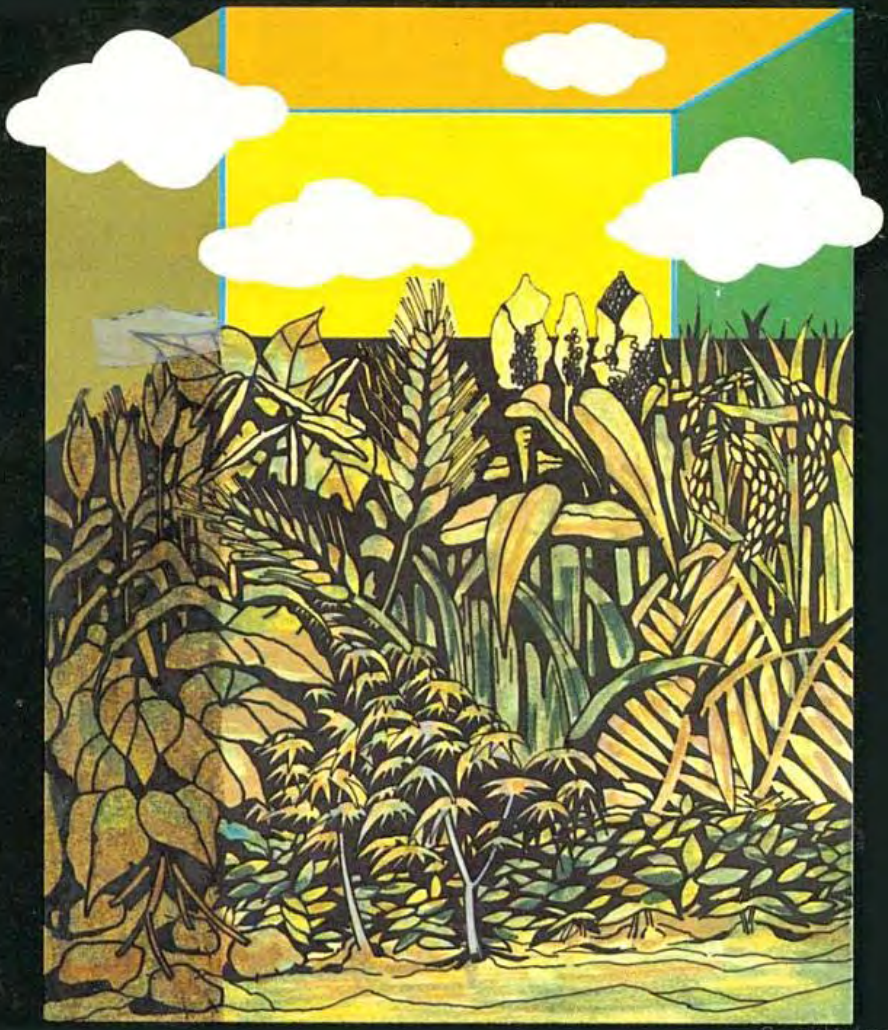
Potential Productivity of Field Crops Under Different Environments

International Rice Research Institute



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Symposium on

Potential Productivity of Field Crops Under Different Environments

1983
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FOREWORD

The International Rice Research Institute is primarily concerned with a single crop, rice. Most of IRRI's research and training programs are oriented toward this crop, which is the most widely eaten by the low-income population of the world.

Our concern, however, is not only the rice crop, but also the rice farmer. The farmer has found, through trial and error, that under appropriate conditions, other crops can complement rice or even replace this important food crop, often with more total food production and greater benefit to the farmer and his family.

This increased concern for crops that can complement or replace rice in the cropping systems of rice farmers led to the Symposium on the Potential Productivity of Food Crops Under Different Environments, which was held at Los Baños, Philippines, 22-26 September 1980.

In the past two decades, much progress has been made in the area of crop physiology that deals with the growth and yield of field crops under different environments. The symposium offered a unique opportunity for crop physiologists working on different crops to meet and discuss their problems.

One of the goals of the symposium was to estimate potential productivity. Potential productivity is an estimate of the upper limit of yield increase that can be obtained from a crop plant. It is, in a way, the most optimistic estimate of crop yield based on present knowledge and available biological materials under ideal management in an optimum physical environment.

Although dramatic production gains have been made in the last 20 years, particularly from rice and wheat, further increases in production are becoming more difficult to attain. A dynamic research program is essential if we are to sustain a dynamic production drive. We cannot be content merely with finding explanations for not achieving the yield potentials of present-day crop varieties. We must find methods for realizing that potential, at least in experimental fields.

The motivation for this Symposium came largely from Dr. A. Tanaka of Hokkaido University and Dr. Shouichi Yoshida, head of the IRRI Plant Physiology Department. They and IRRI scientists Dr. B. O. Juliano and Dr. R. A. Morris organized the symposium.

The papers in this volume were edited by W. H. Smith and Stephen J. Banta, with the assistance of Gloria S. Argosino and Corazon V. Mendoza, assistant editors.

M. S. Swaminathan
Director General

BIOLOGICAL BASIS PHYSICAL ENVIRONMENT, AND CROP PRODUCTIVITY

CLIMATE

J. Elston

Climate and weather help determine cropping systems and yields of individual crops. The information that we have about the relations between climate and cropping systems is mostly statistical and has obvious limitations. Temperature and water balance seem to determine the distribution of crops.

Our understanding of the control of climate and weather upon yields has a sounder intellectual base but still needs a large amount of systematic experimental work on leaf growth and death, respiration, and mineral uptake and translocation. The total dry matter produced by a crop is closely related to intercepted radiation.

It is a truth, nearly universally acknowledged by agronomists, that the dry matter produced by a crop is proportional to the photosynthetically active radiation intercepted by the crop (see Milthorpe and Moorby 1979). Dry matter production depends upon:

- the photosynthetically active radiation above the crop;
- the appearance, rate of growth, duration, and death of the leaves that compose the intercepting canopy; and
- the structure of the canopy.

The economic yield of the crop then depends upon the distribution of the dry matter among the various organs of the individual plants.

The productivity of the crop is the yield of the plants expressed per unit of a particular factor that limits production. Limiting factors include solar energy, labor, and plant nutrients. Several of them may operate as limiting factors at the same time. The total production of the crop is the productivity multiplied by the quantity that represents the limiting factor. Solar radiation is a flux to the surface of the crop and is measured per unit area. Therefore, our first analysis of productivity is usually of yield per unit area (Elston and Dennett 1980).

There must be at least three parts to an analysis and understanding of the ways in which climate and weather determine potential and actual yield. First is the determination of the real quantities of the climatic variables at a particular place. Second is

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the way in which these climatic variables determine the leaf area, canopy structure, total dry matter, and economic yield of a particular crop at that place. Third is the way in which climate, weather, available genotypes, and social and economic factors come together to determine possible and actual cropping patterns and farming systems.

Both *climate* and *weather* are difficult to define. Lamb (1969) defined climate as the totality of the weather experienced at a given place. He suggested that we think of it as long-range meteorology. In agricultural meteorology, we can think of weather as being the real atmospheric conditions experienced in a particular place at a particular time. Clearly, the concept of climate involves some smoothing of the variations in weather.

Meteorological factors vary continuously in space and time and do not necessarily change in phase with each other. No natural classification of climate, based upon consistent foundations that are internal to meteorology alone, is possible. Instead, climates have been defined by their biological consequences. For example, Koppen's grand classification, which has been used to define the parish of the International Crops Research Institute for the Semi-Arid Tropics, uses the great vegetation groups of the world to define climatic groups.

In agriculture we are concerned with many climatic classifications. Each classification exists for a special purpose: perhaps to distinguish tsetse fly areas from those areas without the pest, or to define the productive possibilities of a rice-growing system. The most general, and least exact, schemes are those used to classify farming systems.

The actual yield of a particular crop at one place in one year can be thought of as having two components. One relatively stable component is the long-term average yield which depends upon the genetic potential of the crop, the way it is grown, and the climate. The other component is the departure of the actual yield of a particular year from the average yield. It depends primarily upon the weather of that year, either directly through weather factors or indirectly through the effect of weather on the incidence of pests and diseases and on the timeliness of the operations used in growing the crop.

ASSESSMENT OF CLIMATE IN AGRICULTURE

Climate is an abstraction relating the aerial environment to time and place. A farming system is also an abstraction, relating physical, chemical, biological, and human features to time and place. Climate helps determine farming systems, setting a wide range of possibilities that are then narrowed by other factors.

The physical components of climate have a more straightforward analysis than most of the other components of a farming system mainly because:

- The relevant variables are more easily defined. It is easier, for example, to define water balance or temperature than it is to define risk or stability.
- Some variables, especially rainfall and temperature, have been systematically measured at some places for relatively long periods. (However, not all the measurements are reliable.)
- The laws of physics dealing with energy and matter provide constraints to any

study, and may not be violated.

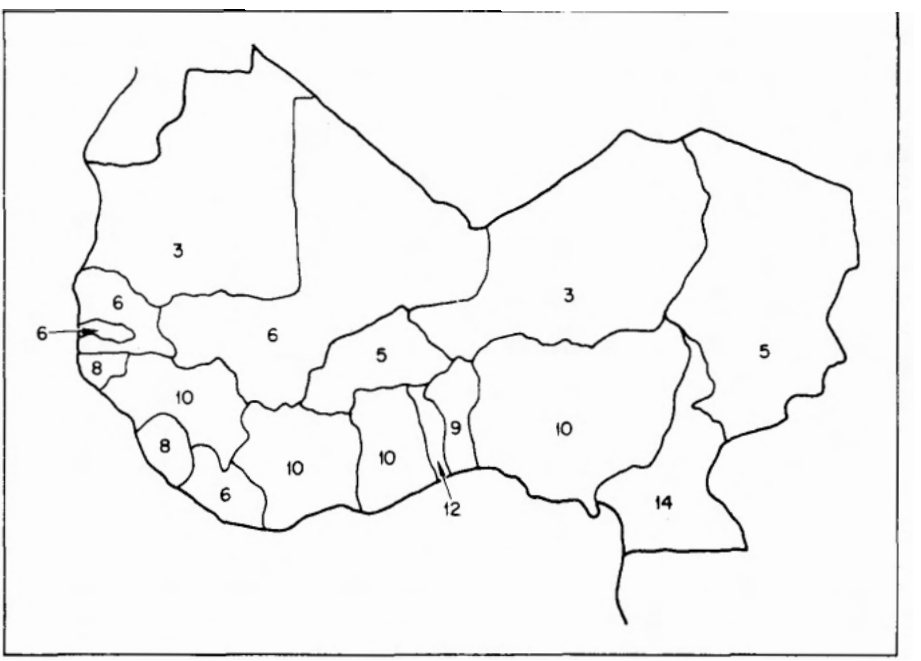
- The mechanisms of the atmosphere that control climatic variables are simpler than those in some other parts of a farming system, and are partly understood.
- It is relatively easy to set parameters for any analysis, providing constraints with some real meaning rather than statistical values determined from regressions.

Climate and farming systems

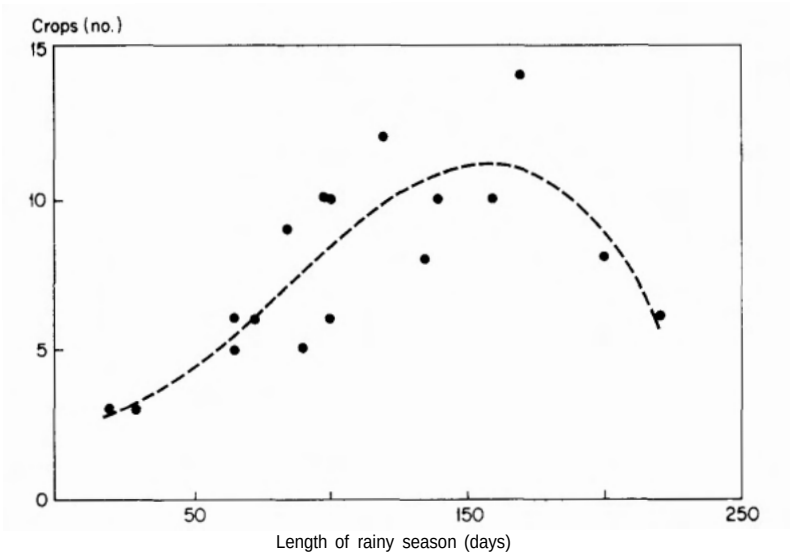
Any analysis must start with an examination of simple cropping systems in simple environments. My colleagues, Michael Dennett and Chris Speed, and I have therefore chosen to look at the cropping system of West Africa, using FAO statistics for species, area, and yield. West Africa has a relatively simple climatic system and rainfall changes more or less regularly with latitude.

In West Africa the number of crops grown in a country changes relatively systematically with latitude (Fig. 1). Only a few crops occupy more than 1% of the total cultivated area in the northern countries, but a number of the southern countries have more than 10 main crops. This change can be related statistically to the length of the rainy season (Fig. 2), defined as the period, in days, when rainfall exceeds potential evaporation.

The proportion of the cultivated land that is used for a particular crop can also be related statistically to the length of the rainy season (Fig. 3). There are characteristic patterns from the dry and wet regions. Millet and sorghum, for example, occupy more than 80% of the total cultivated area in the driest northern regions and are



1. The number of crops in the countries of West Africa. A crop is counted when it occupies at least 1% of the total cultivated area of a country.



2. The number of crops grown in West Africa is a function of the length of the rainy season in days, plotted as the duration of the period when rainfall exceeds potential evaporation.

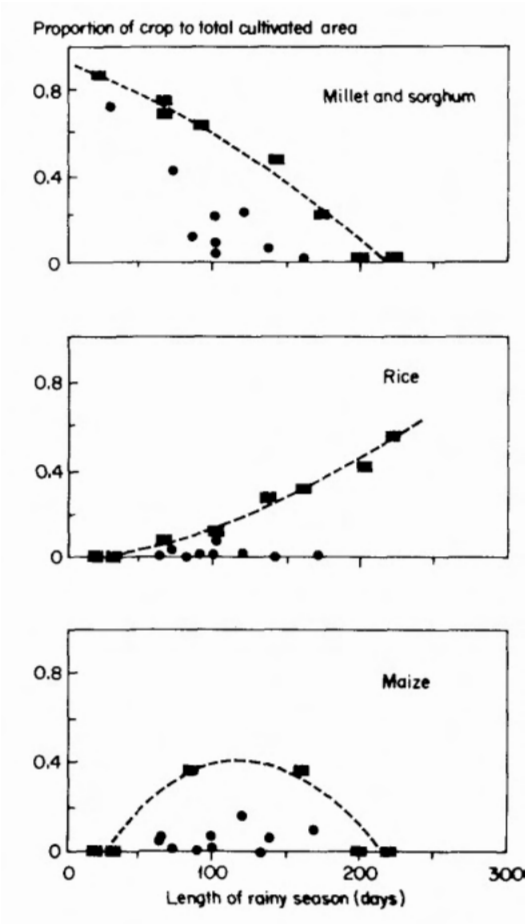
hardly featured in the wettest regions, while rice shows the reverse pattern. Clearly, there are also other places where more of a particular crop could be grown. This is especially true for rice and maize. Soils and cultural and economic constraints modify the control exercised by climate on cropping systems. Nevertheless, the results show a match between the climate and the distribution and relative importance of a crop.

Weather and actual yield

Statistical studies of the relation between weather and the yields and value of a crop have an honorable history (Beveridge 1922, Fisher 1924). With increasing measurements of weather variables and crop yields, it is not possible to relate yield variations from year to year to weather variations. For example, tobacco yields in northern Europe are positively correlated with summer temperature anomalies (Dennett et al 1980). The regression equations explain about 65% of the variation in the yields by variation in temperature and rainfall for the period 1955-72.

Similar relatively simple relations exist between variations in rainfall, representing its water balance, and yields of the crops in our study of West Africa. There is a simple linear correlation between the mean estimated yield of sorghum in Nigeria from 1966 to 1976 and the departure of the rainfall from the mean rainfall for each of the years during the period (Fig. 4). (This was a period of low rainfall for the region). The regression accounts for 70% of the variation in yield and appears to remain a reasonable estimate when tested with the yields for 1977 and 1978.

These statistical relations can be used to assess its present sensitivity of yield to variations in the climatic factors examined. For example, tobacco leaf yields in northern Europe increase on the average by 0.2 t/ha for each 1°C increase of

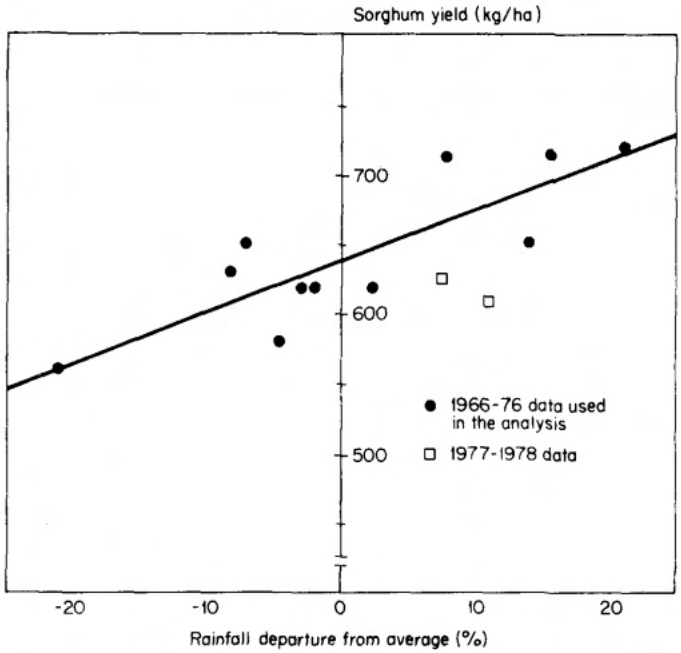


3. The relative importance, as a fraction of the total cultivated area, of millet and sorghum, rice, and maize in the countries of West Africa plotted against the length of the rainy season.

summer temperature. Sorghum yields in Nigeria increase on the average by 4 kg ha for each 1% increase in rainfall. Moreover the equations can be used to predict yields, with reasonable reliability on occasions. Yields of millet and sorghum for 1961-65 and estimates of yields for 1977 and 1978 were compared with calculations from the regressions established for 1966-76 (Fig. 5). The correlation coefficient is 0.80 and is highly statistically significant. The high correlation is due in part to the differences in mean yields between the countries.

These statistical relationships are not always linear. Indeed there is almost a prior expectation that yields should decrease with an extreme anomaly on either side of the average. This certainly happens in Senegal for both groundnut (Fig. 6) and rice (Fig. 7). In both cases, yield drops in extremely wet and extremely dry seasons. The decreases in wet seasons may not necessarily be ascribed to effects of rainfall on growth and hence on yield. They could result from the changed incidence of pests and diseases or to difficulties in agricultural operations.

Statistical relations of the sort just discussed can be determined exactly for a particular crop in a particular place over a particular period, but they can never be



4. The relation between sorghum yields in Nigeria and the departure from the average of the May to October rainfall, 1966-76.

general. We do not know what confidence to place in such relations.

There are great conceptual difficulties in our present approaches to the relations between climate and farming systems. The biological and social components are extremely complex and their interactions, even more so. The ordinary methods of experimental science and agronomy are not adequate. However, the ideas of operational research, systems analysis and synthesis, and modeling can be used for analyzing the relation between climate and farming systems. These ideas, coming from warfare, economics, and science fiction, fit easily into studies of agriculture.

CLIMATE, WEATHER, AND PHYSIOLOGICAL MODELS

A measure of the state of a crop, such as leaf area index (LAI) or dry weight per unit of land, at a given moment, is the sum of a set of processes. For example, the processes of photosynthesis, mineral uptake, respiration, and abscission determine the dry weight. Each process has a rate, which describes a transfer of energy or matter or a change in number. The rates can usually be easily measured by plant physiologists. These processes exist because there are physiological mechanisms that transform or transport energy and matter. The mechanisms are biochemical or biophysical. These mechanisms respond to a number of environmental inputs, which partly determine the rates of the processes and hence the state of the crop.

The rates of the processes change as the environmental factors such as radiation, temperature, or water balance vary. Ultimately, the outcome of the processes should

be predictable, systematic *M* not random. However, we do not understand the processes and their responses to the environment well enough for this predictability to be universal. A general scheme often lacks precision and one that has statistical precision often lacks generality.

Where the outcome of a set of processes can be predicted from fundamental knowledge, we can construct a deterministic model of the system, relating the state variable to climatic factors. Frequently, however, we have to use some elements of guesswork, fudge, and statistical relation. Models then contain a stochastic element.

The states of a crop

LAI, total dry weight per unit area of land, and economic yield are the easiest set of crop state variables to consider at the moment. LAI helps determine the amount of photosynthetically active radiation that is intercepted and so helps determine the total dry weight. The total dry weight is distributed among the various organs of the plant, including the parts that become the economic yield. A simple two-way table can be made, relating crop state variables to processes (Table 1). This is straightforward, if we know all the processes.

The rates of change of state variables, dS, dt, can then be written as functions of the processes, P_1 to P_9.

$$dS_1/dt = f(P_1 \times P_2 \times P_3) - P_4,$$

where f relates volume to leaf area;

$$dS_2/dt = (P_5 + P_6) - (P_2 + (P_8);$$

and

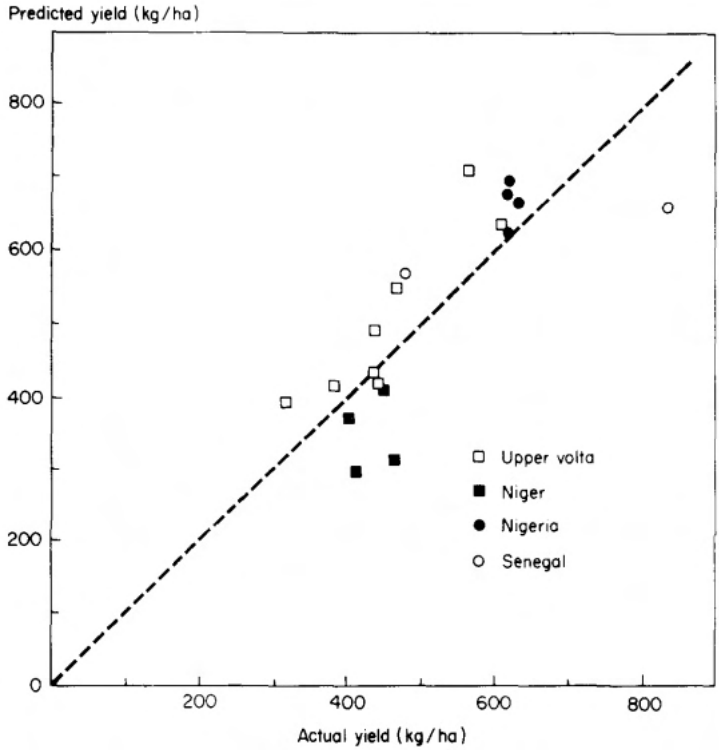
$$dS_3/dt = P_9\,[(P_5 = P_6) - (P_7 + P_8)] + [(P'_5 + P'_6) - (P_7 + P_8)]$$

where P' is a process in the yield tissue.

Table 1. A simple scheme relating various physiological processes to the state of crop variables such as leaf area index, total dry weight, and economic yield.

Process	State of variable[a]		
	Leaf area index S_1	Total dry weight S_2	Economic yield S_3
Leaf initiation (P_1)	+		
Cell division (P_2)	+		
Cell expansion (P_3)	+		
Leaf death (P_4)	–		
Gross photosynthesis (P_5)		+	+
Mineral uptake (P_6)		+	+
Photorespiration (P_7)		–	–
Dark respiration (P_8)		–	–
Translocation (P_9)			+

[a] + = gain, – = loss.



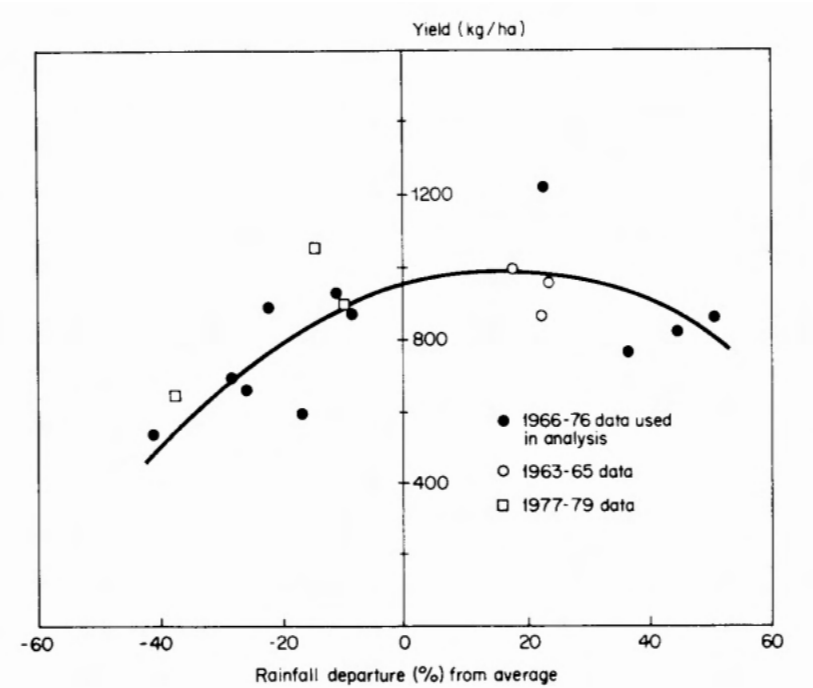
5. Predicted and actual yields of millet and sorghum in 4 countries of West Africa.

The equations for matter express conservation laws. The state at a particular time is the sum of *dS/dt* from the start of growth until that time. The use of this sort of scheme ensures a systematic approach to analysis and measurement and directs attention to relations that we do not understand or have neglected.

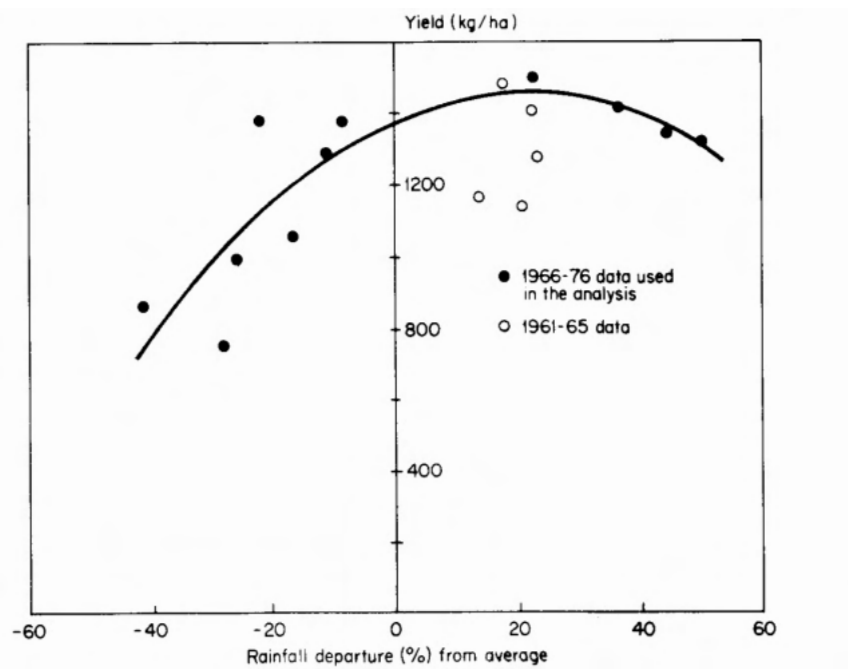
Rates as functions of climate and weather

Now we need to write the rate of each process as a function of the meteorological variables that control it, and to have the relevant measurements of those variables. But this is often extremely difficult as genetic differences, environmental and physiological history, complex reactions and interactions, microclimatic variation, and our own inadequate knowledge all complicate attempts to express these relations quantitatively. There is, for rice, a fine book edited by Dr. S. Yoshida (IRRI 1976) that presents much of the information in an organized and scholarly way. The contributions from former and present IRRI staff members form an intellectual justification for the work of the institute. However, for most crops the necessary experiments have not been done or the information has not been collected. Even for rice and the other cereals there is an enormous amount of work still to be done.

Any brief generalization must be vague, incomplete, and inaccurate. The rate of leaf initiation depends primarily upon temperature and is often a linear function of



6. Relation between groundnut yields in Senegal and the departure from the average of the May-October rainfall.



7. Relation between rice yields in Senegal and the departure from the average of the May-October rainfall.

temperature within the field range of a particular crop. Leaf growth depends upon temperature and water stress, both seeming to operate primarily through cell number. It is also strongly influenced by nitrogen nutrition and by internal controls. Leaf death seems to be influenced by temperature and water stress, but it too is strongly dependent upon internal controls. Physiologists have not given sufficient attention to the processes determining leaf area, so we lack information, especially from field experiments. The omission is surprising because most agricultural operations affect leaf area rather than photosynthetic efficiency. Moreover, the physiological changes that have occurred during plant domestication have been in the size and duration of the photosynthetic system rather than in the photosynthetic rate (Evans 1976). The control of leaf area by temperature and water stress is the first important effect of climate and weather upon yield.

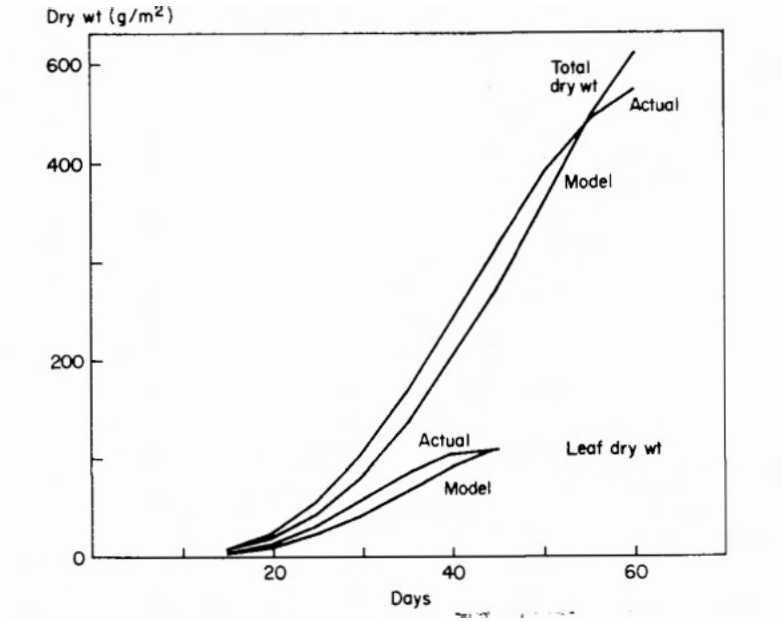
The net photosynthetic rates of a crop (Baker and Meyer 1966 for cotton), crop growth rate (Biscoe and Gallagher 1978 for various cereals), the total dry matter production (Monteith 1977 for various crops), and sugar yield (Scott et a1 1973 for sugar beet) are all linear functions of intercepted radiation. The analysis of the relation between leaf area, canopy structure, intercepted radiation, and photosynthesis has been most successful (Saeki 1963, Monteith 1972). The photosynthetic rate of a unit of leaf area depends upon irradiance, leaf temperature, and water stress, but it is also strongly influenced by internal controls such as the photosynthetic pathway.

We have less knowledge of mineral uptake, photorespiration, and dark respiration. Fortunately, as quantities, they are all smaller than photosynthesis. Dark respiration probably depends upon previous photosynthesis and temperature but has very strong internal controls. Mineral uptake is certainly influenced by soil temperature and perhaps by rate of evaporation.

Translocation is often represented in models by a partition coefficient, such as harvest index, because it is so little understood. It is affected by temperature, but apparently can adapt to changes in temperature, and there are strong internal controls.

The state of development of a crop, usually represented by numbers, like the number of tillers per unit area or the number of fertile florets per inflorescence, is important in determining yield. Again, our experimental information and our understanding are inadequate. However, the rates of development, and hence the developmental stage, may depend upon day length, temperature, and assimilate supply.

All these inadequacies, inconsistencies, and apparent experimental idiocies combined to force a tolerance for ambiguity upon the agricultural meteorologist — a tolerance which does not easily fit the training of experimental scientists. Fortunately, we are now beginning to develop quantitative models of some predictive value, which are partly based upon a real understanding of the relations between weather and physiology. It is not that they are done well, but it is surprising that they work at all. For example, my colleagues John Littleton, Michael Dennett, and John Monteith have predicted the total dry weight and the leaf dry weight for cowpea crops at the International Institute of Tropical Agriculture, Ibadan, from measurements of temperature and solar radiation (Fig. 8).



8. Modeled and actual total dry weight and leaf dry weight for a cowpea crop at Ibadan (based upon Elston and Dennett, 1980).

CONCLUSIONS

The total dry weight of a crop is proportional to the intercepted solar radiation when nutrients, water supply, pests, and diseases do not limit growth. The quantity of intercepted radiation then depends upon leaf area, canopy structure, and solar irradiance. Leaf area depends upon temperature. Most crops, however, experience water stress, poor nutrition, and pests and diseases. Statistical correlations for yields and distribution of field crops are usually done with temperature and rainfall. Temperature and rainfall, representing the water balance, are most likely to limit leaf growth, and hence the interception of radiation in the majority of the field crops.

ACKNOWLEDGMENTS

Michael Dennett, John Littleton, and Chris Speed have all helped me substantially.

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A SOIL BASE FOR PRODUCTIVITY ESTIMATES

R. Dudal, G. M. Higgins, A. H. Kassam, and A. Pécrot

Recent completion of the FAO/Unesco *Soil map of the world* has provided an inventory of the main soils of the globe and an opportunity to incorporate the attributes of the various soils into general assessments of productivity potential of land areas.

The soil units classified in this inventory occur under a wide but identified range of slope, texture, phase, and climatic conditions. Individual mapping units designated by the inventory comprise, in addition to the dominant soil, a wide range of associated soils which may be of equal or even greater agricultural potential. Generalizations on agricultural potentials of major soil regions, which fail to take these and other factors into account, are of limited value as shown by the comparison of individual length of growing period zone results for selected countries.

Many other factors contribute to potential productivity from a given land area. Given the correctness of the soil factors used in the model, an eightfold difference in productivity is postulated. Similar large differences in estimates of potential result when the same soil is assessed for the same crop under different moisture regimes. Fourfold differences in production potential are postulated for the same crop, under the same climate, on the same soil, but under two slope conditions. Changes in input levels are postulated to result in twelvefold differences in overall productivity potential within a uniform soil and climatic regime. Given more specifcally adapted land use systems, even larger differences would undoubtedly result.

These assessments add weight to the growing conviction that realistic estimates of long-term potential productivity can only be made through an interdisciplinary approach that considers all contributing attributes of land, crop, and land use. Matching crop requirements with land properties and formulating production systems for optimum exploitation of the physical environment are prerequisites to determining optimum production potential. The need for incorporation of socioeconomic and management factors in such assessments is now also well recognized.

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Soil is an important factor contributing to the production potential of a land area. Climate, crop, production inputs and methods, land improvement, and socioeconomic factors are among other components to consider in assessing the production potential of a land area. Lack of qualification and definition of these factors accounts for the widely varying estimates of the global extent and potential of cultivable land.

Recent projections by the Food and Agriculture Organization (FAO 1979a) reveal that 60% more food will have to be produced in the year 2000 to meet acceptable nutritional levels for the increased world population. Estimates of land production potentials are required to ascertain where and how the needed production increases can be obtained. Answers are needed to such questions as:

— Where are the areas of highest potential for different crops under various levels of inputs, and what are their extents?

— Where are the areas that would benefit most from land improvements and changes in systems of production, and what are their extents? and

— What levels of investment are required for realizing the additional production?

Soil inventories contribute to the solution of these questions.

This paper summarizes current knowledge on the extent and distribution of major soils in the developing world and discusses the role of this knowledge in an interdisciplinary assessment of rainfed production potential.

A GLOBAL INVENTORY OF SOIL RESOURCES

The expansion of soil survey activities in the early 1950s resulted in the increasing availability of soil maps. Knowledge of the world's soils also increased markedly. Aggregation of country soil inventories, however, was hampered because survey methods, nomenclature, and legends and systems of classification varied widely. Accordingly, global and regional assessments of soil resources were difficult.

Recognizing these facts, FAO and the United Nations Educational, Scientific and Cultural Organization (UNESCO), in cooperation with the International Society of Soil Science (ISSS), embarked in 1961 on the preparation of a soil map of the world on the scale of 1:5 million. Intensive soil correlation was an important element of the program and an international agreement on the legend was reached in 1968. This global soil inventory was completed in 1978 and the 19 maps with accompanying texts (FAO 1969-1980) were presented to the 11th ISSS Congress at Edmonton, Canada.

The reliability of the map differs from area to area, depending on the accuracy and detail of the material used for its compilation. Table 1 shows the kinds of information available in the different parts of the world and provides a picture of global soil survey coverage. Class I areas are systematic soil surveys in which the boundaries are based on physiographic data while the composition of the mapping units is based on field studies. In Class II and Class III areas, boundaries are derived from interpretation of general information on landform, geology, climate and vegetation, and from scattered soil studies.

Only about a fifth of the world's soils have actually been surveyed. The highest percentage of survey coverage is in Europe, and the lowest in Africa. When percen-

Table 1. Global soil survey coverage (%).

	Class I	Class II	Class III
Africa	7.5	38.0	54.5
Asia	19.0	49.0	32.0
Australia	11.0	61.0	28.0
Europe	16.3	23.7	-
North and Central America	28.0	16.0	56.0
South America	14.6	45.9	39.5
World	21.0	40.0	39.0

tages are calculated after deduction of arid regions and permafrost areas, which are rarely surveyed, Class I surveys cover 10.8% of Africa, 23.3% of Asia, 15.4% of Australia, 80.2% of Europe, 46.1% of North and Central America, 15.0% of South America, and 28.2% of the world.

To ensure reliable identification and correlation in areas far apart, the soil units are defined in terms of observable and measurable properties of the soil itself. The key properties have been selected on the basis of generally accepted principles of soil formation. The definitions of diagnostic features and horizons are drawn on the successive approximations of the United States Department of Agriculture (USDA) soil classification and are in accord with *Soil taxonomy* (Soil Survey Staff, S.C.S., USDA 1975).

The legend of the map comprises 106 different soil units, the nomenclature and definitions of which are given in Volume I, *Legend of the soil map of the world* (FAO 1974).

The mapping units employed on the maps are associations of soil units and are usually composed of a dominant soil and of associated soils. Each of the latter occupies at least 20% of a mapping unit area; important soils which cover less than 20% of a mapping unit area are considered inclusions.

The mapping unit symbol of the soil associations also indicates the textural class, slope class, and phase as follows:

The textural class applies to the dominant soil; there are three textural classes: coarse textured, medium textured, and fine textured.

Slope classes indicate the slope that dominates the mapping unit area; 0-8% slopes, 8-30% slopes, and slopes greater than 30%.

Phases indicate land characteristics that are not reflected by the composition of the soil association but are significant to land use or management of the land. The 12 phases are: stony, lithic, petric, petrocalcic, petrogypsic, petroferric, phreatic, fragipan, duripan, saline, sodic, and cerrado.

MAIN SOILS OF THE DEVELOPING WORLD

To date, global interpretations of the *Soil map of the world* have been confined to considerations of the dominant soil in each mapped soil association. Using such data Buringh et al (1975) have estimated the world's potential agricultural land as 3.7 billion ha, and Dudal (1978) has computed global extents of major soil units (Table 2).

Table 2. Distribution of the major soils of the FAO/Unesco *Soil map of the world.*

Soil associations dominated by	World	
	Million ha	Percent
Fluvisols	316	2.4
Gleysols	622	4.7
Regosols and Arenosols	1,330	10.1
Andosols	101	0.7
Vertisols	311	2.4
Solonchaks and Solonetz	268	2.0
Yermosols	1,176	8.9
Xerosols and Kastanozems	896	6.8
Chernozems, Greyzems, and Phaeozems	408	3.1
Cambisols	925	7.0
Luvisols	922	7.0
Podzoluvisols	264	2.0
Podzols	478	3.6
Planosols	122	0.9
Acrisols and Nitosols	1,050	8.0
Ferralsols	1,068	8.1
Lithosols, Rendzinas, and Rankers	2,263	17.2
Histosols	240	1.8
Miscellaneous land units (rice fields, salt flats, rock debris, shifting sands, etc.)	420	3.2
	13,180	100.0

More precise assessment of the total extent of soils can be obtained by considering all the constituent soils delineated in a mapping unit. Such assessments have been achieved for the Developing World by the FAO agroecological zones project (1978) providing, by country and by region, the extent of individual soil units subdivided by texture class, slope class, and phase.

The relative distribution of soil units in each mapping unit, according to the mapping unit composition with respect to the number of associated soils and inclusions, is shown in Table 3. A summary of the extent of major soil units, slope classes, texture classes, and phases in the five regions of the developing world is in Table 4.

The overall picture is by no means constant within individual regions. In the driest of the regions (Southwest Asia), Yermosols, Lithosols, and Regosols are the most extensive. In the moister Central American region, the more weathered Luvisols and Cambisols are of greatest extent. The most humid of the regions, South America and Southeast Asia, have mainly the highly leached Ferralsols, Acrisols, or both. Africa, with a wide range of moisture conditions, has a relatively equal distribution of Lithosols, Yermosols, Arenosols, and Ferralsols.

The main general characteristics and limitations of these more extensive soils have been described by Dudal et a1 (1974) and Dudal (1980) and are briefly summarized below. The soils are listed in the order of their areas (Table 4), and a general correlation with the USDA *Soil taxonomy* is given in parentheses. Precise definitions and correlations are given in the *Legend* of the FAO/ UNESCO *Soil map of the world.*

Table 3. Relative distribution of dominant soil, associated soil(s), and inclusion(s) expressed in percentage of area of the mapping units according to the composition of the mapping unit.[a]

Percentage of area dominant soil	Associated soil(s)		Inclusion(s)	
	No.	Percentage of area	No.	Percentage of area
100	0	0	0	0
70	1	30	0	0
60	1	30	1	10
60	2	20 + 20	0	0
50	2	20 + 20	1	10
30	3	20 + 20 + 20	1	10
50	1	30	2	10 t 10
40	1	30	3	10 + 10 + 10
50	1	30	4	5 + 5 + 5 + 5
40	2	20 + 20	2	10 + 10
30	2	20 + 20	3	10 + 10 + 10
40	2	20 + 20	4	5 + 5 + 5 + 5
30	3	20 t 20 t 20	2	5 + 5
25	3	20 + 20 + 20	3	5 + 5 + 5
24	3	20 + 20 + 20	4	4 + 4 + 4 + 4

[a]Associations dominated by Lithosols are allocated a slightly different distribution, namely: Lithosol - associated soil: ½ + ½ distribution of the area; Lithosol - associated soils: 1/3 + 1/3 + 1/3 distribution of the area.

Lithosols

Soils which are limited in depth by continuous, coherent, and hard rock at a very shallow depth. Limitations to production are a very low rooting volume, frequently steep topography, and surface stoniness.

Ferralsols (oxisols)

Strongly weathered soils of the tropics, consisting mainly of kaolinite, quartz, and hydrated oxides, and with a low base exchange capacity.

Limitations include a low level of plant nutrients; low cation exchange capacity and weak retention of bases; fixation and deficiency of phosphates, particularly on fine textured soils; relatively high losses of nitrogen and bases through leaching in humid areas; acidity with resultant aluminum toxicity; trace element deficiencies; and possibly microelement toxicities.

The degree of these limitations may vary considerably between the different kinds of Ferralsols. Acric Ferralsols show a higher aluminum toxicity than the orthic units which, in turn, have higher aluminum contents than the rhodic group (Van Wambeke 1974). In humid areas, Ferralsols under a semideciduous forest have a considerably higher content of plant nutrients in the surface layer than those under an evergreen forest.

Yermosols (Aridisols *pro parte*)

Soils of arid areas in which moisture stress permanently limits plant growth for rainfed production. When water is available, fertility problems may result from a high calcium carbonate content and a reduced availability of phosphorus. Yer-

Table 4. Distribution and extent (million ha) of major soils in the 5 regions[a] of the developing world.

	S. E. Asia		S. W. Asia		Africa		S. America		C. America		Total	
	Area	%	Area	%	Area	%	Area	%	Area	%	Area	%
Major soil units												
Lithosols	90.4	10.1	173.9	25.6	397.7	13.2	185.7	10.4	43.6	16.0	891.3	13.4
Ferralsols	15.9	1.8	–	–	322.5	10.7	425.7	23.9	0.8	0.3	764.9	11.5
Yermosols	30.1	3.3	190.2	28.0	373.8	12.4	56.3	3.2	20.4	7.5	670.8	10.1
Acrisols	197.7	22.0	2.1	0.3	92.6	3.1	290.1	16.3	14.9	5.5	597.4	9.0
Arenosols	24.8	2.8	37.0	5.5	329.3	10.9	90.6	5.1	0.2	0.1	481.9	7.3
Luvisols	97.6	10.9	10.2	1.5	257.0	8.5	80.3	4.5	31.9	11.8	477.0	7.2
Regosols	27.5	3.0	89.9	13.3	264.7	8.8	41.9	2.3	15.7	5.8	439.7	6.6
Cambisols	122.3	13.6	20.2	3.0	111.6	3.7	51.5	2.9	24.1	8.8	329.7	5.0
Gleysols	49.5	5.5	2.6	0.4	130.4	4.3	117.9	6.6	8.6	3.2	309.0	4.7
Fluvisols	54.6	6.1	15.7	2.3	101.4	3.4	64.4	3.6	5.4	2.o	241.5	3.6
Vertisols	57.9	6.5	5.7	0.9	105.0	3.5	24.8	1.4	13.2	4.8	206.6	3.1
Xerosols	12.6	1.4	40.7	6.0	100.9	3.3	37.8	2.1	11.4	4.2	203.4	3.0
Nitosols	37.5	4.2	–	–	98.5	3.2	36.5	2.1	11.6	4.3	184.1	2.8
Solonchaks	17.3	1.9	49.0	7.2	51.3	1.7	24.0	1.3	0.4	0.1	142.0	2.1
Others	56.0	6.2	16.7	2.4	69.8	2.8	235.5	13.2	69.4	25.6	447.4	6.8
Miscellaneous land units	5.9	0.7	24.1	3.6	204.8	6.8	19.9	1.1	–	–	254.7	3.8
Total	807.6		678.0		3,011.3		1,782.9		271.6		6,641.4	
Phases												
Stony	13.7	1.5	128.0	18.9	334.8	11.1	22.6	1.3	0.2	0.1	499.3	7.6
Lithic	78.0	8.7	46.4	6.9	62.7	2.1	1.9	0.1	46.5	17.9	235.5	3.6
Petric	7.0	0.8	–	–	83.5	2.8	47.3	2.7	–	–	137.8	2.1
Saline	27.3	3.0	36	0.5	24.2	0.8	36.3	2.0	1.3	0.5	92.7	1.4
Cerrado		–	–		–	–	73.1	4.1	–	–	73.1	1.1
Petrocalcic	–	–	11.0	1.6	39.3	1.3	16.0	0.9	2.4	0.9	68.7	1.0
Petroferric	9.6	1.1	–	–	48.4	1.6	–	–	–	–	58.0	0.9
Sodic	0.1	0.1	0.4	0.1	16.1	0.5	24.9	1.4	–	–	41.5	0.6
Petrogypsic	–	–	11.7	1.7	11.7	0.4	–	–	–	–	23.4	0.4
Duripan	–	–	–	–	1.1	0.1	–	–	0.4	0.2	1.5	0.1
Sodic/Saline	0.6	0.1	–	–	1.0	0.1	–	–	–	–	1.6	0.1
No phase	673.3	84.7	476.9	70.3	2,388.5	79.2	1,560.8	87.5	220.8	80.4	5,408.3	81.1

	S. E. Asia		S. W. Asia		Africa		S. America		C. America		Total	
	Area	%	Area	%	Area	%	Area	%	Area	%	Area	%
Texture classes												
Coarse	90.6	10.1	170.5	25.1	915.0	30.4	264.5	14.8	18.4	6.8	1,459.0	22.0
Medium	502.8	56.0	363.3	53.6	1,634.9	54.3	694.4	39.0	167.4	61.6	3,362.8	50.6
Fine	304.2	33.9	144.2	21.3	461.4	15.3	824.0	46.2	85.8	31.6	1,819.6	27.4
Total	897.6		678.0		3,011.3		1,782.9		271.6		6,641.4	
Stope classes												
0-8 percent	361.2	40.2	302.5	44.6	1,723.1	57.2	935.8	52.5	94.0	34.6	3,416.6	51.4
8-30 percent	273.8	30.5	214.1	31.6	1,025.4	34.1	528.2	29.6	109.7	40.4	2,151.2	32.4
>30 percent	262.6	29.3	161.4	23.8	262.8	8.7	318.9	17.9	67.9	25.0	1,073.6	16.2
Total	897.6		678.0		3,011.3		1,782.9		271.6		6,641.4	

[a]Country composition of the regions is given in appropriate volumes of the agroecological zones project (FAO 1978, 1979b, 1980a, and 1980b).

mosols with high gypsum contents may cause major engineering problems for irrigation construction.

Acrisols (Ultisols p.p.)

Soils of tropical and subtropical areas with a subsurface horizon of clay accumulation, low base saturation, and low weatherable mineral content. Acrisols have limitations similar to those of Ferralsols. Under natural conditions, nutrient reserves are concentrated in the surface horizon. Acrisols are also sensitive to erosion because of unfavorable structure in the surface layer and decrease of permeability in the argillic B horizon. Short-term surface waterlogging mag occur. These soils are easily damaged by compaction and loss of surface structure when heavy equipment is improperly used for deforestation or tillage operations. The argillic B horizon is an asset for moisture and nutrient retention.

Arenosols (Psamments p.p.)

Soils derived from sands, showing weak horizon differentiation.

Their low natural productivity is due to a general lack of nutrients in coarse textured quartzy materials, low water and nutrient retention, low cation exchange capacity, and a deficiency in minor elements normally bonded to clay or organic matter.

Luvisols (Alfisols p.p.)

Soils of tropical, subtropical, and temperate areas with a subsurface horizon of clay accumulation, a medium to high base saturation, and with weatherable minerals. They do not have major limitations related to acidity, calcium deficiency, or long-term phosphate fixation. The saturation complex is dominated by calcium; as a result, microelement deficiencies may occur. Sensitivity to erosion, particularly under conditions of inadequate crop cover, is a major hazard. Low aggregate stability and surface sealing result in runoff and impeded emergence.

Subsurface layers of plinthite, ferruginous concretions, or hardpans are present in higher rainfall areas. Erosion of such soils is particularly damaging through exposure of layers unfit for crop growth.

Regosols (Orthents and Psamments p.p.)

Soils formed from medium- to coarse-textured materials and showing no profile development. When sandy their limitations for plant growth are comparable to those for Arenosols. On medium-textured materials, Regosols often result from active erosion through a continuous removal of surface layers. Weak structure leads to compaction and soil degradation.

Cambisols (Ochrepts)

Soils of initial profile development showing transitional characteristics to more strongly developed soils.

Constraints in the various types of Cambisols (vertic, ferralic, calcic, dystric, gleyic) are similar, but normally less pronounced than those of the more developed Vertisols, Ferralsols, Luvisols, Acrisols, Gleysols.

Gleysols (Aquents, Aquepts, Haplaquolls)
Soils in which excess water is a major factor in their formation and a serious limitation to upland crop production in the rainy season. The base status of Gleysols is usually related to the nutrient content of the surrounding upland soils. Profile development varies considerably. In high rainfall areas Gleysols often contain plinthite or concretionary layers in depth.

Fluvisols (Fluvents)
Weakly developed soils formed from alluvial deposits in active floodplains.

The great variability of these soils does not permit characterization of the nutrient status for the group as a whole. The nutrient status of Fluvisols is related to the materials from which they are derived and these materials are not necessarily adjacent. Flood hazard is a common limitation of Fluvisols. A special mention should be made of thionic Fluvisols which are widespread in the tropics. Waterlogging under natural conditions and extreme acidity after drainage characterize these soils.

Vertisols (Vertisols)
Heavy textured soils developed from swelling clays, forming wide and deep cracks when dry. Limitations are related to the physical properties of these soils. Tillage is hampered by stickiness when wet and hardness when dry. Base saturation is high. with calcium and magnesium dominating the sorptive complex. These soils are susceptible to erosion and seasonal waterlogging.

Xerosols (Ustollic and Xerollic Aridisols)
Soils of dry areas, excluding the strongly saline and sodium-saturated soils. Xerosols suffer from moisture limitations and have a nutrient status similar to that of Yermosols. As with the Yermosols, special attention must be paid to engineering problems in Xerosols high in gypsum or with gypsiferous layers in the subsoil.

Nitosols (Paleudults, Paleudalfs p.p.)
Soils of tropical and subtropical regions showing features of strong weathering and a deeply developed subsurface horizon of clay accumulation.

Nitosols have similar but more favorable chemical properties than Ferralsols. A subdivision is made into dystric and eutric Nitosols; the latter have medium to high base saturation and usually no limitations from exchangeable aluminum. The deeply argillic B horizon and the progressive textural change with depth enhance moisture and nutrient retention and reduce erosion hazards in comparison with Acrisols.

Solonchaks (Salorthids)
Soils showing a high concentration of soluble salts which result in low osmotic potential of the soil solution.

In these soils plants suffer from moisture stress (osmotic drought) and hindrance to normal ion uptake. Depending on the nature of the salts present, different

elements may be in excess. The economic implications involved in reclaiming saline soils are a major consideration to increased production.

SOIL IN A PRODUCTIVITY MODEL

A knowledge of the extent and characteristics of soils in an area allows incorporation of soil factors in models assessing land production potentials. One such model has recently been developed and applied by FAO (1980) to assess production potentials of lands and their potential population supporting capacities. The model provides an opportunity to consider the contribution of soils to productivity (Fig. 1).

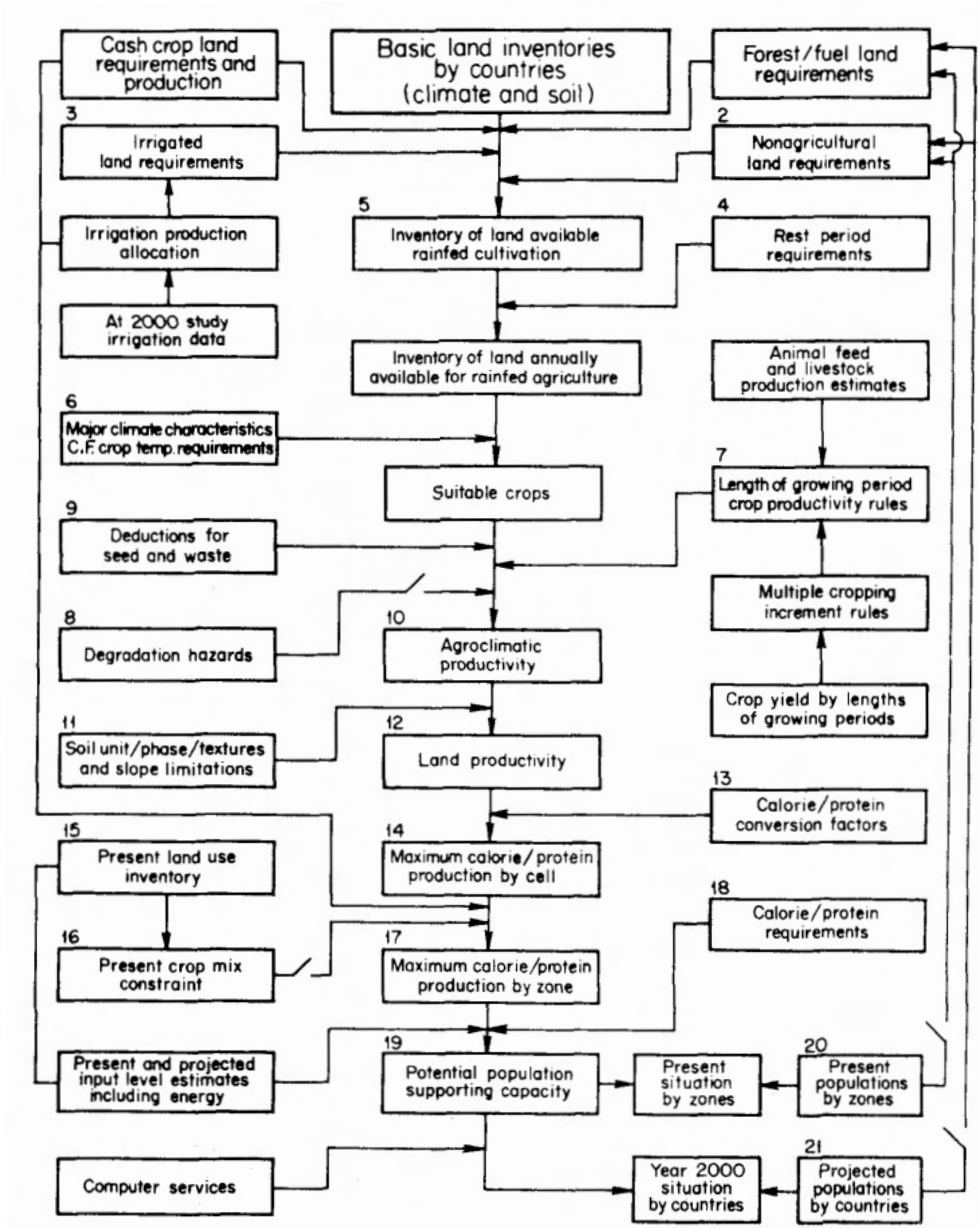
Developed in collaboration with the Food and Agriculture Programme of the International Institute for Applied Systems Analysis, the model is applied for 3 levels of inputs circumstances, and each assessment considers 16 crops to ascertain maximum potential calorie production. Basic to each assessment, as shown at the head of the flow chart (step 1), is the soil and climatic inventory. This land resource base comprises overlay of a climatic inventory onto the previously described FAO/UNESCO *Soil map of the world.* The climatic inventory differentiates major climates characterizing thermal conditions (e.&. warm tropics, cool tropics) and lengths of growing period zones characterizing moisture conditions (e.g. 120-150 days zone, 270-300 days zone) as described in FAO (1978). Measurement of the unique climate/soil areas resulting from this combination allows quantification of the land resources of all developing countries in terms of climatic and soil conditions, and as related to crop adaptability (Kassam et al 1977).

Higgins and Kassam (1980) reported that the land inventory quantifies the extent of each individual soil unit by country, by phase, slope, and texture class as it occurs in each major climate and growing period zone.

Land resource inventory analysis, to ascertain maximum potential calorie production, considers first the land required for nonagricultural use, irrigation production, and rest (fallow) period requirements. Deductions of land required for these uses result in country inventories of land annually available for rainfed cultivation. Each data cell of this inventory (more than 35,000 data cells for Africa) is then analyzed separately for all 16 crops of the study to ascertain which use is most productive under the cell's soil and climatic conditions.

This is achieved by first applying major climate/crop temperature requirement rules as formulated by Kassam (1980a) to ascertain suitable crops which can be considered further. Individual crop productivity rules (incorporating multiple cropping), as determined by Kassam (1980b) and livestock productivity rules (Blair Rains and Kassam 1980) are then applied, and deductions for seed and waste (also crop dependent) follow. Subsequently, appropriate degradation hazard rules are introduced to arrive at *agroclimatic productivity* estimates. Application of limitations imposed by soil, phase, slope, and texture limitations then allows computation of *land productivity* under the cultivation of the 16 assessed crops.

The next step is to calculate calorie-protein production from the different crops through application of crop calorie-protein composition rules. The crop giving the highest calorie-protein production in each cell is selected (Shah and Fischer 1980) and the sum of the production from each cell in a length of growing period zone



1. Model for assessing production potentials of lands and their potential population-supporting capacities.

records the maximum potential calorie-protein production from each zone in each country. The constraint of retaining the present crop combination on all land is included in the low level of input assessment to allow for continued dietary preference for presently grown crops. Data on current crop combinations in each growing period zone are derived from land use inventories.

Once the potential calorie-protein production for each growing period zone is ascertained (rainfed and irrigated production), application of country-specific per capita calorie-protein requirements allows computation of the potential population supporting capacity in each zone and country. The computed potential population supporting densities (persons per ha) are compared with present data on population density to identify critical zones where potential sustained production from land resources is insufficient to meet the food needs of the population. Country population projections for the year 2000 are also compared with country potential population supporting capacities to identify countries which will meet critical problems of food production for future populations.

In the model, soil considerations function in 3 ways:

a. by modifying the agroclimatic productivity according to the soil, slope, texture, and phase composition of each cell to estimate potential land productivity under each crop;
b. by determining, in combination with major climate, length of growing period and crop, the rest period requirement of each cell; and
c. by contributing to the degradation hazard assessment of each cell.

To achieve the required soil modifications of agroclimatic productivity, all soil units, slope classes, texture classes, and phases of the FAO UNESCO *Soil map of the world* have been rated in terms of the severity of their limitations to the production of each crop. These ratings have been formulated for the three input levels, assuming a suitable rainfed production climate, and are based on how well the soil conditions of a soil unit match with the soil requirements of each crop. Definition of the crops' soil requirements is therefore a prerequisite. Examples of the soil ratings employed (Sys and Riquier 1980) are shown in Table 5.

A rating of S1 signifies no or only minor soil limitations to crop growth under the stated level of inputs and that the land productivity potential is reflected by the agroclimatic productivity potential. A rating of S2 indicates that some soil limitations will adversely affect crop growth and that the land productivity potential should accordingly be one class lower than agroclimatic productivity potential. The N rating indicates severe soil limitations that make crop growth not possible or, at best, very limited, despite a suitable climate.

Soil factors also enter into the model through the rest period requirement input. Many tropical and subtropical soils cannot be continuously planted to annual food crops without undergoing degradation. Such degradation is marked by decreased crop yields and a decline in soil structure, nutrient content and other physical, chemical and biological attributes. Under traditional farming systems, degradation is prevented or diminished by alternating some years of cultivation with periods of rest (fallow). Even under a technically advanced cultivation system, as considered in the model, some rest period may be required on certain soils to permanently maintain land productivity.

The length of the rest period is dependent on crops, input level, and soil and climatic conditions. The model considers the duration of the rest period in computing land productivity potential. Data on rest period requirements have been compiled by Young and Wright (1980). Table 6 cites examples of rest period requirements formulated for major soils under various climates and input levels.

Table 5. Ratings of selected soil units for specific rainfed crops.[a]

Soil unit	Pearl millet			Maize			Cassava			Bunded rice		
	Low	Int.	High	Low	Int.	High	Low	Int.	High	Low	Int.	High
Regosols												
Calcaric	S1	S1	S1	S2	S1/S2	S1/S2	N	S2	S2	S2	S1/S2	S1/S2
Dystric	S2	S1/S2	S1	S2	S1/S2	S1	S2	S1/S2	S1	S2	S2	S2
Lithosols	N	N	N	N	N	N	N	N	N	N	N	N
Arenosols												
Cambic	S2	S1/S2	S1	N	S2/N	S2	S2	S2	S2	N	N	N
Albic	S2/N	S2/N	S2/N	N	N	N	S2/N	S2/N	S2/N	N	N	N
Cambisols												
Dystric	S2	S1/S2	S1	S2	S1/S2	S1	S2	S1/S2	S1	S2	S1/S2	S1
Calcic	S1	S1	S1	S2	S1/S2	S1/S2	N	S2	S2	S2	S1/S2	Sl/S2
Vertic	S2/N	S2	S2	Sl/S2	S1	S1	S2/N	S2	S2	S1	S1	S1
Luvisols												
Orthic	S1	S1	S1	S1	S1	S1	S1	S1	S1	S1	S1	S1
Chromic	S1	S1	S1	S1	S1	S1	S1	S1	S1	S1	S1	S1
Ferric	S2	Sl/S2	S1/S2	S2	S1/S2	S1/S2	S2/N	S2/N	S2/N	S2/N	S2/N	S2/N
Cleyic	S2/N	S2/N	S2/N	S2/N	S2/N	S2/N	N	N	N	S1	S1	S1
Acrisols												
Orthic	S2	S1/S2	S1	S2	S2	S1/S2	S2	S1/S2	S1	S2	S1/S2	S1
Ferric	S2	S1/S2	S1	S2	S2	Sl/S2	S2	S1/S2	S1	S2/N	S2/N	S2/N
Plinthic	S2/N	S2/N	S1/N	S2/N	S2/N	S2/N	S2/N	S2/N	S1/N	S2	S2	S1/S2
Ferralsols												
Orthic	S2	S2	S1/S2	S2	S2	S2	S2	S2	S1/S2	S2	S2	S2
Xanthic	S2	S2	S1/S2	S2	S2	S2	S2	S2	S1/S2	S2	S2	S2
Rhodic	S2	S1/S2	S1	S2	Sl/S2	S1/S2	S2	S1/S2	S1	S1/S2	S1/S2	S1/S2

[a]Input levels are low, int. (intermediate), and high. S1 = none or minor soil limitation to crop growth under the stated level of input, S2 = some soil limitations to crop growth. N = severe soil limitations.

Table 6. Rest period requirement, expressed in terms of cultivation factor[a], for some major soils in the warm tropics.

Soil	Low inputs		Intermediate inputs		High inputs	
	>270 days	<120 days	>270 days	<120 days	>270 days	<120 days
Regosols	10	20	30	45	50	50
Arenosols	10	20	30	45	so	50
Cambisols	35	40	65	60	85	80
Luvisols	25	35	50	55	70	75
Vertisols	40	45	70	75	90	90
Gleysols	60	90	80	90	90	90
Acrisols	15	20	40	60	65	75
Ferralsols	15	20	35	40	70	75

[a] Cultivation factor is the number of years in which it is possible to cultivate the land, as a percentage of the total cultivation and noncultivation cycle. Length of growing period is >270 and <120 days.

The third input that considers soil factors is degradation hazard. This is important in sustained assessments of productivity, and depends on the degree of conservation measures assumed. In the model, the degree of conservation measures assumed is linked to the level of inputs being assessed. The low level of inputs assumes no soil conservation measures corresponding to maximum rates of soil loss according to soil, climate, and crop. The intermediate level of inputs assumes simple conservation measures, corresponding to a rate of soil loss reduced by half. The high level of inputs assumes complete soil conservation measures corresponding to no significant soil loss.

Potential rates of soil loss have been computed by Arnoldus (1980) using a parametric method incorporating climate, soil, topography, and crop factors. Climatic aggressivity was determined for each length of growing period (LGP) zone. Multiplication by the factors formulated for each soil and crop estimated the rate of soil loss. Table 7 shows the erodibility classes of selected soil units.

The following rates of soil loss are used to modify the estimates of land productivity potentials.

Rate of soil loss (t/ha per annum)	*Postulated long-term productivity losses*
< 12	No change in land productivity potential.
12 to 50	50% of very productive land downgrades to productive land; remainder remains unchanged.
51 to 100	100% of all productive land downgrades by one productivity class.
101 to 200	50% of all productive land downgrades by one productivity class; remainder downgrades to nonproductive land.
>200	All productive land downgrades to nonproductive land.

Table 7. Examples of soil erodibility classes.

Soil	Erodibility class[a]	Soil	Erodibility class[a]
Calcaric Regosols	I	Chromic Luvisols	II
Dystric Regosols	II	Ferric Luvisols	I
Lithosols	I	Gleyic Luvisols	II
Cambic Arenosols	I	Orthic Acrisols	II
Albic Arenosols	I	Ferric Acrisols	I
Dystric Cambisols	II	Plinthic Acrisols	III
Calcic Cambisols	II	Orthic Ferralsols	I
Vertic Cambisols	III	Xanthic Ferralsols	I
Orthic Luvisols	II	Rhodic Ferralsols	I

[a] I = slight, II = moderate, III = severe

RESULTS

Applying the three soil-related inputs to the assessed agroclimatic productivity potential permits assessment of the relative importance of these soil factors to land production potential. Such application has been made for Orthic Ferralsols and Orthic Luvisols (Table 8) planted to cassava and sorghum in 2 lengths of growing period (LGP) zones (150-180 and 240-270 days).

Considering the effects of soil factors alone, the results show that Orthic Luvisols have a production potential of 4.3 million cal/ha per annum compared with Orthic Ferralsols with 2.8 million cal. The Orthic Luvisols maintain their superior production potential for both crops in both LGP zones, for both slopes, and at all three levels of inputs.

The results also show that differences in production potential of similar (or greater) magnitude were due to differences in LGP zone and crop, e.g. an average of 4.8 million cal from cassava in both zones (i.e. average of 7.2 and 2.3) compared with 2.3 (i.e. average of 1.3 and 3.3) for sorghum, a difference of 109 percent when soil, LGP zone, slope and level of inputs are all considered together.

These estimates of potential are for two pure soil units with comparable slope and texture conditions — circumstances that seldom occur in reality. Normally there is a wide diversity of soil unit composition, slope, texture, and phase conditions within and between similar major soil mapping units.

Consequences of such variations are reflected in Table 9, which presents production potentials for large areas dominated by the same major soil unit in the warm tropics in Africa. The data are computed potential population-supporting capacities for selected LGP zones within countries where more than half of the total extent of the LGP zone is composed of the same major soil unit. This infrequent situation precludes the possibility of comparing all major soil units in like manner. The comparison is made for the high level of inputs and the assessment is for the crops producing maximum calories.

The results show as great a variation within the same soil in a single LGP zone as between soils in the same zone, e.g. 6.4 to 12.7 within Ferralsols in the 270-300 days LGP zone and 8.9 to 12.7 between Luvisols and Ferralsols.

These variations and the lack of consistent differences in production potential

Table 8. Assessments of potential production (cal x 10^6/year) of 2 soil units in the warm tropics.

	Orthic Ferralsols					Orthic Luvisols					Average input	AVERAGE input	AVERAGE crop	OVERALL AVERAGE input	OVERALL AVERAGE crop	OVERALL AVERAGE LGP
	'a'	'b'	Av input	Av crop	Av LGP	'a'	'b'	Av input	Av crop	Av LGP						
240-270 days growing period zone					3.4					5.1						4.3
Cassava				6.1					8.3						4.8	
Low input	0.9	–	0.5			1.9	–	0.9			0.7	0.4		0.4		
Intermediate input	6.1	0.7	3.4			11.0	–	5.5			4.5	2.6		2.3		
High input	21.6	7.4	14.5			27.8	9.3	18.6			16.6	9.4		7.7		
Av slope	9.5	2.7				13.6	3.1									
Av soil	6.1					8.3										
Sorghum				0.7					1.8				1.3		2.3	
Low input	0.1	–	0.1			0.2	–	0.1			0.1					
Intermediate input	0.4	–	0.2			1.8	–	0.9			0.6					
High input	2.5	0.9	1.7			3.9	1.3	2.6			2.2					
Av slope	1.0	0.3				2.2	0.4									
Av soil	0.7					1.8										
Average slope	5.3	1.5				7.8	1.8									
Average soil	3.4					5.1										
150-180 days growing period zone					2.2					3.4						2.8
Cassava				1.5					3.0				2.3			
Low input	0.1		0.1			0.9	–	0.5			0.3	0.4				
Intermediate input	1.0	0.1	0.6			4.4	0.2	2.3			1.5	2.0				
High input	5.7	1.9	3.8			9.1	3.0	6.1			5.0	6.0				
Av slope	2.3	0.7				4.8	1.1									
Av soil	1.5					3.0										

	Orthic Ferralsols					Orthic Luvisols					Average input	AVERAGE input	AVERAGE crop	OVERALL AVERAGE input	OVERALL AVERAGE crop	OVERALL AVERAGE LGP
	'a'	'b'	Av input	Av crop	Av LGP	'a'	'b'	Av input	Av crop	Av LGP						
Sorghum				2.8					3.8				3.3			
Low input	0.5	0.1	0.3			1.3	-	0.7			0.5					
Intermediate input	2.7	1.0	1.9			4.8	0.9	2.9			2.4					
High input	9.1	3.1	6.1			11.6	3.9	7.8			7.0					
Av slope	4.1	1.4				5.9	1.6									
Av mil	2.8					3.8										
Average slope	3.2	1.1				5.4	1.4									
Average soil	2.2					3.4										
AVERAGE slope	4.3	1.3				6.6	1.6									
OVERALL AVERAGE slope	5.4	1.5														
OVERALL AVERAGE soil	2.8					4.3										

[a] Av = 1st order average, Average = 2d order average; AVERAGE = 3d order average; OVERALL AVERAGE = 4th order average. 'a' slope = 0-8%; 'b' slope = 8.30%. LGP = length of growing period.

Table 9. Potential population-supporting capacities of selected length of growing period (LCP) zones dominated by specific major soil units.

LGP zone (days)	Capacity (persons/ha)		
	Ferralsols	Luvisols	Lithosols
270-300	12.7 (Congo) 11.9 (Cameroon) 11.1 (Sudan) 6.4 (Sierra Leone)	12.6 (Togo) 10.2 (Ghana) 8.9 (Benin)	
240-270	12.7 (Angola) 11.6 (Zimbabwe) 8.1 (Burundi) 6.7 (Sierra Leone)	11.3 (Togo) 10.9 (Benin) 8.9 (Ghana)	
210-240	12.1 (Zimbabwe)	12.5 (Benin) 9.3 (Ghana) 8.2 (Togo) 7.9 (Upper Volta)	
180-240	10.7 (Zaire)	11.1 (Zimbabwe) 8.9 (Benin) 8.4 (Ghana) 7.6 (Nigeria)	4.2 (Guinea)
150-180	6.8 (Malawi)	8.7 (Benin) 6.8 (Senegal) 5.8 (Cent. Afr. Rep.)	3.4 (Guinea)

between major soil units are undoubtedly caused by the heterogenous composition of these major soil mapping units.

Productivity potential of lands in Africa has been assessed and selected results are presented in Table 10. The data are for the warm tropics and comprise assessments of potential population-supporting capacities for LGP zones and related dominant major soil units. The assessment incorporates all information on individual soil unit, slope, texture, and phase composition of the soil mapping units contained in the *Soil map of the world.*

The results show overall potential population-supporting capacities ranging from 0 to nearly 12 persons per hectare, depending on level of inputs and climate soil circumstances. A fourfold increase in potential population-supporting capacity is postulated as a consequence of moving from the low level of inputs to the intermediate level. This reflects increased productivity per hectare, not only from increased yields, but also from reduced rest period requirements, reduced degradation, and increased optimization of crop choice as best suited to the different soil and climatic conditions. The threefold increase postulated between the intermediate and high levels of inputs also reflects further increased productivity even when possible production from slopes greater than 14% are assumed negligible because of the restrictions set by mechanization.

Table 10. Potential population supporting capacities (persons/ha) of lands in Africa in the warm tropics, at 3 levels of inputs

Length of growing period zone (days)	Extent (million ha)	Main soils (%)	Potential population-supporting capacity		
			LOW inputs	Intermediate inputs	High inputs
365[a]	20	Ferralsols (68) and Gleysols (17)	1.8_7	7.9_9	11.9_9
365	128	Ferralsols (48) and Gleysols (22)	1.6_1	4.8_9	12.5_5
330-364	75	Ferralsols (49) and Arenosols (12)	1.3_7	5.3_3	11.1_7
300-329	73	Ferralsols (39) and Arenosols (13)	1.4_4	6.0_7	13.4_3
270-299	128	Ferralsols (33) and Arenosols (17)	0.8_8	4.7_0	10.2_1
240-269	133	Ferralsols (35) and Luvisols (13)	0.9_2	4.4_3	11.5_8
210-239	130	Ferralsols (28) and Luvisols (16)	0.6_6	2.8_9	10.5_4
180-209	226	Luvisols (24) and Ferralsols (13)	0.4_9	2.1_5	8.3_7
150-179	175	Luvisols (27) and Vertisols (13)	0.5_0	2.3_3	9.0_3
120-149	114	Luvisols (24) and Arenosols (18)	0.1_4	0.7_6	5.2_1
00-119	72	Arenosols (27) and Lithosols (11)	0.0_8	0.2_5	3.1_8
75-89	58	Arenosols (34) and Lithosols (11)	0.0_6	0.1_4	1.5_6
0-74	371	Regosols (20) and Arenosols (20)	0.0_3	0.0_4	0.0_6
0	181	Yermosols (34) and Lithosols (27)	0.0_0	0.0_0	0.0_0
			0.5_0	2.0_9	6.1_4

[a] Year-round humid growing period.

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BIOENERGETICS OF GROWTH OF SEEDS, FRUITS, AND STORAGE ORGANS

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The amount of substrate required for growth of seeds, fruits, and other storage organs is computed for 23 major crops. The computations are based on knowledge of the biochemical conversion processes that occur during growth, and the biochemical composition of the storage organs. The amount of substrate required for maintenance processes in these organs is estimated from literature data. The procedures in calculating the growth processes are explained and justified. The substrate requirement for synthesis of 1 kg of the total storage organvaries from 1.3 to 2.4 kg glucose, and from 1.6 to 5.5 kg glucose when the substrate is expressed per kg of the storage organ principal component. Synthesis of 1 kg of the total storage organ requires 0.02-0.3 kg amides, or 0.02-0.4 kg amides/ kg of the principal component. Respiration during growth is also computed.

There is good evidence that there is no scope for improvement of the efficiency with which plants convert substrates into storage organs. Higher yields per unit of substrate can be achieved only by the production of energetically cheaper storage organs. Maintenance of the storage organs during their development consumes 6 to 25% of the total substrate requirement for their growth. Research should further quantify this fraction and indicate the scope for breeding and selection of varieties with lower maintenance requirements.

The assumption that the efficiency of transfer of nitrogen within the plant toward seeds, fruits, and storage organs is 100% is probably incorrect.

This paper addresses the question of how much substrate is required for the growth of seeds, fruits, and other storage organs. An experimental approach is cumbersome

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and requires elaborate measurements for each species. A theoretical approach, however, seems feasible; it has no major problems, and is fast and fairly reliable. We show how to calculate the amount of substrate required for synthesis, transport, and maintenance processes occurring during the growth of seeds, fruits, and other storage organs.

Knowing the substrate requirement for growth, we can compute the yield of a crop using the amount of available substrate. The substrate requirement can also be used inversely to indicate the amount of extra substrate needed for the formation of 1 additional kg of end product.

The substrate for growth consists of carbohydrates and amino acids. Concurrent assimilation processes are almost exclusively the source of substrate for storage organs of tuber crops. In other crops, a considerable fraction of the substrate is supplied by the breakdown of starch and protein in vegetative organs. In grain crops particularly, this process is important and might become even more so (Lupton 1980). Both substrate sources are important in seed legumes. The two types do not come from the same source in the same proportion; the fraction of carbohydrates that generally comes from photosynthesis is larger than that which comes from amino acids. In wheat, for example, most of the grain protein comes from nitrogenous compounds in vegetative parts, whereas most of the carbohydrate comes from photosynthesis (Spiertz 1978). Regardless of where the substrate comes from, the bulk of the organic carbon (C) that is provided to growing seeds, fruits, or storage organs is always in the form of simple carbohydrate molecules (such as glucose and sucrose), and the nitrogen comes almost exclusively in the form of organic nitrogen in amino acids.

The term *storage organ* is used to indicate the major agricultural product of a crop — grain, fleshy or dry fruits, tubers, or other vegetative storage organs. The term includes components that are indispensable for organ formation, such as chaff, seed coat, hulls, and pods. The total weight of the storage organ, rather than the weight of only the principal fraction, is considered because it represents more truly the energy required by the crop to produce that organ. The *relative substrate requirement* is defined as the amount of substrate required to form 1 kg of storage organ. The substrate is expressed in glucose and amino acids when it is supplied by photosynthesis directly, and in starch and protein when vegetative tissues are their source. The numerical values of the substrate requirements are slightly different in each situation.

The present approach to determining the substrate requirement is basically a biochemical one (in which conversion processes are analyzed), rather than a statistical one (in which results of agronomical experiments are correlated with environmental factors). The approach has been developed and described earlier (Penning de Vries et a1 1974, Penning de Vries and Van Laar 1977). Some of those earlier calculations have been refined for this paper, particularly those pertaining to breakdown of proteins in vegetative tissue, and to synthesis of protein and lignin. Some experiments evaluating the approach are discussed. The emphasis, though, is on the presentation of a simplified scheme to compute the relative substrate requirement of seeds, fruits, and other storage organs, and the scheme's application to the major

crops. All calculations are on a dry matter basis. The nitrogen utilization efficiency within the plant is assumed to be 100%; this assumption is discussed in a separate section. The efficiency of carbon utilization is one of the results of the computations presented.

In this paper, the approach is not applied to vegetative parts of crops, partly because this was done elsewhere (De Wit et a1 1978), and partly because of the more complex situation — involving the direct interaction of growth and photosynthesis, the form in which nitrogen is absorbed from the soil — and uncertainties about the importance of maintenance processes.

BASIC CONCEPTS

Growth of storage organs is almost completely heterotrophic because most of the growing cells do not photosynthesize. This is obvious for belowground storage organs, but not quite so for those growing in light. Although their outer cell layers photosynthesize, growth of those cells contributes little to the overall dry weight increase. Photosynthetic products from outer cell layers can be transported to inner cells, but most of the organic carbon is probably transported as very simple molecules. It is assumed that the products excreted by the cells from outer layers are identical or energetically similar to those supplied by the phloem. Therefore, growth of all storage organs is considered as completely heterotrophic. This does not contradict the observation that photosynthesis by aboveground storage organs can contribute significantly to the substrate for growth.

Growth includes the conversion of substrate molecules into specific components and their subsequent incorporation into the cellular structures of the storage organ. Some carbohydrates are combusted to provide the energy to drive the growth reactions, and for translocation of the substances into and out of cells and through the plant. The result is the production of CO_2 related to these processes, which is called *synthesis respiration.* Living cells exhibit another carbon-consuming process called *maintenance.* Maintenance occurs continuously in living cells; the CO_2 production that results from it is called maintenance respiration (m.r.r.). The distinction of those two components of respiration and of carbon-consuming processes in plants goes back to McCree (1970), and has received a theoretical treatment (cf. Barnes and Hole 1978). There is no indication of other carbon-consuming processes that need consideration.

Efficiency of synthesis processes

This section summarizes an earlier paper (Penning de Vries et al 1974).

An example of a simple equation that represents a synthesis process is the formation of the amino acid lysine from glucose and ammonia. From biochemical handbooks (Dagley and Nicholson 1970), it appears that this equation can be represented by:

$$1 \text{ glucose} + 2\ NH_3 + 2\ (NAD)H_2 + 2\ (ATP) \rightarrow 1 \text{ lysine} + 4\ H_2O \qquad (1)$$

(units = gmol, compounds in parentheses serve only as carriers). The hydrogen and energy (ATP) needed are obtained by the combustion of glucose:

$$0.219 \text{ glucose} + 0.316\ O_2 + 0.684\ H_2O \rightarrow 2\ (NAD)H_2 + 2\ (ATP) + 1.316\ CO_2 \quad (2)$$

The sum of these equations, expressed in grams (the number of gmol × the respective molecular weights), is:

$$1.000 \text{ g glucose} + 0.155 \text{ g } NH_3 + 0.046 \text{ g } O_2 - 0.665 \text{ g lysine} + 0.264 \text{ g } CO_2 + 0.272 \text{ g } H_2O \quad (3)$$

Similar equations can be derived for synthesis of almost all organic components of plants; the quantity of those compounds for which the biosynthetic pathway is really unknown is small; therefore, their cost of synthesis is usually negligible. During simulation of synthesis of complicated components, such as proteins, the reaction equations of the monomers (amino acids) must be added, weighted according to their relative importance, and the cost of polymerization accounted for. During these processes, some energy must be spent to repair enzymes. It corresponds to the energy of roughly 1 ATP molecule per amino acid formed, according to earlier estimates. There are few additional complications. Almost no energy seems to be required for obtaining the immense degree of organization of polymers into organelles and cells.

For synthesis of highly complex products (such as nucleic acids, organelles, and even biomass), a reaction equation can be derived with only the terms: glucose, oxygen, nitrogen, minerals, the end products themselves, carbon dioxide and water.

The multitude of organic components in plants can be separated by their cost of synthesis into five groups: carbohydrates (glucose, sucrose, starch, fructosan, cellulose, hemicellulose, etc), proteins (true proteins, free amino acids and amides, nucleic acids, nucleotides), lipids (fats, oils), lignin (a polymerized product of components like coniferyl alcohol), and organic acids (tri-carbinic acid cycle acids, oxalic acid, etc.). Values characterizing the synthesis and concurrent respiration of these groups are given in Table 1. They are similar to those published earlier, except that the values for lignin are slightly modified as a result of new information about its synthesis (Sarkanen and Ludwig 1971). The synthesis of components within each group are similar; differences are less than 10%. But the differences between groups are considerable. These conclusions were drawn earlier (Penning de Vries et al 1974) based on an analysis of the sensitivity of the conversion equations to changes in the relative importance of the constituents within each group over a reasonable range.

The processes are assumed to occur at a maximal efficiency and yields in Table 1 are generally high. Only when the specific energy content (Joule per g) increases considerably (as during lipid synthesis), or when an expensive process takes place (such as the reduction of NO_3) is the yield low and the respiratory loss high. (NO_3 reduction during protein synthesis is presented only for reference; it is assumed that storage organs grow exclusively with organic nitrogen).

Absorption of glucose and inorganic molecules into the cells is an active, energy-demanding process. Its cost is not well known (Ziegler 1975), but seems to be on the order of 1 ATP/molecule. Accounting for this cost of import, but neglecting the small effects of interactions between syntheses of different components, the amounts of glucose and amides required for syntheses of components and their concurrent respiration are given in Table 2.

Table 1. Glucose required for synthesis of 1.000 g of a component, and concurrent respiration, expressed in CO_2 and in O_2.

Component	Glucose consumed (g)	CO_2 produced (g)	O_2 consumed (g)
Proteins (with NH_3)	1.623	0.416	0.222
Proteins (with NO_3)	2.475	1.666	0.431
Carbohydrates	1.211	0.123	0.099
Lipids	3.030	1.606	0.352
Lignin	2. 119	0.576	0.189
Organic acids	0.906	-.045	0.270

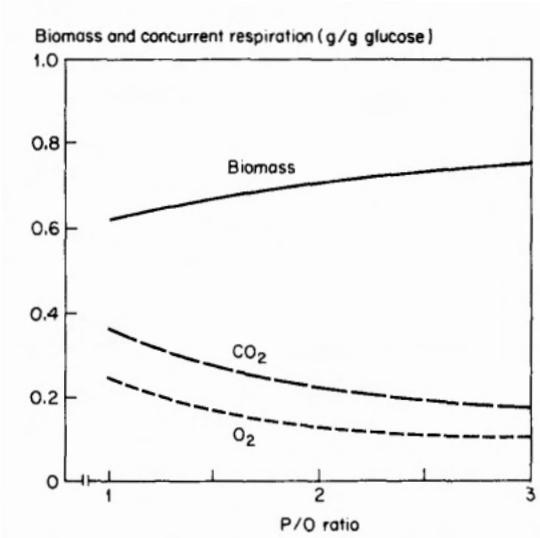
Table 2. Glucose and amides required for synthesis of 1.000 g of a component (inluding the cost of importing glucose, amides, and minerals into the cell) and the concurrent respiration.

Component	Glucose consumed (g)	Amides consumed (g)	CO_2 produced (g)	O_2 consumed (g)
Proteins	0.948	0.768	0.544	0.250
Carbohydrates	1.242	0.	0.170	0.133
Lipids	3. I06	0.	1.720	0.435
Lignin	2.174	0.	0.659	0.248
Organic acids	0.929	0.	-.011	0.296
Minerals absorbed	0.050	0.	0.073	0.053

Much of the basic information used in the computations has been obtained in research with microorganisms. It is likely, though, that the biochemistry of plants is not much different. Moreover, sensitivity analysis has shown that the choice of pathway for synthesis of components is often of minor importance. For these calculations, one additional, but not necessarily correct assumption has been made: that the efficiency of ATP production from glucose is maximal and constant (2 ATP from glycolysis and a P/O ratio of 3). Indeed, such high efficiencies have often been observed in plant cells (Bandurski 1960). Slightly lower values have been reported in germinating seeds (Flavell and Barratt 1977). Considerably lower P/O ratios have been observed in roots (Lambers 1979) as a result of the intensive use of an alternative pathway for $NADH_2$ oxidation. Although this pathway exists in shoots and storage organs, it seems to be used to a limited extent (Solomos 1977). Moreover, as most of the organic carbon goes into the skeletons of the end product. the relative substrate requirement of the growth process is not very sensitive to the assumed maximum efficiency of energy generation. The efficiency must be reduced considerably to have a noticeable effect (Fig. 1).

Efficiency of synthesis from glucose plus amino acids

The synthesis from glucose of all nonnitrogenous compounds is similar. The substrate for growth of the storage organs consists not merely of glucose, but includes amides as well. This is unlikely to change the pathways of synthesis of nonnitrogenous compounds. There are indications that the unloading of the phloem near the storage organ is largely a passive process, so the assumption that the energy of 1 ATP molecule is needed for absorption of 1 monomer into the cell is no



1. Relation between the yield of the synthesis of biomass from 1.000 g glucose and concurrent respiration at different levels of efficiency of energy generation in cells, expressed as P/O ratio (from Penning de Vries et al 1974).

underestimation (cf. Mengel 1980). The active process of transport through the phloem probably requires little energy and is neglected. The values characterizing the synthesis of these organic plant components of Table 2 are therefore applicable to storage organs.

The syntheses of nitrogenous compounds from amino acids and from glucose and inorganic nitrogen differ. Synthesis from amino acids varies because of variations in the amino acid compositions of the substrate and the end product. The simplest of the many possible combinations occurs when the amino acid composition of the proteins in the storage organ is the same as the composition of the mixture supplied by the phloem, so that no conversions need to take place. This situation is described by the reaction equation:

$$1.156 \text{ g amino acids} + 0.206 \text{ g glucose} + 0.220 \text{ g } O_2 \rightarrow 1.000 \text{ g protein} + 0.302 \text{ g } CO_2 + 0.280 \text{ g } H_2O \quad (4)$$

Equation 4 accounts only for the cost of polymerization, tool maintenance, and uptake into the cells, It is the average equation for synthesis of a few proteins.

A much more expensive synthesis occurs when the organic nitrogen is provided in the form of amides in which each carbon skeleton carries two amino groups. In this situation, many new carbon skeletons of amino acids have to be formed from glucose, and many of the remaining skeletons of glutamine and asparagine are transformed into other molecules. In the phloem of many plants, it is usual for the amides, glutamine, and asparagine to make up more than 80% of the total nitrogen transported, although they are only a small fraction of the amino acids in the proteins (Ziegler 1975). Valine (Tammes and Van Die 1964), proline, or arginine (Pate 1973) can also constitute more than 10% of the nitrogen in the phloem. Nitrate is absent in the phloem (Ziegler 1975). The conversion of amides and glucose into proteins can be represented by the equation:

$$0.76 \text{ g amides} + 0.948 \text{ g glucose} + 0.250 \text{ g } O_2 \rightarrow 1.000 \text{ g protein} + 0.544 \text{ g } CO_2 + 0.422 \text{ g } H_2O \quad (5)$$

The composition of the amino acids of equation 5 (64.6% glutamine by weight. 33.55 asparagine, and 1.9% cystein, hence 0.197 g N g amides) resembles compositions that have often been observed in the phloem. Equation 5 was used to calculate the substrate requirements in Table 2. For every combination of a glutamine-asparagine mixture and the amino acid composition of a protein, there is a specific reaction equation. Equation 5 is the average of nine combinations of the glutamine-asparagine mixture and of three storage proteins. The three proteins gluten corn, arachin, and gluten wheat, were chosen from a group of nine that in an earlier analysis (Penning de Vries et al 1974) were judged to have the low, medium, and high energy demands. The amide compositions used were those that result from the breakdown of those three proteins (equation 12). It was assumed that the standard pathways for synthesis were followed, always by the most efficient alternatives. A recent review of amino acid metabolism (Miflin and Lea 1977) supports this suggestion.

The computations that yielded equation 5 indicate the variability of the terms of the equation resulting from differences in the biochemical compositions of substrate and product. Of the nine equations computed, the one with the highest amount of glucose involved was

$$0.693 \text{ g amides} + 1.124 \text{ g glucose} + 0.220 \text{ g } O_2 \rightarrow 1.000 \text{ g protein} + 0.590 \text{ g } CO_2 + 0.447 \text{ g } H_2O \quad (6)$$

The one with the lowest amount of glucose was

$$0.869 \text{ g amides} + 0.797 \text{ g glucose} + 0.270 \text{ g } O_2 \rightarrow 1.000 \text{ g protein} + 0.485 \text{ g } CO_2 + 0.451 \text{ g } H_2O \quad (7)$$

Keeping in mind the types of proteins selected for this exercise, equation 5 may be rewritten as

$$0.77 \text{ g} \pm 0.1 \text{ g amides} + 0.94 \pm 0.15 \text{ g glucose} + 0.25 \pm 0.02 \text{ g } O_2 \rightarrow 1.000 \text{ g protein} + 0.55 \pm 0.05 \text{ g } CO_2 + 0.43 \pm 0.03 \text{ g } H_2O \quad (8)$$

It appears that the ratio of amide to glucose is much more variable than their sum. and that their concurrent synthesis respiration is remarkably constant.

Breakdown of starch and protein

Transport of organic carbon and of nitrogen toward the storage organs occurs mainly in the form of sucrose and amides (Van Die and Tammes 1975, Ziegler 1975). Because other organic components are present in small amounts, only breakdown into glucose and amides is considered. In vegetative plant parts, only carbohydrates (predominantly starch) and proteins serve as the sources of these components.

As a basis for calculations, glucose is chosen as the substrate carbohydrate, rather than sucrose, merely for convenience. Sucrose is easily formed from glucose:

$$2\,\text{glucose} + 2\,(\text{ATP}) \rightarrow 1\,\text{sucrose} + 1\,H_2O \tag{9}$$

The reaction occurs during phloem loading (c.f. Mengel 1980). The reverse reaction is similar, but it does not yield ATP. Sucrose is 5% lighter than glucose per carbon atom. The breakdown of starch into glucose is a simple enzymatic hydrolysis. This yields the equation:

$$1.000\,\text{g starch} + 0.094\,\text{g}\,H_2O + 0.031\,\text{g}\,O_2 \rightarrow 1.082\,\text{g glucose} + 0.043\,\text{g}\,CO_2 \tag{10}$$

For protein breakdown, there is a similar choice of what to start with and what to end with. The simplest degradation process is hydrolysis into amino acids. By including energy demand for loading the phloem and assuming that tool maintenance requires the same amount of energy as synthesis (which may be an overestimation), the average equation becomes:

$$\begin{gathered}1.000\,\text{g protein} + 0.082\,\text{g glucose} + 0.096\,\text{g}\,O_2 + \\ 0.110\,\text{g}\,H_2O \rightarrow 1.166\,\text{g amino acids} + 0.122\,\text{g}\,CO_2\end{gathered} \tag{11}$$

The average equation that describes the complex process of the breakdown of gluten corn, arachin, and gluten wheat proteins is:

$$\begin{gathered}1.000\,\text{g protein} + 0.095\,\text{g}\,H_2O + 0.384\,\text{g}\,O_2 \rightarrow 0.768\,\text{g amides} + 0.370\,\text{g glucose} \\ + 0.341\,\text{g}\,CO_2 + (0.027\,\text{gmol ATP})\end{gathered} \tag{12}$$

All amino acids were assumed to be broken down into asparagine or glutamine. Again, the pathways followed for breakdown are standard. If any cysteine was present in the protein, it was assumed to be transported as a sulfur carrier. Remaining carbon skeletons are rebuilt into glucose by gluconeogenesis reactions. Equation 12 is very close to that calculated earlier (Penning de Vries and Van Laar 1977).

Equation 12 shows that a net production of ATP results from protein breakdown, similar to the amount obtained by the combustion of 9.128 g glucose. That energy is estimated to be 5 to 10 times smaller than that required for maintenance of the tissue during the period in which it exports these amides. The excess energy prevents some other glucose molecules from being combusted. To account for this saving, equation 12 is modified to:

$$\begin{gathered}1.000\,\text{g protein} + 0.172\,\text{g}\,H_2O + 0.247\,\text{g}\,O_2 \rightarrow 0.768\,\text{g amides} + \\ 0.498\,\text{g glucose} + 0.153\,\text{g}\,CO_2\end{gathered} \tag{13}$$

Again, we can estimate the variability of the coefficients of the equation. The extremes calculated are:

$$\begin{gathered}0.880\,\text{g protein} + 0.070\,\text{g}\,H_2O + 0.326\,\text{g}\,O_2 \rightarrow 0.768\,\text{g amides} + \\ 0.237\,\text{g glucose} + 0.271\,\text{g}\,CO_2 + (0.023\,\text{gmol ATP})\end{gathered} \tag{14}$$

and:

$$\begin{gathered}1.118\,\text{g protein} + 0.107\,\text{g}\,H_2O + 0.482\,\text{g}\,O_2 \rightarrow 0.768\,\text{g amides} + \\ 0.505\,\text{g glucose} + 0.434\,\text{g}\,CO_2 + (0.039\,\text{gmol ATP})\end{gathered} \tag{15}$$

The variability can be shown by:

$$1.00 \pm 0.15 \text{ g protein} + 0.1 \pm 0.04 \text{ g } H_2O + 0.38 \pm 0.15 \text{ g } O_2 - 0.768 \text{ g amides} + 0.37 \pm 0.2 \text{ g glucose} + 0.34 \pm 0.1 \text{ g } CO_2 + (0.3 \pm 0.1 \text{ gmol ATP}) \quad (16)$$

Combining equations 4 and 11, we see that for the breakdown and resynthesis of 1 g of protein. at least 0.288 g glucose is required, and probably 0.450 g glucose (equations 5 plus 13). The glucose requirement may even be as high as 0.578 g glucose g protein (equations 5 plus 12). This glucose is converted into CO_2 and H_2O. Protein breakdown and resynthesis thus appear to be an expensive process.

Effects of species and environmental variables

As there is no indication that different species produce the same product via energetically different biochemical pathways, the efficiencies of synthesis of specific components are assumed to be equal among all species of higher plants. The relative substrate requirement, of course, is not necessarily similar among species as biochemical compositions of storage organs differ.

Temperature and drought stress probably do not affect the efficiency of synthetic processes, though they may modify the rate, and the composition of the storage organ as well. Fertilization and other cultural practices may also influence the biochemical composition of the storage organ, and its relative substrate requirement, but only indirectly.

The effect of growth substances on changing the cost of biosynthesis has not yet been analyzed. It seems unlikely that growth substances modify the efficiency, but rather change the biochemical composition of tissues and redirect the flow of substrate to different organs. Growth substances modify morphology more than the carbon balance.

Maintenance processes

This section estimates the intensity of respiration that results from maintenance processes in storage organs. Some of the information presented was discussed earlier (Penning de Vries 1975). Maintenance processes counteract spontaneous degradation of proteins, membranes, and ion gradients in cells. The cost of maintenance processes per unit of time is a multiplicate of the rates of the processes and their specific cost. Degradation and resynthesis of proteins within cells was estimated earlier to require the equivalent of 0.24 g glucose/ g protein. With a turnover rate of about 15%/ day, this corresponds to 28-53 mg glucose/ g protein per day, or 7-13 mg glucose/g total dry weight per day in vegetative tissues.

Maintenance of ion gradients was estimated to require the energy of 6-10 mg glucose/ g dry matter per day. The average rates of maintenance processes, however, are only known approximately, and even less is known of their fluctuations. Therefore, it is still impossible to predict with reasonable certainty from basic data the rate of maintenance respiration (m.r.r.). It is still obtained from measurements: 1) by extrapolation of rates of respiration at diminishing rates of growth, or 2) growth suppresion in starvation experiments. Determined in this way, maintenance processes consume 7-60 mg glucose/g dry matter per day in vegetative tissues at normal temperatures.

Such m.r.r. values should not be extrapolated without further analysis of storage organs because they differ functionally from vegetative tissues.

Storage organs may grow relatively fast. Maintenance respiration seems to be more intense in rapidly growing tissue than in slowly growing tissue. The intensity of maintenance processes (m, expressed in gmol ATP per g dry matter per hour) in bacteria at 35°C has been found to be related to the growth rate (μ, in g/g per hour in the following way:

$$m = 0.0023 + 0.072\,\mu \tag{17}$$

(Van Verseveld, 1979). which can be transplanted into:

$$M = 0.26 + 0.34 \times RGK \tag{18}$$

where M is m.r.r. (g glucose/g dry matter per day) and RGR is the relative growth rate (g/g per day). Even after correcting for high temperature at which the observation was made, the basic value of m still appears to be about IO times higher in bacteria than the m.r.r. in plant cells when expressed in the same units. This may not be amazing, considering the high protein content of bacteria cells and the large surface-to-volume ratio, both of which can be expected to stimulate maintenance processes. However, if such a relation of M with RGR holds in plants — for which there are some qualitative arguments (Penning de Vries 1975) — then it would follow that the m.r.r. in plants is usually dominated by the first term of equation 18 but also that the m.r.r. may be stimulated considerably at the RGR attained by very young organs.

On the other hand most of the proteins in storage organs are inactive and stabile, and energy requirements for their maintenance are probably near zero. Protein turnover is consuming about half of the total maintenance requirement so that the cost of maintaining storage organs is expected on a theoretical basis to be in the range of 4 to 30 mg glucose g per day in cereals and in legumes. For tuber crops and tree crops, which accumulate large amounts of starch or oil, this estimate is probably too high.

Actual measurements of the maintenance respiration rate are scarce. Flinn et al (1977) measured in detail the gas exchange and growth of developing pea fruits at an average temperature of 19° C. They calculated an average m.r.r. of 4 mg CO_2/dry matter per day by subtracting the synthesis respiration (0.324 g CO_2 biomass formed, computed according to the procedure described in Figure 2) from the total respiration reported. This m.r.r. value may be too low, because the amino acid mixture in the phloem contained a larger variety of amino acids than was assumed in our calculation. A value of 8 mg CO_2/g per day for this experiment is therefore retained.

Hole and Barnes (1980) also analyzed data from similar experiments with developing pea fruits and concluded that the m.r.r. of large fruits was about 15 mg CO_2/g per day at 15°C. Their regression analysis, however, leads to an unrealistically low value for the synthesis respiration of only 0.073 g CO_2/ g biomass. When the value of 0.324 g CO_2/gfor the synthesis respiration of pea fruits is again adopted, reinterpre-

Component	Fraction of biomass (g/g)	Glucose consumed (g)		Amides consumed (g)		CO_2 produced (g)		O_2 consumed (g)	
Carbohydrates	0.40	(1.211)	0.484	(0)	–	(0.123)	0.049	(0.099)	0.040
Proteins	0.21	(0.948)	0.199	(0.768)	0.161	(0.544)	0.114	(0.250)	0.052
Lipids	0.23	(3.030)	0.697	(0)	–	(1.606)	0.369	(0.352)	0.081
Lignin	0.08	(2.119)	0.170	(0)	–	(0.576)	0.046	(0.189)	0.015
Organic acids	0.04	(0.906)	0.036	(0)	–	(-.045)	-.002	(0.270)	0.011
Minerals	0.04	(0)	–	(0)	–	(0)	–	(0)	–
	+		+		+		+		+
	1.00		1.586		0.161		0.576		0.199

For import of: 1. glucose 1.586/180. = 0.0088
2. amides 0.161/139. = 0.0012
3. minerals 0.04 /100. = 0.0004 +

0.0104 gmol ATP

Generation of ATP: 0.049 g glucose + 0.052 g O_2 → 0.071 g CO_2 + 0.0104 gmol ATP
(4.737) (5.053) (6.947) (1)

Final equation:

1.635 g glucose + 0.161 g amides + 0.251 g O_2 + 0.04 g minerals → 1.000 g biomass + 0.648 g CO_2

2. Procedure used to compute the glucose and amides required for the synthesis of 1.000 g biomass. [a]Numbers within parentheses are those of Table 1; those for protein are calculated from equation 5. Numbers outside the parentheses are the results of calculations for cotton bolls. Cost of import of substrates and minerals are expressed in gmol ATP. ATP generation occurs according to the normal pathway; the numbers in parentheses below the equation represent the ratio of the weights of these molecules. If some glucose required for maintenance is to be accounted for, its amount can be added to the equation to calculate maintenance respiration. The final equation is the sum of the conversion and energy generating processes.

tation of their data leads to a m.r.r. of about 10 mg CO_2/g per day and thus retained of Flinn's experiment. Hole and Barnes also observed that in very young fruits, where RGR exceeds 0.5 g/g per day, the m.r.r. is much higher — 180 mg CO_2/g per day. However, as the period during which this very high m.r.r. was observed lasted only a few days and only a small amount biomass was maintained at 180 mg CO_2/g per day, its effect on the total maintenance requirement was small. Therefore, this complication is neglected in the following computations.

In developing ears of wheat plants, the m.r.r. was initially 15-19 mg CO_2/g per day at about 18°C, and dropped in later stages (Vos 1981). Schapendonk and Challa (1981) report an almost linear decrease of the m.r.r. from 23-10 mg CO_2/g dry weight per day in growing cucumber fruits at 22°C. They found a large temperature effect: the m.r.r. was about 4 times as high at 28°C as at 16°C. Thornley and Hesketh (1972) reported a fairly constant value of 7-11 mg CO_2/g per day for cotton bolls 1 to 40 days old. Mutsaers (1976) concluded that the m.r.r. diminishes during cotton boll development and computed an average rate of 9 mg CO_2/g per day. Particularly for

root crops and tree crops, data on the m.r.r. are lacking. The only value found in literature is 7 mg CO_2/g per day, which Hunt and Loomis (1979) used in sugar beet growth simulation.

On the basis of this limited data, we adopt the preliminary conclusion that the m.r.r. equals 15 mg CO_2 g dry weight per day. Its equivalent of 10 mg glucose/g dry weight per day is used to calculate the substrate requirement for maintenance of growing storage organs of all species with the exception of root and tree crops. For those crops, a fixed value for the whole growth period is adopted. Arguments are provided below.

Maintenance respiration is generally sensitive to temperature. However, this is probably of secondary importance only, because the average temperature during the growth of the storage organs does not vary much from one site to another or from one year to another. In addition, the duration of the storage organ growth period tends to be shorter at higher temperatures. The effects on the m.r.r. of other environmental factors are probably not large, but they have not been quantified.

EVALUATION OF THE BIOCHEMICAL APPROACH

The biochemical approach to conversion and growth processes has been evaluated by comparing computations with experimental results. Unfortunately, synthesis and maintenance processes always occur simultaneously, and their substrate consumption or CO_2 production cannot be separated. Final proof of the correctness of the biochemical approach must wait until the intensity of maintenance processes can be predicted. Moreover, most experimental data are not sufficiently accurate to permit precise evaluation.

Observed and predicted growth or respiration rates, or both, have been compared for a maize embryo growing on a glucose solution in darkness (Penning de Vries 1974); the daily respiration of whole plants in relation to their daily photosynthesis at various growth rates (Penning de Vries 1975); and the yield of seedlings of maize, beans, and groundnuts germinating in darkness at two temperatures (Penning de Vries and Van Laar 1977). Generally, there was fair agreement between the measured and predicted substrate requirements, growth rates, and respiration rates. Thornley and Hesketh (1972) analyzed the growth and respiration of cotton bolls and concluded that 0.74 ± 0.1 g boll and 0.38 ± 0.15 g CO_2 were formed per 1.00 g of substrate. This value is a little lower than that computed for cotton in Figure 2: 0.648 g CO_2/g biomass, or 0.33 g glucose/0.74 g biomass. Yokoi et al (1978) measured a value for the synthesis respiration of germinating beans close to the theoretical value. Vos (1981) found a synthesis respiration relative to the growth rate in developing wheat ears of 0.24 g CO_2/g biomass increase a value slightly below the theoretical 0.28 g CO_2/g, possibly because there was little lignin synthesis at the time of measurement, hence less respiration. Schapendonk and Challa (1980) confirmed that the computed synthesis respiration efficiency of a growing cucumber fruit (0.15-0.17 g CO_2/g) was close to the theoretical efficiency (0.16-0.21 g CO_2/g), considering the biochemical composition of the fruit. The theoretical substrate requirements of growth processes in various crops in various stages of development are in line with observations of Yamaguchi (1978).

Except for the growth of fibrous roots no experimental data indicated that the efficiency of biosynthesis deviates significantly from that computed on a theoretical basis. It is confirmed in almost all papers that temperature has no effect on efficiency.

By inverted reasoning, Penning de Vries et a1 (1979) determined the rate of growth (expressed as synthesis of structural dry matter) in intact plants by measuring the rate of respiration, subtracting maintenance respiration, and computing the rate of synthesis from the remaining synthesis respiration.

SUBSTRATE REQUIREMENTS FOR GROWTH OF STORAGE ORGANS

Data characterizing crops

To calculate substrate requirements, data on the biochemical composition of storage organs were needed. In addition to the biochemical composition of the final product after threshing, cleaning, and technological processing, the composition of the raw product was needed (final product plus hulls, seed coats, pods, and inflorescences) to fit our definition of storage organ. The fractions these parts contribute to the total weight of the storage organs are presented in Table 3.

The biochemical compositions of whole storage organs of various crops also are given in Table 3. Two problems were involved in constructing Table 3: 1) not all appropriate data could be found and 2) data that were obtained usually concerned only the final product and not the total storage organ, which required adjustments of reported biochemical compositions. The ash fraction reported in literature is interpreted as oxide ash, about 60% of which is minerals. Organic acids are rarely reported. We assumed that the quantity of organic acids equaled that of minerals because both are often chemically coupled into salts. The amount of lignin is also rarely reported. Van der Meer (1979) states that lignin is an important constituent of fiber, although some lignin is present elsewhere in the biomass. The lignin in the principal fraction of storage organs is usually very low (Hartley 1978), but fairly high in the enveloping tissues. The lignin fraction in stems of graminoids is often above 20% (Sarkanen and Ludwig 1971) and is assumed to be similar for other support tissues. Although it is a significant constituent of many aboveground storage organs, its quantification remains difficult. The carbohydrate fraction in Table 3 is equal to the difference between 100% and the sum of the other groups.

The biochemical fractions reported in Table 3 are median values. A range is indicated when several sources of data were encountered. If a few were found, only the most complete data set was used. The data are based on more than 40 literature references. The principal source of information about storage organ components and about the biochemical composition are given. Sugarcane is not really a storage organ but is included as basis of comparison with other crops.

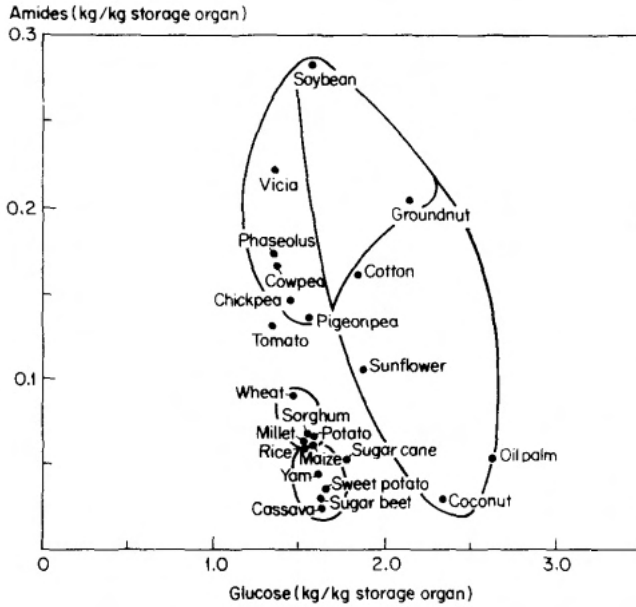
The biochemical compositions of the storage organs are fairly characteristic per species, but are not really fixed. They can be influenced by cultural measures, variety, and weather. Examples of how fertilization affects the protein content were given by Kramer (1979). He also presented examples of differences in protein content of wheat cultivars. Franke (1976) shows that groundnut has higher lipid and lower protein content at higher growth temperatures.

Table 3. Characterization of storage organs of the major crops. The fraction that the principal commercial product forms of the total storage organ is indicated (column 2) to facilitate the use of these data in combination with different types of data about crop yield. The average moisture content of the harvestable storage organ (column 10) is also given. The biochemical composition of the whole storage organ is presented in columns 4-9. Principal sources of information are given; most data are adjusted to account for the different biochemical composition of the hull, seed coat or inflorescence.

Crop	Storage organ	Major components	Biochemical composition of storage organ (dry product, %)						Av moisture content (%) of harvesrable storage organ	Principal source of data [a]
			Carbohy-drate	Protein	Lipid	Lignin	Organic acid	Minerals		
Cassava *(Manihot esculenta)*	Tuber	Tuber 100%	87	3	1	3	3	3	52	A
Chickpea *(Cicer arietinum)*	Pod with secda	Pod 15-25% Seed 85-75%	65 50-70	19 16-31	6 2-9	4 3-4	3 3-4	3 24	11 10-20	B
Coconut palm *(Cocos nucifera)*	Coconut	Copra 42%, stony endocarp 33%, pericarp 25%, no lignin and all fat in crop	39 35-42	4 3-5	28 26-31	25	2	2	25	C
Cotton (*Gossypium* sp.)	Bolls	Seed 65%, lint 35% (of which 94% cellulose)	40 36-44	21 18-24	23 22-24	8	4	4	8	E,F
Cowpea *(Vigna unguiculata)*	Pod with seeds	Pod 15-25%[b] Sccd85-75%,	61	22	2	7	3	4	11	F
Faba bean *(Vicia faba)*	Pod with seeds	Pod15-25%, Seed 85-75%	55 48-60	29 24-33	1 1-2	7 6-8	3	4 3-5	11	F
Field bean *(Phaseolus vulgaris)*	Pod with seeds	Pod 15-25% Seed 85-75%	60 53-66	23 16-31	2 1-3	7	4	4 3-5	11	F
Groundnut *(Arachis hypogaea)*	Pod with seeds	Pod 25-40% Seed 75-60%	14	27	39	14	3	3	5	E
Maize *(Zea mays)*	Cob	Seed 70%, rest 30%; no protein and 70% lignin in rest	75 70-80	8 5-11	4 2-6	11	1	1	13 10-19	D,N
Millet *(Pennisetum typhoides)*	Ears	Grain 60%, rest 40%	69 62-73	9 7-15	4 3-6	12	3	3 2-3	10 7-16	E,F
Oil palm *(Flaeis guineensisis)*	Palm nut	Stalk 17% fruit 83% of which is	37	7	48	4	2	2	47	G,P

		mesocarp 75% and shell and kernel 12.5% each								
Pigeonpea *(Cajanus cajan)*	Pod with seeds	Pod 15-25%, Seed 85-75%[b]	60	20	2	10	4	4	13	F
Potato *(Solanum tuberosum)*	Tuber	Tuber 100%	78 73-81	9 6-13	0 0-I	3	5	5	76 63-87	H
Rice *(Oryza sativa)*	Inflores-cence with seeds	60% grain 20% chaff. 20% stalk	76 73-81	8 6-9	2 0-3	12	1	1 0-2	12 11-14	E,F,Q
Sorghum *(Sorghum bicolor)*	Inflores-cence with seeds	60% grain, 20% chaff, 20% stalk[c]	72 67-74	9 7-13	3 3-4	12	2	2 1-2	10 8-16	I
Soybean *(Glycine max)*	Pod with seeds	Pod 20-40% Seed 80-60%	29 20-34	37 32-47	18 14-22	6 3-6	5 2-5	5 2-7	7 5-10	F, R
Sugar beet *(Beta vulgaris)*	Beet	Beet 100%	82 73-87	5 3-9	0 0-1	5	4	4 1-8	77	H
Sugarcane (*Saccharum* sp.)	Whole tops	Millable cane 50-60% in which 9-13% sugar	57	7	2	22	6	6	73	J
Sunflower *(Helianthus annuus)*	Inflores-cence with seeds	Kernels 44% hulls 23%[d] inflorescence 33%; almost all oil and no lignin in kernels	45 29-51	14 12-20	22 18-31	13	3	3 3-4	6	E, K
Sweet potato *(Ipomoea batatas)*	Tuber	Tuber 100%	84	5	2	3	3	3	70 50-80	A
Tomato *(Lycopersicum esculentum)*	Fruit	Fruit 100%	54 51-57	17 16-18	4 2-6	9	8	8 8-10	94 93-95	L
Wheat (*Triticum* sp.)	Inflores-cence with seed	Grain 85% Inflorescence 15%	76 73-79	12 9-15	2	6	2	2	13 9-18	M,N
Yam (*Dioscorea* sp.)	Tuber	Tuber 100%	80	6	1	3	5	5	70 60-80	F

[a]A= Onwueme 1978. B = Vander Maesen 1972, C= Purseglove 1975, D= Farle 1977, E= Benedictus 1980, F= Purseglove 1974. G=Orr and Adair 1967, H= Brouwer 1976, I = Franke 1976. J= Nathan 1978, K= Carter l978, L= Herrmann 1979, M = Brouwer 1972, N= Sibma pers. comm., O= Dantuma and Klein Hulze pers. comm., P= Corley, pers. comm., Q= Van Keulen pers. comm., R= Gupta et al 1973. [b] In analogy to Faba bean, [c] Own estimate. [d] In analogy to rice.



3. Glucose and amides required for growth of 1 kg of total storage organ. Data are from Table 4.

The period during which about 90% of the growth of storage organs occurs must be specified to estimate the total cost of maintenance processes during the growth period. This period is assumed to be 30-40 days for the formation of grain in cereals (Spiertz 1978, Andersen and Andersen 1980), sunflower (Dantuma, pers. comm.), and cotton (Thornley and Hesketh 1972). In legumes, the period of formation of pods with seeds is assumed to be 20-30 days (Flinn et al 1977, Oliker et a1 1978). Assuming that the average time that biomass needs to be maintained equals half its growing period, a total of 0.175 and 0.125 g glucose/ g dry matter is added to cereals and legumes, respectively. Storage organs of root and tree crops grow for 80 days or more, sometimes up to 400 days. A fixed value of 0.4 g glucose/g dry matter for the whole growth period is adopted for these crops. This value corresponds with a growth period of 80 days and the value of m.r.r. mentioned above. The same total maintenance cost is used to calculate the substrate requirement for growth of cassava, yam, coconut, and oil palms because their longer growth period is probably compensated for by a lower m.r.r. Sugarcane is included in this group with the highest maintenance requirements for comparison with other crops in Figure 3.

Results

The procedure described to compute the cost of synthesis and of maintenance is summarized in Figure 2. This procedure was also applied to calculate the requirements for growth of other storage organs. Two types of results are presented in Table 4: the quantity of substrate provided by the phloem and needed in the growing storage organ for synthesis of 1 kg of product, and the associated quantity of starch and protein broken down if the substrate is supplied at the expense of vegetative tissue.

Table 4. Characterization of substrate requirements for growth of 1 kg of a storage organ.

Crop	Substrate (kg) involved in growth of I kg product[a]					Substrate (kg) involved in breakdown to form substrate for 1 kg product[b]		
	Glucose (1)	Glucose (2)	Amino acids	CO_2 (1)	CO_2 (2)	Starch	Protein	CO_2
Cassava, tuber	1.64	1.24	0.023	0.793	0.206	1.50	0.030	0.069
Chickpea, pod with seed	1.42	1.29 (1.21-1.30)	0.146 (0.12-0.24)	0.539	0.356 (0.28-0.45)	1.22	0.190	0.082
Coconut palm, coconut	2.37	1.97 (1.93-2.(12)	0.031 (0.02-0.04)	1.338	0.751 (0.72-0.80)	2.17	0.040	0.100
Cotton, boll	1.81	1.63 (1.62-1.64)	0.161 (0.14-0.18)	0.905	0.648 (0.62-0.68)	1.58	0.210	0.100
Cowpea, pod with seed	1.35	1.23	0.169	0.503	0.320	1.15	0.220	0.083
Field bean, pod with seed *(Vicia faba)*	1.31	1.19 (1.18-1.19)	0.223 (0.18-0.25)	0.517	0.334 (0.31-0.37)	1.08	0.290	0.080
Field bean, pod with seed *(Phaseolus vulgaris)*	1.35	1.22 (1.22-1.24)	0.177 (0.12-0.24)	0.507	0.324 (0.29-0.38)	1.14	0.230	0.084
Groundnut, pod with seed	2.11	1.99	0.207	1.139	0.956	1.83	0.270	0.120
Maize, cob	1.56	1.39 (1.36-1.42)	0.06I (0.04-0.08)	0.580	0.323 (0.28-0.37)	1.40	0.080	0.073
Millet, ear	1.54	1.36 (1.36-1.40)	0.069 (0.05-0.12)	0.584	0.327 (0.30-0.38)	1.38	0.090	0.073
Oil palm, palm nut	2.53	2.13	0.054	1.548	0.961	2.31	0.070	0.110
Pigeonpea, pod with seed	1.38	1.26	0.154	0.511	0.328	1.18	0.200	0.081
Potato, tuber	1.57	1.17 (1.17-1.18)	0.069 (0.05-0.10)	0.797	0.210 (0.20-0.24)	1.4l	0.090	0.074
Rice, inflorescence with seed	1.53	1.36 (1.34-1.36)	0.061 (0.05-0.07)	0.554	0.297 (0.26–0.32)	1.38	0.080	0.071

Table 4 continued

Crop	Substrate (kg) involved in growth of 1 kg product[a]					Substrate (kg) involved in breakdown to form substrate for 1 kg product[b]		
	Glucose (1)	Glucose (2)	Amino acids	CO_2 (1)	CO_2 (2)	Starch	Protein	CO_2
Sorghum, inflorescence with seed	1.53	1.36 (1.36-1.37)	0.069 (0.05-0.l0)	0.571	0.314 (0.30-0.35)	1.37	0.090	0.073
Soybean, pod with seed	1.58	1.46 (1.32-1.50)	0.284 (0.244.36)	0.806	0.623 (0.60-0.65)	1.29	0.370	0.112
Sugar beet, beet	1.62	1.22 (1. 18-1.26)	0.038 (0.024.07)	0.794	0.207 (0.20-0.24)	1.47	0.050	0.071
Sugarcane, whole tops	(1.78)	1.38	0.054	–	0.333	1.25	0.070	0.064
Sunflower, inflorescence with seed	1.87	1.69 (1.63-1.83)	0.108 (0.094.15)	0.889	0.622 (0.56-0.80)	1 .66	0.140	0.093
Sweet potato, tuber	1.65	1.25	0.038	0.817	0.230	1.50	0.050	0.072
Tomato, fruit	1 .36	1.24 (1.201.27)	0. 13 1 (0.124.14)	0.513	0.330 (0.29-0.37)	1.18	0.170	0.077
Wheat, inflorescence with seed	1.45	1.27 (1.27-1.28)	0.092 (0.07-0.12)	0.535	0.278 (0.27-0.29)	1.28	0.120	0.074
Yam, tuber	1.60	1.20	0.046	0.800	0.213	1.45	0.060	0.072

[a] Processing that occurs in all storage organs; (1) = requirement for synthesis plus maintenance, (2) = requirements for synthesis only; numbers in parentheses represent variations due to variations in biochemical composition of the storage organ. [b] These processes may occur in vegetative tissues. Values are calculated according to equations 10 and 13, for situation (1).

The amount of glucose required for synthesis only and the sum of that needed for synthesis and maintenance are specified. Also given is the CO_2 production for synthesis and for synthesis plus maintenance together. These details will facilitate reconstruction of the final results of the calculations, and, if the reader desires, use of alternative assumptions (e.g. about cost of maintenance) and repetition of the computations. The variations in substrate requirements due to the variations in the biochemical composition are only indicated for the synthesis. The calculations to arrive at columns 7-9 are performed according to equations 13 and 10. The amounts of protein equal those indicated in Table 3, as the efficiency of transfer of nitrogen is supposed to be 100%. If respiration (column 9) is compared with measurements, it should be remembered that maintenance respiration of vegetative organs is not yet accounted for.

Table 4 indicates that it is particularly the lipid content of storage organs that makes them expensive to produce. The requirements for maintenance increase the total requirements for growth, but do not disturb the picture that evolved as a result of cost of synthesis, except for tuber crops in which maintenance requires a considerable fraction of the substrate. However, the intensity of maintenance respiration processes is not well known, and deserves further crop physiological research. The efficiency of carbon utilization for synthesis of storage organs can be computed in different crops with the data from Tables 1, 3, and 4 (columns 3, 4). Carbon utilization efficiency appears to be about 0.80 g C/g C; groundnut has the lowest efficiency (0.70) and potato the highest (0.89).

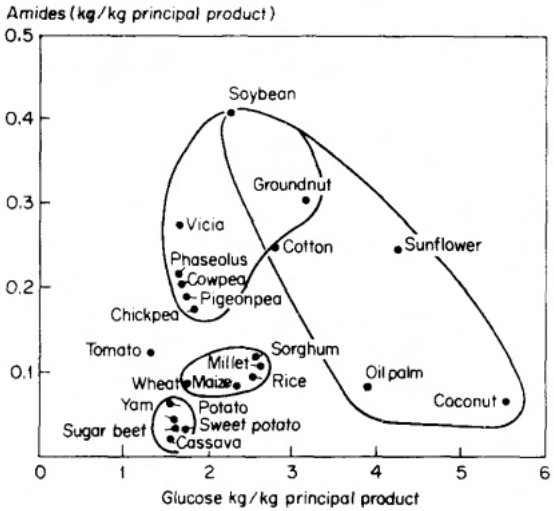
The results given in Table 4 are those of the whole growth period of the storage organ. The concentration of components may change during growth: protein synthesis is sometimes relatively advanced and at later stages the synthesis of carbohydrates and lipids is emphasized. One example is in the growth of lupin seeds (Atkins et al 1975); both growth efficiency and respiration per unit dry weight change during the growth period. This possible complication requires careful consideration when predicted efficiencies and respiration rates are compared with measured values.

Sinclair and De Wit (1975) calculated the substrate requirement for growth of seeds in a way similar to the one presented here. The most important differences are that we include the requirements for synthesis of components supporting or enveloping the principal product, and account for the cost of maintenance of the storage organ. Figure 3 presents the substrate requirements in a graphical way that permits the distinction of crop groups — cereals, legumes, beets and tubers, and oil-rich seeds — on the basis of substrate requirements.

The requirements for growth expressed per kilogram of the principal component are plotted in Figure 4. This is one way to show the economic cost of the principal product. Figure 4 exaggerates the differences between crops, as valuable by-products are ignored.

EFFICIENCY OF NITROGEN UTILIZATION

Calculations of nitrogen utilization assume that no nitrogen gets lost in the processes of breakdown, transfer, and resynthesis, but the value might not be 100%. There probably is a physicochemical loss from the formation and volatilization of NH_3. During breakdown of some amino acids, NH_4^+ is formed probably as a normal



4. Amounts of glucose and amides required for growth of 1 kg of the principal component of the storage organ. Data from Tables 3 and 4.

intermediate in cells as a result of protein turnover for cell maintenance, and photorespiration (Woolhouse 1980). Novozamski and Houba (1977) found 2-25 meq NH_4^+ kg dry matter in leaves (or about 0.2-1.4%) of their total organic nitrogen. NH_4^+ is not volatile, but it is in equilibrium with H^+ plus volatile NH_3. The pK of this protonization reaction is 9.25, so at the actual pH of the cell protoplasma of 6.8-7.0 (Kramer 1955) or 6.0-7.0 (Lehninger 1970), the NH_3 concentration is 2,000-200 times lower than that of NH_4^+. Because of the high solubility of NH_3 in water relative to air, the equilibrium concentration of NH_3 (g m^3) is about 600 times lower in air. This leads to a range of possible NH_3 concentrations of 0.007-0.9 mg NH_3/m^3 in the air in intercellular spaces. The NH_3 concentration in the ambient air of unpolluted environments is lower than 8 nbar (Farquhar et al 1979), or 0.-0.006 mg NH_3/m^3, which is often lower than that in leaves. At a concentration difference of 0.01 mg NH_3/m^3 across the stomatal resistance, a flow of about 0.2 kg N/ ha per day occurs in a crop with open stomata and a leaf area index (LAI) of 5 (a resistance of 100 seconds/m for 10 h per day). Such rate of nitrogen loss could be easily sustained by NH_4^+ that results from the metabolic turnover of proteins in crops, which amounts to 7-100 kg protein, ha per day. Farquhar et ai (1979) measured the NH_3 efflux of maize leaves under natural conditions and observed rates up to 20 g N/ha per day in a small number of samples.

This loss may proceed continuously and go undetected during the vegetative period. Its rate might increase in the reproductive phase, during which the break-down of amino acids and NH_4^+ production are stimulated. In addition, nitrogen is transported through the phloem which has a pH of about 8.0 (Ziegler 1975) and where the ratio of NH to NH_4^+ is 10-100 times higher than that in leaf cells. Atkins et al (1975) indicated that the concentration of NH_3 (presumably of NH_4^+) in endo-spermic fluid of lupin seeds was as high as 70 meq liter of fluid, about 5 times higher than the values reported by Novozamski and Houba (1977). Wetselaar and Farquhar (1980) reviewed NH_3 volatilization and reported nitrogen losses of 0.5-2.0 kg

N/ha per day during a few weeks at the end of the growing season. The losses could not be attributed to leaching or internal redistribution.

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PHYSIOLOGICAL ASPECTS OF PRODUCTIVITY IN FIELD CROPS

A. Tanaka

There are two levels in agricultural technology: one to obtain relatively high yields with limited inputs, and the other to obtain maximum yields with a given amount of solar energy and ample inputs. At these levels, relative productivity and potential productivity control the yield, respectively.

The improvement of crop yields in acid soil areas with adequate temperature and soil moisture conditions is discussed.

Relative productivity is determined by high aluminum tolerance when no or a limited amount of lime is used, low phosphorus adaptability when soil pH is reasonably well adjusted, and efficiency to utilize nutrient elements when pH and phosphorus levels are improved. Searching for crop species and breeding of varieties which are high in relative productivity will help farmers with limited inputs for now, but eventually it will be necessary to increase the efficiency of the inputs.

Potential productivity is controlled by the efficient use of solar energy. The photosynthetic rate per unit leaf area (Po) is higher in C-4 than in C-3 plants. The difference in the crop growth rate (CGR) between the C-4 and C-3 plants however, is, not that great because the CGR is not always controlled by the source potential. Improvements in the po or the canopy architecture are beneficial only when the source is the limiting growth factor. With available improved varieties, the sink potential is frequently the limiting yield factor during the growth of the harvesting organ. The harvest index differs among crops due to varying relative durations of the harvesting organs to the total growth durations, and also in relative strength as the sink between the leaf and stem and the harvesting organ.

With longer growth duration of a crop, there will be higher yield because the crop receives more solar energy. With higher protein or lipid content of the harvesting organ, there will be more primary photosynthetic products needed to produce a unit amount of

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harvesting organ ("equivalent yield"). So, the potential productivity of various crops should be compared in terms of "equivalent yield per day in the field." If the recorded maximum yields of various crops are expressed in this term, the range of productivity among various field crops is narrow, although it is slightly higher in maize and potatoes, and slightly lower in field beans.

In statistics or agronomy crop yield is generally equivalent to the weight of the harvested organ at a certain water content of a crop occupying a unit field area. Crop yield expressed in this manner has only a limited physiological significance because growth conditions (climate and soil) and genetic characteristics (growth duration and chemical composition of harvested organs) differ in each crop. Although yields of root crops are far higher than those of grain crops, the actual difference is not large because these yields are expressed in fresh weight in root crops, and in air-dry weight in grain crops.

The ratio of the world's average yield to the highest country yield is lower in field beans, groundnut, sorghum, and cassava (Table I) because these crops are frequently grown under stressed conditions. Productivity should therefore be defined as the efficiency of crops to utilize natural resources or agronomic inputs to produce the harvested organ.

Agricultural technology has two levels: 1) that for obtaining relatively high yields with limited inputs, and 2) that for obtaining maximum yield with a given amount of solar energy by trying to eliminate all other stresses with ample inputs. In the second level, temperature may limit yield because controlling it in field crop production is expensive.

This paper discusses crop production in acid soil areas with adequate temperature and soil moisture.

Table 1. World's average yield and highest country yield of various field crops (FAO 1979).

Crop	World's average yield (t/ha)	Highest country yield (t/ha)		Ratio of world's average yield to highest country yield
Rice	2.54	6.96	(Gabon)	0.36
Wheat	1.78	5.73	(Netherlands)	0.31
Maize	2.96	7.44	(New Zealand)	0.40
Sorghum	1.30	4.79	(Spain)	0.27
Sugarcane	55.3	153.4	(Peru)	0.36
Potato	14.5	34.4	(Netherlands)	0.42
Sweet potato	8.4	23.9	(Sudan)	0.35
Cassava	9.1	32.3	(Cook Islands)	0.28
Sugar beet	32.3	50.0	(Belgium-Lux embassy)	0.65
Soybean	1.51	3.36	(Italy)	0.45
Beans, dry	0.57	2.43	(Egypt)	0.23
Groundnut in shell	0.98	3.79	(Malaysia)	0.16

In the first-level technology, the ability of crops to produce high yield under stress or with limited amount of inputs is defined as relative productivity. When farmers cannot afford to apply lime to correct soil pH, crop tolerance for soil acidity is the key factor that controls relative productivity. When farmers can afford to correct soil pH but can not improve phosphorus status, crop adaptability to low phosphorus condition is the key factor. When pH and the phosphorus status are properly adjusted, crop efficiency to utilize nutrients from limited amounts of fertilizers is the key factor.

Yield will be controlled by the amount of solar energy available to the crops when farmers can afford to apply ample amounts of fertilizers after soil improvement at the second-level technology. Under such a condition potential productivity is the key factor. Efficiency may differ among crop species because of differences in the genetic potential and the present level of breeding.

RELATIVE PRODUCTIVITY

Acid soils are widely distributed in humid regions in the world and occupy a considerable portion of potential agricultural lands in the tropics. A large portion of the areas remain unreclaimed or are used only for extensive agriculture or animal husbandry with minimum inputs because soil fertility is low (Sanchez 1976). For socioeconomic reasons, it is frequently more realistic in such areas to plant crops that can tolerate soil acidity or can adapt to low phosphorus than to improve the soil condition. Cassava is frequently grown on such soils in the tropics.

Socioeconomic changes may help to improve adverse soil factors. In Japan, areas with volcanic ash soils remained unreclaimed until 1950 because of their low fertility. Small subsistence farmers using minimum inputs grew buckwheat, foxtail millet, barnyard millet, sweet potato, and upland rice on such soils because those crops were adapted to volcanic ash soils. In the 1950s, however, farmers made these areas productive by applying ample amounts of lime and phosphatic materials, which the government had subsidized (Tanaka 1977a).

In areas where soils are naturally rich or have been enriched, farmers may aim at higher yields by applying limited amounts of fertilizers. Crop efficiency in using nutrient elements becomes the key factor. Based on this characteristic, farmers select crop species which need only a limited amount of fertilizer.

Tolerance for soil acidity

Primary growth-retarding factors of acid soils are low pH or high concentrations of aluminum or manganese in the soil solution. These soils are frequently low in available phosphorus, various cations, and some microelements. It is therefore important to identify the key adverse factor of a given acid soil.

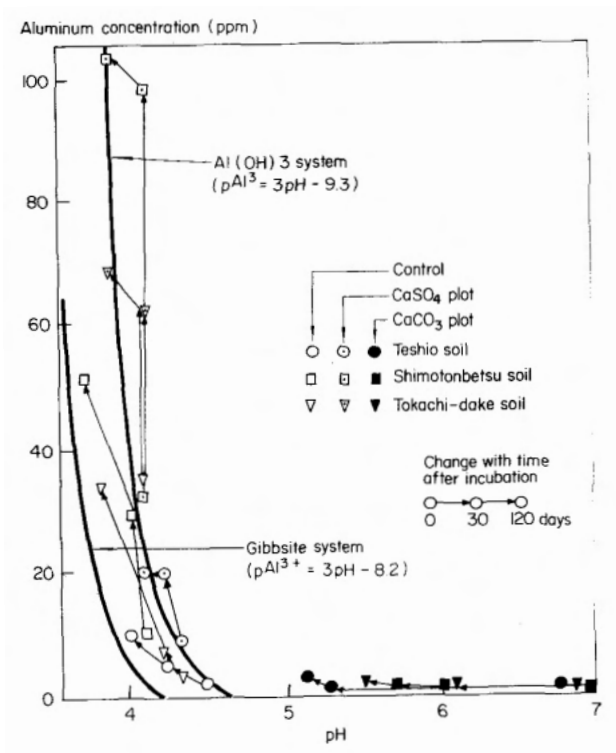
Tolerances for low pH per se, high alummum, and high manganese were compared among about 50 commonly grown crop species in Japan, under a water culture condition. Tolerance for soil acidity among those crops was also compared by growing them in plots with soil pH of 4.5 and 6.5 (established by applications of H_2SO_4 or $CaCO_3$ to a soil with pH 5.5). Ample amounts of nitrogen, phosphorus, and potassium were applied. Results indicated that the major factor controlling soil

acidity tolerance was high aluminum tolerance (Tanaka and Hayakawa 1975a, b). Among *Gramineae* species, rice and oats are tolerant of high concentrations of aluminum while wheat and barley are susceptible to soil acidity and high concentrations of aluminum.

Application of lime to an acid soil increases the pH and decreases the aluminum concentration in the soil solution (Fig. 1, Tanaka and Hitsuda 1980). The relation between pH and aluminum concentration appears to follow the behavior of $Al(OH)_3$ (Errikson 1952) and gibbsite (Lindsay and Moreno 1960): the concentration is extremely low at a pH above 5.0, and increases rapidly at a pH below 4.5. The adverse effect of low pH per se becomes apparent only at a pH below 4.0 (Arnon and Johnson 1942) where the major factor of growth retardation is the high aluminum concentration in the soil solution. Between pH 4.0 and 5.0. aluminum concentration rather than low pH per se is the important factor. At a pH above 5.0, neither low pH per se nor high aluminum concentration retards crop growth.

Since the critical aluminum concentration causing growth retardation differs among crop species, some crops can be grown on an acid soil without lime application, while others can be grown only after a large application of lime depending upon their high aluminum tolerance. When a farmer cannot afford to apply sufficient lime, he has to grow aluminum-tolerant crop species (Table 2).

In some acid soils, especially those with impeded drainage. manganese concentration in the soil solution may be high. Crop species susceptible to high manganese, e.g. field bean, may suffer from manganese toxicity on some acid soils.



1. pH and aluminum concentration of the soil solution in 3 acid soils treated with $CaCO_3$ or $CaSO_4$. Hokkaido, Japan.

Rice has high soil acidity tolerance. When a soil is kept submerged, the pH increases while the aluminum concentration in the soil solution decreases (Tanaka and Navasero 1966). Manganese concentration in the soil solution may be high, but rice has tolerance for that. Wetland rice can therefore be grown on acid sulfate soils on which no other crop, except pineapple, can be grown. Under such conditions, however, iron concentration in the soil solution can be extremely high and wetland rice may suffer from iron toxicity (Tadano 1976).

Adaptability to low phosphorus conditions

When soil acidity is the key limiting factor, lime application is a prerequisite. Even with lime, however, crop yield is generally low in most acid soils without applied phosphorus.

If low phosphorus soils with limited or no phosphatic materials have to be reclaimed, it is necessary to grow crops or varieties that are adapted to low phosphorus conditions. Rice, maize, sorghum, and sweet potato are adapted to such conditions (Table 3). Cassava grows better than other field crops on low pH and low phosphorus soils (Cock and Howeler 1978). It is not certain, however, if it is tolerant of high aluminum concentration.

Low phosphorus adaptability is a result of ability of roots to absorb phosphorus and to withstand low phosphorus content in the plant. The phosphorus content in the leaves necessary to maintain active growth is much higher in tomato than in rice (Tadano and Tanaka 1980). Low phosphorus adaptability, however, is mostly the result of the ability of roots to absorb phosphorus from growth media low in phosphorus. Phosphorus application will become necessary after phosphorus in the soil is exhausted by successive harvests of crops that deplete soil phosphorus.

Species or varieties adapted to low phosphorus conditions may be recommended

Table 2. Tolerance for high aluminum concentrations in various field crops (Tanaka and Hayakawa 1975a).

Very strong	Strong	Medium	Weak	Very weak
Buckwheat	Oats	Maize	Onion	Carrot
Rice	Soybean	Field beans	Barley	Spinach
	Broad bean	Cabbage	Sugar beet	Celery
		Wheat	Cucumber	
		Barnyard millet	Sorghum	
		Pea	Turnip	
		Eggplant		

Table 3. Adaptability to low phosphorus conditions [Fox et al 1974, McLachlan 1976, Sommer 1936, Tadano and Tanaka (1980), Tidmore 1930].

Strong	Medium	Weak
Rice	Wheat	Sugar beet
Maize	Barley	Tomato
Azuki-bean	Soybean	Pea
Sorghum	Field beans	Cotton
Sweet potato	Potato	Lettuce
Buckwheat		

for the time being to farmers who grow crops on soils low in phosphorus and who have no money to buy enough fertilizer. Use of mycorrhizas to extract soil phosphorus, which cannot be used by the roots of crops, may also be beneficial.

Studies have been conducted to improve the effect of rock phosphate and to increase the efficiency of phosphorus fertilizers by placement (Fenster and Leon 1979).

Efficiency in using nutrient elements

After soil pH and phosphorus have been improved, crops may respond positively to applications of potassium, magnesium, sulfur, zinc, or copper, depending upon the crops. The amount of available nitrogen in the soil usually controls yield.

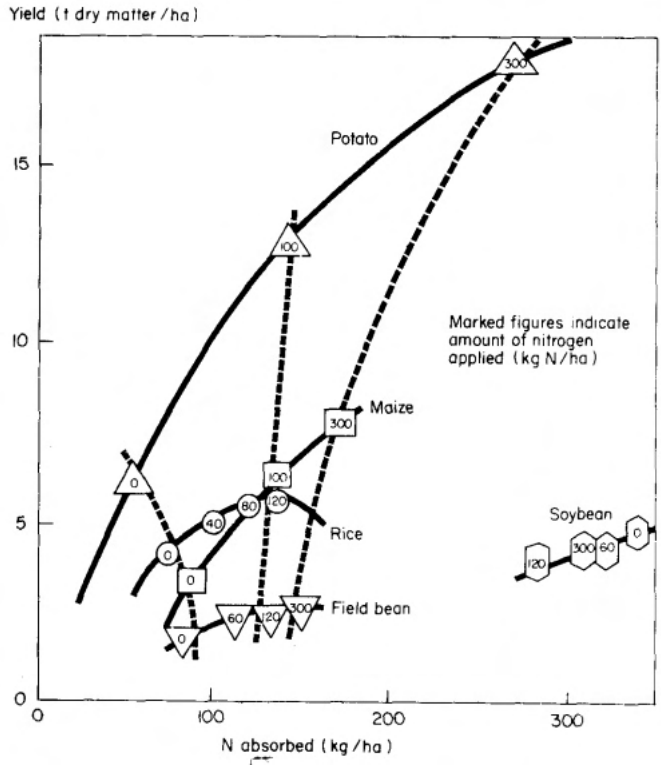
The yield of crops with a limited supply of combined nitrogen (ammonium or nitrate) differs considerably among species. With the aid of *Rhizobium*, legume crops can fix N_2 which is abundant in the air. Soybean is more active than field bean in N_2 fixation (Tanaka et al 1978). In some cereal crops, microorganisms living in the rhizosphere fix N_2. The amounts of nitrogen fixed have been reported to be large in sugarcane, maize, rice, and wheat.

Various crops grown in fields at Hokkaido University responded differently to varying amounts of applied nitrogen (Fig. 2). Even without nitrogen application, soybean accumulated a large amount of nitrogen by N_2 fixation. Soybean responded negatively to nitrogen application at certain levels because of retardation of N_2 fixation by combined nitrogen. In potato, the amount of nitrogen absorbed was slightly less without nitrogen application but increased with nitrogen application. Among crops the difference in absorbed nitrogen at 100 kg applied N was small. Nitrogen absorption was larger in potato and smaller in field beans at 300 kg applied N/ha. The yield was higher in crops that absorbed more nitrogen at high nitrogen application.

A farmer who grows few crops but cannot afford to use liberal amounts of fertilizers has to decide which crop to fertilize. Maize, soybean, potato, and sugar beet grown with and without any fertilizer in plots which have received the same treatments for more than 50 years, responded to nitrogen, with maize > potato -sugar beet >soybean; to phosphorus, with sugar beet > potato - soybean> maize; and to potassium, with potato> sugar beet> soybean> maize (Table 4). The result indicates that a limited amount of nitrogen, phosphorus, and potassium should be applied to maize, sugar beet, and potato, respectively.

Efficiency of a nutrient element to produce the organ to be harvested can be expressed by the amount of the harvested organ produced by a unit amount of the element absorbed by a crop. Efficiency differs among crop species (Table 5). For example, one gram of absorbed P produced more than 300 g of the harvested organ in potato or sweet potato, and only 150 g in wheat, soybean, field beans, or groundnut. This indicates that phosphorus is more efficient in sweet potato than in soybean. However, the phosphorus content of the harvested organ was 0.17% and 0.59% on dry matter basis in sweet potato and soybean, respectively.

Also related to soil fertility management is the distribution of absorbed nutrient elements between the harvested organ and the residue. The percentage distribution



2. Amount of nitrogen absorbed and yield at different levels of nitrogen application in various field crops in Hokkaido. Crops were tested on similar soils on a Hokkaido University farm, but during different years.

Table 4. Average yields of crops with no nitrogen, phosphorus, or potassium, 1978-79.

Treatment	Average yield [a] (%)			
	Maize	Potato	Sugar beet	Soybean
No nitrogen	8	41	48	112
No phosphorus	87	78	59	79
No potassium	95	24	51	55

[a]Relative to yield with 3 fertilizer ingredients.

of potassium in the organ to be harvested is only 10% in rice or wheat and more than 50% in potato or soybean (Table 5). If only the harvested organ is removed from the field and all the residues are returned to the soil, the amount of potassium which can be recycled in crop production differs considerably among crop species. In general the percentage distribution of nitrogen and phosphorus is high in the organ to be harvested; the percentage distribution of magnesium is moderate while that of potassium and calcium is low. This point should properly be considered in the study of cropping systems in relation to soil fertility.

Table 5. Efficiency of nutrient elements absorbed by crops to produce harvested organ and nutrient in harvested orgain in relation to total amount absorbed.

Crop[a]	Efficiency of absorbed nutrient (g dry matter of harvested organ per g nutrient absorbed)			Nutrients (%) in harvested organ		
	N	P	K	N	P	K
Rice (ab)	40	205	44	65	67	11
Wheat (ab)	23	151	20	61	70	9
Maize (ab)	37	215	29	69	69	14
Sorghum (b)	44	191	38	58	63	17
Soybean (ab)	13	154	21	85	88	58
Field bean (a)	18	151	25	78	76	31
Groundnut (b)	11	125	24	56	56	18
Sweet potato (b)	50	321	29	45	54	35
Potato (a)	47	320	33	58	16	65
Sugar beet (a)	30	225	26	35	40	26

[a] (a) Average of 5 cases of intensive farmers in Hokkaido, Japan, in 1977 and 1978, (b) A case at IRRI (Physiology Department 1978), (ab) Average of (a) and (b).

POTENTIAL PRODUCTIVITY

Recorded maximum yield is high in root crops and sugarcane but low in grain legumes (Table 6).

Yield is higher and growth duration longer in sugarcane, sugar beet, and cassava. Potato and sweet potato have higher yield and harvest index than the other crops. The yield of grain legumes is lower, and their grains contain more proteins and lipids than other crops.

In discussing crop productivity, the following points should carefully be considered:

- The rate of dry matter production of a crop occupying a unit field area (crop growth rate, CGR) can be expressed by the leaf area index (LAI) multiplied by the net assimilation rate (NAR).
- With a given LAI the NAR is a function of the photosynthetic rate per unit leaf area (Po) at high light intensities and the degree of mutual shading which is controlled by canopy architecture.
- The total dry matter production can be expressed by the average CGR during growth multiplied by the growth duration.
- Organs to be harvested such as grains in cereals or grain legumes, tubers in potato, and roots in cassava, sweet potato or sugar beet, are a portion of the total dry matter produced.
- Chemical composition of the organ to be harvested differs among crop species. More energy is required to produce a unit amount of proteins or lipids than to produce the same amount of starch.

Photosynthetic rate of leaves

The Po is higher in C-4 than in C-3 plants (Table 7). Varietal difference in the Po has also been reported in various crops.

The comparisons were generally based on Po measured at considerably high light intensities at a leaf age when the Po is at its peak. As the Po of a leaf changes with age,

Table 6. Recorded maximum yield of various field crops.

Crop	Maximum yield[a] (t/ha, dry matter)	Growth duration (days)	Harvest index	Equivalent yield per day (g glucose/ m^2 per day)
Rice	14 (ST)	190	–	10.0
	11 (T)	125	0.50	11.9
Wheat	12 (TM)	–	–	–
	8 (T)[b]	120	0.35	9.3
Maize	22 (TM)[c]	–	–	–
	13 (ST)	130	0.50	14.3
Sorghum	7 (T)	80	0.50	11.9
Sugarcane	[22] (T)	365	[0.35]	[6.6]
Potato	20 (ST)	–	–	–
	18 (TM)	162	0.80	14.3
Sweet potato	17 (TM)[d]	180	0.80	11.7
Cassava	28 (T)	365	0.60	9.6
Sugar beet	[19] (ST)	240	[0.45]	[8.7]
Soybean	7 (TM)[d]	120	0.45	11.8
Field beans	5 (T)[e]	90	0.45	8.6
Groundnut (seeds)	5 (TM)[d]	140	0.40	9.3

[a]Data on maximum yield and growth duration are from Cooper (1975). TM, ST, and T indicate data obtained in temperate areas, subtropics, and tropics. Figures in [ ] are expressed in sugar. [b]Values obtained at Centro Internacional de Mejoramiento de Maiz y Trigo. [c]Values attained by a farmer in Michigan, USA. [d]Data from Japan. [e]Data from International Center for Tropical Agriculture.

Table 7. Photosynthetic rate of leaves (Po) and crop growth rate (CGR) of various crops.

crop	Po[a] (mg CO_2/dm^2 per h)	CGR[b] (g/m^2 per day)
Rice	30-40, 34-41	25, 36, 23, 55
Wheat	58-12, 28-39	19, 18, 30
Maize	60-80, 86, 21-85	30(48), 52, 31, 78, 55
Sorghum	79-90, 60	51
Sugarcane	100, 34-86	31
Potato	25-35, 26	24(31), 23, 35
Sweet potato	21-26	21
Cassava	30	18, 22, 43
Sugar beet	30	31, 24, 28
Soybean	30-35, 43, 22-43	22, 21, 17
Field beans	30-40, 23-31	14(32)

[a]Values obtained at Hokkaido University, and those listed by Cifford (1974), the CIAT Annual Report (1978), and Murata (1980). [b]Data in parentheses are from densely planted crops at Hokkaido University. All other values came from Monteith (1978). Cooper (1975), Gifford (1974), Evans (1975), Murata (1980), Cock (1980), and Enyi (1972).

however, it is not so easy to compare the Po among varieties of a species.

Since Po is one of the factors affecting CGR a higher Po means a higher CGR. According to Monteith (1978) CGR was higher in the C-4 than in the C-3 plants (Table 7). But the difference in CGR between C-3 and C-4 plants is much smaller

than expected from the difference in Po (Cooper 1975. Evans 1975). In our study the maximum CGR was slightly higher in maize than in other crops, although such a difference did not exist in the average CGR during the entire growth period of the field crops. In field beans, the maximum CGR at ordinary planting density was far lower than for other crops, but density at very close planting was as high as in other crops.

Studies on genetic materials associated with the evolution of cultivated wheats demonstrated that one important factor that increased dry matter production was increase in the leaf area rather than in Po. In cultivated wheat the Po at its peak was lower than that of its ancestors but was kept high for a longer period during ripening (Evans and Dunstone 1970).

With presently available genetic materials the Po is not necessarily the dominant factor that determines CGR. No evidence shows that potential productivity can be improved by simply increasing the Po.

Canopyarchitecture

In a canopy of plant populations, light distribution is uneven. Lower leaves receive less light because of mutual shading. A horizontal leaf receives more light than a vertical leaf when the sun is directly above the canopy, a horizontal leaf also gives more shade to the lower leaves.

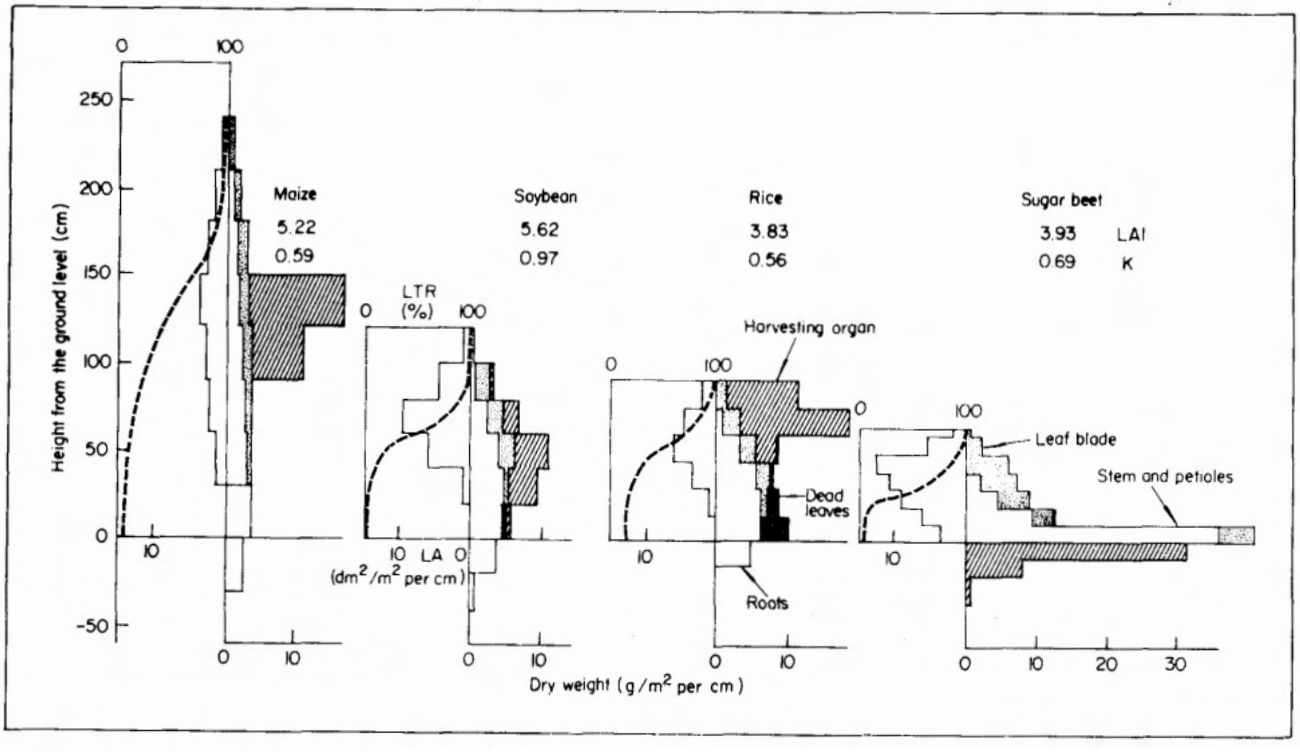
Leaf position is one factor that controls the photosynthetic rate of a plant population. The light intensity *(I)* that passes through a canopy at a given LAI and light intensity from above the canopy *(Io)* is expressed as $I= Ioe^{-k,LAI}$, where k is the extinction coefficient. The higher the k value, the larger the shade produced by a unit leaf area.

Leaf distribution at stratified heights from the ground level and light penetration through the canopy differ among crop species (Fig. 3). In maize the leaves are distributed evenly throughout a height range; in soybean the leaves are concentrated at a certain height, where the light is intercepted intensively; in sugar beet the leaves occur compactly near the ground. In a grain legume such as soybean, the k value is higher than in cereals because large leaves exsert almost horizontally. Large k values of these crops may impose a ceiling to productivity.

In rice that was heavily fertilized with nitrogen, mutual shading can be a problem because LAI tends to be high and leaves tend to bend horizontally. A high yield is therefore possible only with ample nitrogen application on varieties that have a small k value (Tanaka et a1 1966). This concept worked well in the varietal improvement of rice in tropical Asia during the 1960s (Jennings and Beachell 1965).

Plant height is another factor of the architecture. Generally speaking, the shorter the stature. the higher the yield in rice or wheat because lodging occurs when large amounts of nitrogen fertilizer are applied.

But it is not always true that the shorter the plant stature, the higher the lodging resistance. In maize, taller varieties tend to have a higher grain yield; brachytic lines have lower yield because of their compact leaf arrangements (Yamaguchi 1974). In field beans, the grain yield is generally higher in indeterminates than indeterminates (Tanaka and Fujita 1979) because of better light distribution within the canopy.



3. Distribution of dry matter in various organs, leaf area, and light intensity at stratified heights of canopy during active growth of organs lor harvested field crop in Hokkaido.

Balance between photosynthesis and respiration

The relationship between photosynthesis (P), respiration (R), and dry matter production ($\triangle$w) is often expressed as $\Delta W - P = R$. Dry matter production always accompanies respiration which generates the energy for biosynthesis. The growth efficiency (GE) [ΔW ($\Delta W + R$) or $\Delta W/P$] is about 0.65 during the normal vegetative growth of various crops (Tanaka 1977b). At later crop growth stages, however, differences in GE exist for two reasons: a) difference in the chemical composition of the organ to be harvested, and b) difference in the proportion to the total respiration (R) of maintenance respiration (Rm) which is not geared directly to growth.

The Rm-to-R ratio is about 0.2 during the vegetative growth of normally growing crops (Kato and Tanaka 1981). However, it can be higher when the architecture of a canopy is unfavorable as in a tall rice variety with long leaves (Tanaka et al 1966).

Leaf area index

Crops differ in LAI and LAI response to planting density or nitrogen level. The optimum (or ceiling) LAI is about 5-6 in rice or maize, and 3-3.5 in cassava.

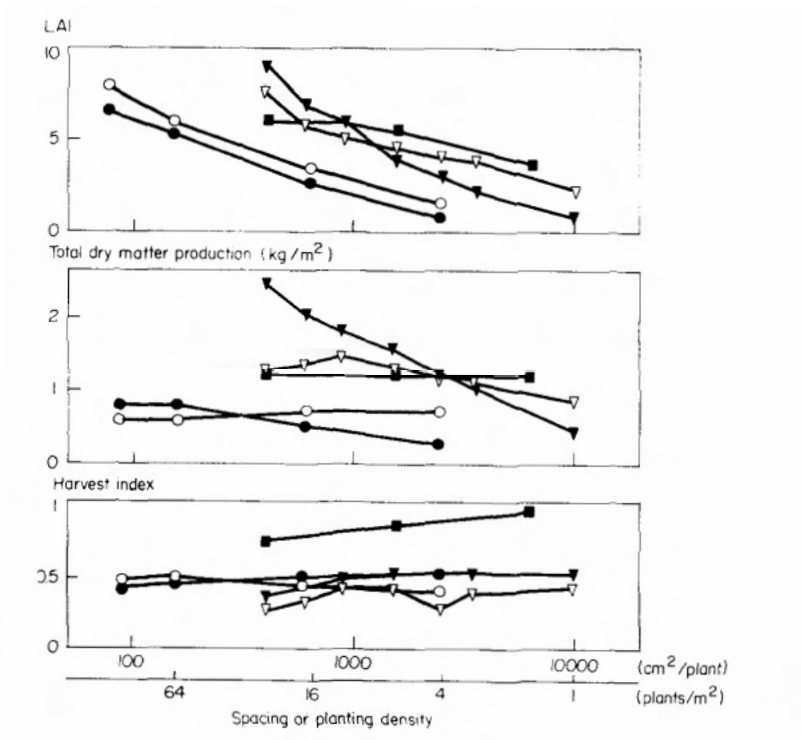
The LAI is determined by the size of each leaf, the number of leaves on a stem (tiller or branch), and the number of stems per unit field area. Change in LAI is caused mainly by the change in stem number. The potential to increase the tiller number is large in rice, moderate in wheat, and small in maize. Varietal difference in tillering or branching ability is also large.

At spacings wider than 1,000cm^2/plant potato, had the highest LAI (Fig. 4). The increase in LAI with planting density was very low in potato but rather high in maize. In maize the LAI of Fukko No. 8, which has no tillering ability, was lower at wide spacings but increased almost proportionally with increase in planting density. The LAI of Golden Cross Bantam, which has tillering ability, was higher at wide spacings, but increase in LAI with planting density was lower.

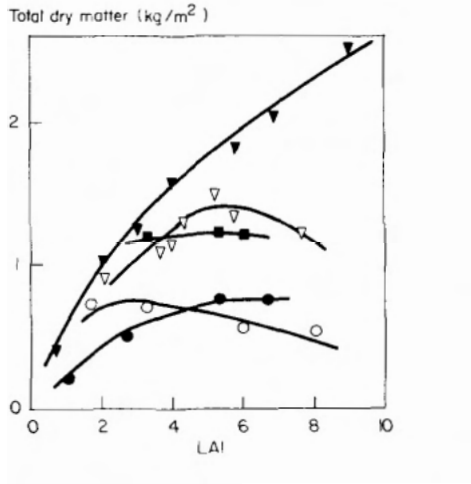
Total dry matter production generally increased with planting density and LAI (Fig. 4). But the relation between LAI and total dry matter production is not a simple one (Fig. 5). Varieties such as Golden Cross Bantam maize or Gin-tebo field beans have an optimum LAI.

The photosynthetic rate of a crop population decreases with increase in LAI because of mutual shading, but increase in respiration is linear. It has been argued that crops have a ceiling LAI rather than an optimum LAI because respiration does not increase linearly with LAI, however, experimental data indicate that both instances exist. Fukko No. 8 maize has ceiling type LAI, Golden Cross Bantam maize has optimum-type LAI (Tanaka and Yamaguchi 1972). In rice a high yielding variety with short, erect leaves that is grown in the dry season has ceiling LAI (Cock and Yoshida 1973). old, leafy varieties grown in the rainy season have optimum LAI (Tanaka et al 1966). Crops with ceiling LAI are easier to manage than those with optimum LAI Excessive application of nitrogen does not have a negative effect on the ceiling LAI.

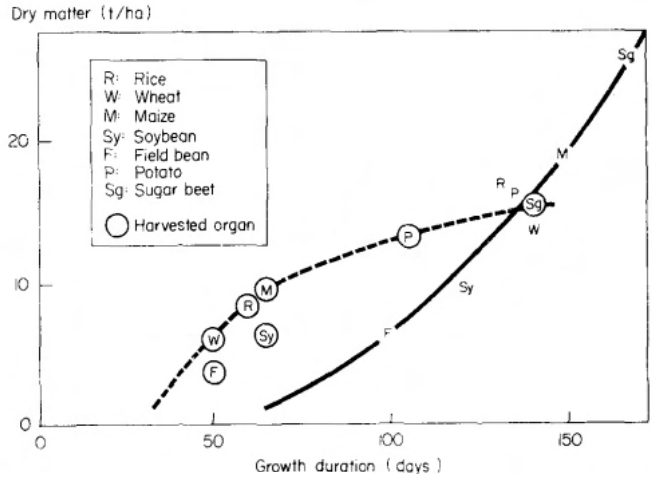
In some root crop or grain legume varieties, the LAI does not increase above a certain limit even at a high planting density (Fig. 3). When LAI exceeds the critical



4. The maximum leaf area index (LAI), total dry matter production, and harvesting index as affected by planting density in various field crops in Hokkaido. Experiments were conducted on the farm of Hokkaido University with ample fertilizers. Field bean: Taisho-kinotoki (determinate) (•) and Gin-tebo (seml-indeterminate) (O) were tested in 1976. Maize: Fukko No. 8 (dent) (▼) and Golden Cross Bantam (▽) were tested in 1969. Potato: Dan-shaku (■) was tested in 1979.



5. Maximum leaf area index (LAI) and total dry matter in various field crops in Hokkaido. (Symbols are the same as those in Figure 4.)



6. Total growth duration and total dry matter of harvested organs of various field crops in Hokkaido. Dry matter of harvested organs is expressed in equivalent yield, and total dry matter is expressed as equivalent yield + weight of leaf and stem. Total growth duration in winter wheat was 320 days, but days with average temperature below 7°C were excluded.

level, the lower leaves, because of mutual shading, receive a light intensity below the compensation point, they suffer from a shortage of respiratory substrates, and eventually defoliate. New leaves continue to develop at the top of the canopy, but the LAI remains almost constant because of the defoliation of lower leaves. In cereal crops the lower leaves die as a result of excessive mutual shading but this generally takes some time. The shaded leaves consume a considerable amount of photosynthates before they die.

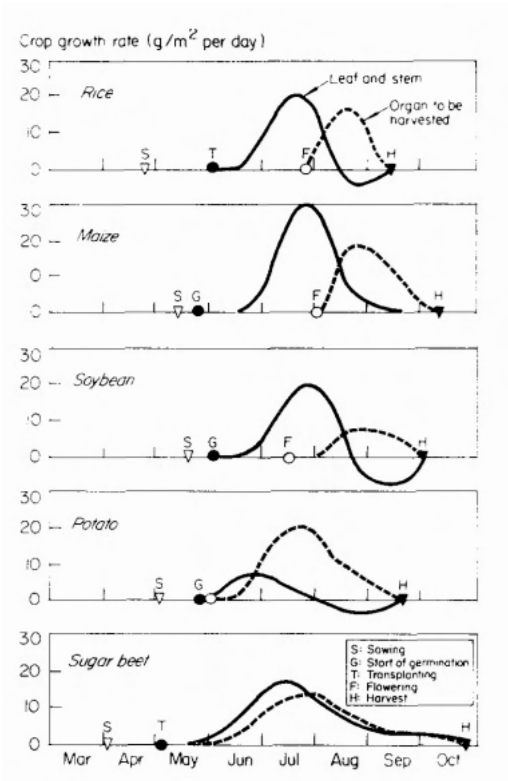
Growth duration

Growth duration is as short as 60 days in some tropical field bean varieties, 4-6 months in rice or maize, and 1-1.5 years in cassava and sugarcane.

In this study, the longer the duration of a crop in the field, the larger the total dry matter production (Fig. 6), and the longer the growth duration of the organ to be harvested, the higher the yield.

The CGR changes with growth (Fig. 7). The proportion of photosynthates in the organ to be harvested and in the other organs changes with growth. In root crops the growth of organs to be harvested starts early and covers a longer period; in cereal crops it starts only after flowering and covers a shorter period.

In most root crops, the length of the total growth period, and of the growth duration of organs to be harvested are directly related to increase in yield. In rice, the period from flowering to harvest is almost constant regardless of the total growth duration. There is also an optimum growth duration for obtaining maximum yield: the longer the growth period, the higher the total dry matter production and the lower the harvest index (Vergara et al 1964). The optimum growth period changes



7. Growth rate of leaf and stem and harvested organ at successive growth stages of various field crops in Hokkaido.

with management practice: the higher the nitrogen level or the planting density, the shorter the optimum growth period.

It is easy to select the best planting season for crops with a short growth period, but if such crops are subjected to adverse conditions, they have no time to recover from the damage before harvest. Crops with a long growth period have a limited range of planting season, but they have time to recover from damage during the growth period.

Harvest index and source-sink relationship

Root crops generally have a higher harvest index because the growth period of organs to be harvested is long relative to the crop's total growth period. Since the shoot and the roots in tubers grow simultaneously for a long period, their relative strength as the sink to accumulate photosynthates is an important factor which controls the harvest index. In sugar beet the harvest index increases only slightly during the growth period because the growth rate of the shoot and the root is almost parallel (Fig. 7). In varietal improvement of sugar beet, a major accomplishment was the improvement of sink potential of the roots which increased the weight of roots and total dry matter production (Thorne and Evans 1964). In potato the tubers dominate the shoot in the competition for photosynthates after a certain growth stage. because the tubers are a very active sink. Leaf growth is suppressed and some

substances in the shoot are retranslocated to the tubers at later growth stages (Fig. 7). resulting in a very high harvest index. In potato breeding, productivity has been increased through the improvement of the tubers' sink potential although the source potential was also improved by an increase in leaf area to support the sink potential (Inoue and Tanaka 1978). Increase in the size of each tuber has made possible the sink potential. The LAI is inversely proportional to the harvest index (Fig. 4), and this suggests that under such a condition, the shoot dominates the tubers as they compete for photosynthates.

In cereal crops until flowering the sink of photosynthates is the leaf and stem then it is the grains. Most of the photosynthates produced after flowering accumulate in the grains, and some amount of the constituents of leaf and stem at flowering may retranslocate to the grains as in the case of rice (Fig. 7). The sink potential of the grains, however, is decided before flowering. The harvest index is therefore determined by the amount of dry matter in vegetative organs produced up to flowering, the sink potential of grains before flowering, the photosynthetic potential during ripening, and the amount of substances in vegetative organs that can retranslocate to the grain during ripening when the sink potential of grains exceeds the source potential. The sink potential of grains can be broken down into yield components — panicle (or ear) number, number of grains per panicle. and potential size of each grain (hull size in rice) — determined during panicle development. As various combinations of yield components give similar sink potentials and various interactions in yield components occur, manipulation of the sink potential is very complicated. In general the increase in sink potential of grains for varietal improvement has been accomplished by increasing the size of each grain at early stages, and then the number of grains. The increase in grain number was accomplished mainly by increasing the panicle number in rice and the grain number per ear in maize. Because grain number is more important than grain size in determining the sink potential and because there is a loose negative correlation between grain number and grain size, maize varieties with small grains appear to be more productive (Tanaka and Yamaguchi 1972).

In grain legumes, the vegetative organs continue to differentiate and grow after the start of blooming, especially in indeterminates. The yield components are node number on the main stem and branches, raceme number per node, pod number per raceme, grain number per pod, and grain size. Generally, pod number is closely correlated with grain yield, and high yielding varieties often have small grains (Tanaka and Fujita 1979). But as large grain legumes command a high price in the market, the breeding of high yielding bean varieties has become a problem.

After the sink potential of grains has been decided in grain crops, ripening is controlled by the relative potential of the sink (grains) and the source (photosynthetic facility). When sink potential is larger than source potential, source potential is the yield-limiting factor, and yield is increased by improving the source. But when sink potential is smaller than source potential, yield is limited by sink potential.

In the 1960s the productivity of tropical rice was remarkably increased by improving source potential through modification of canopy architecture. The approach was successful because the source was the yield-limiting factor in the popular rice varieties. With the present high yielding varieties, the grain yield is often

positively correlated with grain number (Yoshida et a1 1972). This suggests that the sink is the yield-limiting factor at present. Data on currently available maize varieties (Tanaka and Yamaguchi 1972) or field beans (Tanaka and Fujita 1979) show that grain yield was positively correlated with grain number, suggesting that their yield-limiting factor is the sink. In cassava a positive correlation between the yield and the harvest index (Kawano et a1 1978) indicates that the sink potential of roots is one of the yield-limiting factors.

The source potential can be high in maize because this crop is a C-4 plant. This potential, however, is not evident during grain ripening because of limited grain number. Because of this, the CGR during ripening is not necessarily higher in maize than in the C-3 plants. The Po of the ancestors of cultivated wheats is not weak, but this potential is not evident during ripening because their sink potential is low. A proper identification of the yield-limiting factor between the source and the sink is important in increasing potential productivity of crops.

Chemical composition of harvested organs

Harvested organs of crops vary widely in chemical composition (Table 8).

Constituents of the harvested organ are produced from primary photosynthetic products, and during the process some of the primary products are used in respiration to generate the energy required for biosynthesis. In the respiration of harvested organs, the conversion efficiency of starch, proteins, and lipids produced from a unit amount of the primary photosynthetic product (as glucose) are 0.84, 0.38, and 0.31, respectively (Tanaka 1977b, Yamaguchi 1978).

Based on the composition of harvested organs and their conversion efficiencies, the amount of primary photosynthetic product (glucose) to produce a unit amount of the harvested organ (equivalent yield) can be calculated. It is 1.35 for rice and 2.09 for soybean (Table 8).

Comparison of productivity based on dry weight of the harvested organ is not logical because of differences in chemical composition. A logical comparison is that based on equivalent yield. For example, 14 and 7 t grain/ ha are recorded maximum yields for rice and soybean. Thus rice productivity may be considered as twice that of soybean. However, if yields are expressed in equivalent yields, these are 18.9 for rice

Table 8. Chemical composition of harvested organs and equivalent yield of various crops.

Crop	Proteins [a]	Lipids [a]	Carbo-hydrates [a]	Equivalent yield [b]
Rice	8.8	2.7	87.0	1.35
Wheat	12.1	2.3	83.7	1.39
Maize	9.5	5.3	83.7	1.42
Sorghum	8.3	3.1	86.7	1.35
Potato	9.3	0.5	86.3	1.29
Sweet potato	4.2	0.7	92.3	1.24
Soybean	39.0	19.9	35.4	2.09
Field beans	24.1	2.6	69.0	1.54
Groundnut (seeds)	27.7	50.4	19.6	2.59

[a] Crude protein, crude lipid, and the balance between dry matter and crude protein + crude lipid + ash, respectively. [b] In rice for example, 0.088/0.38 + 0.027/0.31 + 0.87/ 0.84 = 1.35.

and 14.6 t/ ha for soybean. The difference in productivity between these two crops, therefore, is not so large as it appears.

Logical method for comparing productivity

The most logical method for comparing productivity is equivalent yield per unit amount of solar energy which the field receives during the crop's growth period. Rice yield has been slightly higher in Spain or Australia than in Japan or Korea, but the amount of solar radiation during the rice season in Spain or Australia is about twice that in Japan or Korea. Productivity is therefore higher in Japan or Korea although it is not certain whether this is due to differences in varietal productivity or in management practices.

When crop species or varieties of different growth duration are grown under conditions where they receive similar amounts of solar radiation, their productivity can be compared by the use of equivalent yield per day in the field.

Based on the data of recorded maximum yield of various crops (Table 6). equivalent yields per day can be determined. The productivity of various crops ranges from 8.6 to 14.3 g glucose/m^2 daily. Since the yield of sugarcane and sugar beet is expressed in sugar, the range would be still narrower. From the figures we conclude that potential productivity is similar among crop species but is slightly higher in maize and potato and slightly lower in field beans, groundnut, and wheat. Possible reasons for higher productivity is a high Po in maize and a large harvest index in potato. For the low productivity the reason may be an adverse canopy architecture in field beans or groundnut.

In areas with high latitudes or altitudes, the frost-free period is limited. It is not possible to grow more than one crop in a year and a crop with a long growth duration and unable to stand low temperatures cannot be grown even once a year. Sugar beet is one of the productive crops in such areas because it is tolerant of low temperatures and has a long duration of root growth. In areas without frost, the situation is more complicated. A crop species with a growth duration of more than 183 days cannot be grown more than once a year in a field, whereas a crop species with a growth duration of less than 121 days can be grown 3 times a year. Climatic conditions also vary every season and crop requirements in every climatic condition differ among crop species. Evaluation of cropping systems in which various crop species are grown should therefore consider equivalent yield per year.

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TROPICAL CROP BREEDING — ACHIEVEMENTS AND CHALLENGES

K. Kawano and P. R. Jennings

All the major food crops were domesticated in the tropics or adjacent areas. Diseases, pests, and cultural practices coevolved over the ages with the crop species. Rich variability of crop germplasm, pests, environments, and cultural practices complicates tropical crop breeding. Yet, the major difficulty in breeding is the need to grapple with the bulk of farming situations that have partial or no access to modern cultural practice technology. Breeding may be relatively easy for the high productivity environments with high cultural technology outside the center of origin of the species. When the crop is a vegetatively propagated perennial, disease resistance may be obtained with relative ease. Where the harvest index is the yield-limiting factor, a quantum yield increase by selection is possible. In contrast, breeding for low productivity environments with low cultural technology inside the center of origin of the crop becomes extremely difficult. If the crop is a sexually propagated annual, obtaining stable disease resistance is a real challenge. If the total biologcal yield is the yield-limiting factor, substantial yield increase by breeding may not be expected. The research emphasis earlier given to the tractable farming situations of high-input technology is shifting to the bulk of tropical farms that have low to medium technology possibilities and where yields are stagnant. These targets for research must be identified in terms of biological, climatic, soil, and socioeconomic factors. A critical issue is identification of cultural practices within the reach of the farmers in each target area. Research plots for varietal selection should be managed at a level within the reach of the average farm. A maximum use of land cultivars within each target area, combined with broad-based and high-volume hybridization, is critical. The major selection criterion should be the overall performance of a population and, secondarily, selection for individual single traits. The final selection should be based on moderate and stable yield over years within a given environment.

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One of man's greatest achievements has been the domestication of crop species, Nearly all the major food crops have been domesticated in the tropics or adjacent areas. Numerous pathogens, pests, and cultural practices coevolved with each crop species in its center or centers of origin. Consequently, the variability in crop germplasm, pests, and cultural practices in the tropics is tremendous. Agricultural advance in the temperate countries constitutes a recent and small chapter in the history of the domestication and evolution of crop production. Yet, modern theory related to crop breeding and production largely developed in the temperate countries and the resulting technology, without appropriate modification, tended to be imported to the tropics. Some of the imported technologies were useful; however, crop improvement in the tropics is now generally recognized as more difficult and complex than originally thought.

The basic difficulty of tropical crop breeding stems from the tremendous variability in crop germplasm, pests, and the cultural systems for crop production, and the highly complex interactions among these factors.

We present several underlying factors about crop breeding in the tropics which may be important in defining the basic strategy for specific crop breeding programs. Many of these factors are not emphasized in textbooks prepared from the temperate area experience.

PHYSIOLOGICAL FACTORS UNDER DIFFERENT ENVIRONMENTS IN DIFFERENT CROPS

A food crop is genetically improved through the improvement of either total dry matter production or harvest index, or both. Harvest index is the proportion of economic yield to the total biological yield of a plant. In cereal crops, it is the proportion of grain weight to the total plant weight. In root and tuber crops, it is the proportion of root or tuber weight to the total plant weight. Total biological yield represents the crop's photosynthetic efficiency while harvest index represents the efficiency of the crop to convert photosynthesized products into an economically valuable form.

We evaluated the relative importance of harvest index and total plant weight to yield at different levels of environmental productivity in rice (Table 1) and cassava (Table 2), using yield data for widely variable germplasm under a range of environments. Two statistics are compared to assess relative importance: the simple correlation coefficient between yield and harvest index or total plant weight, and the relative size of variance of harvest index or total plant weight compared with that of grain or root yield. Environmental productivity is given by the total average yield of each yield trial.

In rice grown in high-yield environments harvest index was much more important to grain yield than total plant weight. In low-yield environments, the importance of total plant weight to rice yield was overwhelming (Table 1).

In cassava, on the other hand, harvest index was important across all the yield levels. The relative importance of total plant weight tended to be greater in the low- than in the high-yield environments (Table 2).

Table 1. Relationship of harvest index (A) and total plant weight (B) to rice gain yield (Y) in diverse environmental conditions[a] in Peru.

Av yield of experiment (t /ha)	r_{YA}	V_A/V_Y	r_{YB}	V_B/V_Y
5.26	0.222	0.381	0.886**	0.997
7.44	0.177	0.414	0.886**	1.065
7.82	0,723**[b]	0.693	0.682**	0.690
8.03	0.591**	0.684	0.536**	0.843
8.14	0.288	0.568	0.574**	0.969
8.14	0.534**	0.672	0.230	0.813
8.81	0.893**	0.911	0.074	0.457
9.13	0.820**	0.673	0.240*	0.386
9.18	0.764**	0.971	0.236	0.810
9.28	0.744**	0.651	0.096	0.567
9.59	0.657**	1.182	0.078	0.727

[a]Data from 11 varietal yield trials conducted on northern coast of Peru. Variation in yields was caused by differences in nitrogen application and plant spacing. The general yield level was high, because of the extremely high productivity of the Peruvian north coast, but the relative yield comparison may be valid. *r* : correlation coefficient. V/V: relative size of variance of harvest index or total plant weight to that of yield (variables are converted into logarithmic scale). [b]**Significant at 1% level.

Table 2. Relationship of harvest index (A) and total plant weight (B) with root yield (Y) in cassava under diverse environmental conditions.[a]

Location[b]	Av yield of experiment (t/ha)	r_{YA}	V_A/V_Y	r_{YB}	V_B/V_Y
Carimagua	4.9	0.813**	0.615	0.840**	0.530
Carimagua	15.3	0.691	0.406	0.932**	0.748
Carimagua	19.1	0.773**	0.640	0.889**	0.712
Caribia	24.1	0.582**	0.710	0.789**	0.738
Caribia	27.3	0.852**	0.690	0.807**	0.438
Caribia	29.8	0.711**	0.499	0.821**	0.760
CIAT	26.3	0.840**	0.956	0.242	0.042
CIAT	27.8	0.817**	0.907	0.409	0.321
CIAT	28.6	0.918**	1.040	0.542	0.254
CIAT	30.4	0.763**	0.823	0.551**	0.476
CIAT	37.2	0.668**	0.108	0.767**	0.670
CIAT	42.1	0.776**	0.767	0.525*	0.404

[a]Data from replicated yield trials in 3 years at 3 locations. r: correlation coefficient. V/v: relative size of variance of harvest Index or total plant weight to that of yield (variables are converted into logarithmic scale). *Significant at 5% level, **significant at 1% level. [b]CIAT = Centro lnrernacional de Agricultura Tropical.

Tropical food crops may be grouped according to the relative importance of harvest index and of total biological yield to economic yield. The first group, exemplified by cassava, includes crops in which harvest index is universally important to economic yield over a wide range of environmental productivity. The second group represented by rice, includes crops in which the harvest index is more important under high-yield environments while total biological yield is more important in low-yield environments.

In crops such as wheat (Syme 1970, McEwan 1973, Donald and Hamblin 1976), barley (Singhand Stoskopf 1971), oats (Sims 1963), and peanut (Duncanet a1 1978),

harvest index is more important in high-yield environments. With these crops it is difficult to analyze which factor is more important under low-yield conditions because very limited attention has been given to the genetic aspect of yield factors in such conditions. However, these crops may fall into the same category as rice.

In field bean, total plant weight is highly correlated with grain yield while harvest index is not (CIAT 1975, 1978). Similarly, in soybean, harvest index is not important to grain yield (Buzzell and Buttery 1977). In tropical maize, total plant weight is highly correlated with grain yield regardless of planting density: harvest index is equally important to grain yield, but only at a high planting density (Yamaguchi 1974).

Field bean, soybean, and maize were studied in comparatively well-managed fields that received adequate fertilizer, irrigation. and weed and pest control, and therefore represent relatively high-yield environments.

Very limited research has been conducted with these crops in low-yield environments. Because in rice and cassava the relative importance of total plant weight to grain yield tends to be greater in low-yield environment, it appears that in field bean, soybean, and maize, total plant weight is also important to grain yield in low-yield environments. Thus, these crops represent a third group, in which total biological yield is important over a wide range of environmental productivity.

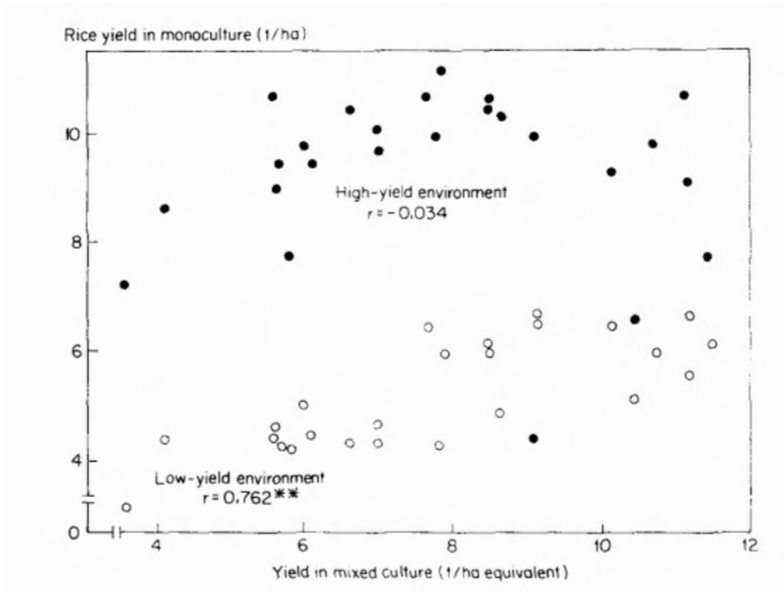
We conclude that the crucial physiological factors related to yield differ drastically according to crop and potential productivity of the environment.

COMPETITION AND EVOLUTION OF CULTIVARS

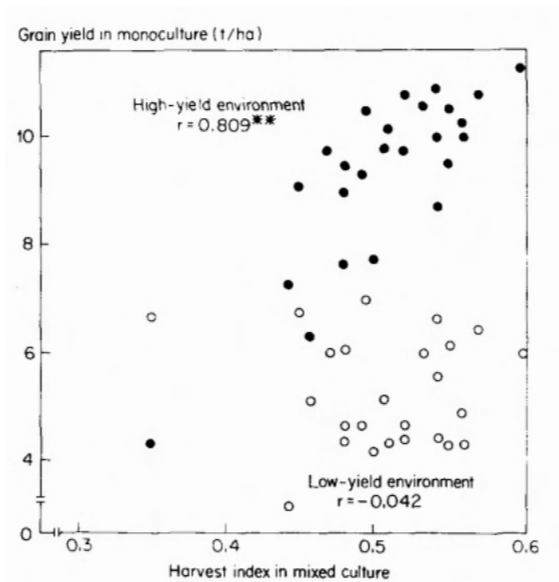
In separate experiments in high-yield environments, 25 genotypes of rice and 20 of cassava of different growth habits were mix-planted in alternate rows with a tester genotype. Yield data for each genotype were compared with those for the same genotype grown in monoculture. The competitive ability of each genotype was given as: yield in mixture - yield in monoculture.

In rice, competitive ability of each genotype in mixed culture was positively correlated with its straw weight in monoculture (r = 0.615**) and negatively with harvest index (r = –0.690**). The genotypes that performed well in mixed culture (defined as strong competitors) had high straw weight and low harvest index. In a low-yield environment, grain yield of each genotype in mixed culture was highly correlated with that of the same genotype in monoculture (r = 0.762**), but in a high-yield environment it was not correlated with grain yield (r = –0.034, Fig. 1). In contrast, in a high-yield environment the harvest index of each genotype in mixed culture was highly correlated with its grain yield in monoculture (r = 0.809**), but in a low-yield environment it was not (r = –0.042, Fig. 2). Thus, selection for harvest index is much more efficient than selection for grain yield itself if the selection target is high grain yield under a high-yield environment. When the objective is increased grain yield under a low-yield environment, selection for grain yield is efficient.

In cassava, competitive ability was highly correlated with stem and leaf weight of the same genotype in monoculture (r = 0.806**) and negatively correlated with harvest index of the same genotype in monoculture (r = –0.859**). Because harvest index is highly important to root yield, competitive ability was negatively correlated

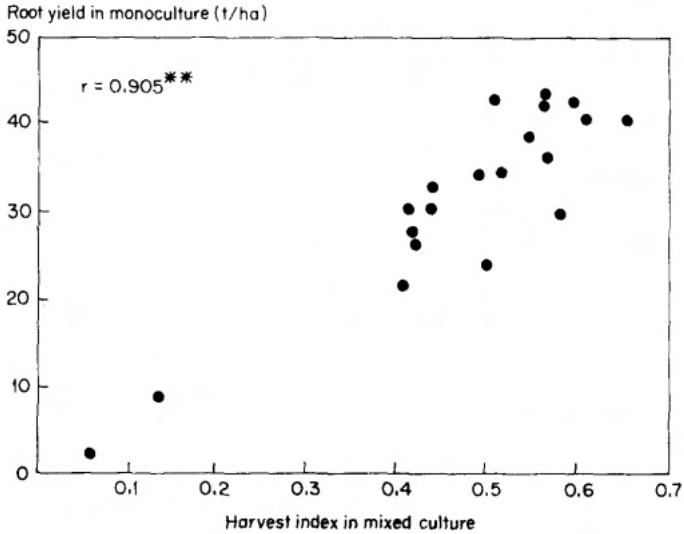


1. Relation between grain yield in mixed culture and that in monoculture of the same rice genotype in high- and low-yield environments.



2. Relation between harvest index in mixed culture and grain yield in monoculture of the same rice genotype in high- and low-yield environments.

with root yield in monoculture (r = −0.703**). Stem and leaf weight, a good indicator of the quantity of stem cuttings required for propagation in mixed culture, was negatively correlated with root yield in monoculture (r = -0.539**). Root yield in mixed culture was correlated with that in monoculture (r = 0.568**). However, harvest index in mixed culture was most closely correlated with root yield in monoculture (r = 0.905**, Fig. 3). Thus, selection for harvest index is more efficient than that for root yield itself when the objective is higher root yield. If genetically



3. Relation between harvest index in mixed culture and root yield in monoculture of the same cassava genotype.

mixed cassava populations are planted at random from available stem cuttings, genotypes with high competitive ability, but low yielding ability, would dominate after several cycles of plantings.

Because the essential part of intergenotypic competition occurs through competition for light interception by different rice genotypes (Kawano and Tanaka 1967, Jennings and Aquino 1968), the genotypes with a high harvest index are expected to be weak competitors because of the relatively fewer resources allocated for stem and leaf expansion. We generalize that genotypes with a high harvest index are weak competitors and those with large total plant weight are strong competitors.

In cassava and its wild relatives, roots are not an indispensable organ for reproduction because seeds and stems are the means of propagation. Cassava cultivars with higher productivity must have evolved mainly through improvement in harvest index because the species must have started from a harvest index near zero. Productivity was gained at the expense of competitive ability.

Seeds are the essential organ for reproduction in grain crops, even in their wild forms. Grain cultivars must have started to evolve from a harvest index higher than zero. Crops such as rice, wheat, oat, and peanut with higher productivity in high-yield environments must have evolved mainly through the improvement in harvest index at the expense of competitive ability.

Competitive ability is positively correlated with yielding ability in monoculture in field bean (CIAT 1977) and in maize (Kannenberg and Hunter 1972). In both crops, yield must have evolved through a delicate balance between improvement in harvest index and in competitive ability. In other grain crops yielding ability in low-yield environments must have evolved in a similar manner.

In the bulk population method of crop improvement, genetically mixed populations are exposed to natural selection. From the available data we speculate that the

method would result in rice genotypes that yield reasonably well in low-productivity environments, in cassava genotypes that yield poorly in medium- to high-productivity environments, and in field beans that may yield satisfactorily in low- or high-yield environments. Farmers' selection and propagation over thousands of years constitute a large-scale bulk population breeding program. Many old land varieties cultivated traditionally in the tropics resulted from this process; they perform quite respectably in their accustomed environments.

The competition studies cited were conducted in high-productivity environments. The present discussion may not be extended to intraspecific competition in low-productivity conditions. Thus, the interaction of competition factors with the adverse yield factors of low-productivity environments should be further studied to establish breeding strategies for these stress environments.

DISEASES AND PESTS

Among the factors that influence the productivity of environments, biological restraints, especially diseases and pests, contribute to low productivity. California, New South Wales in Australia, and the northern coast of Peru are known for extremely high rice yields, and the subtropical elevations of Colombia (Caicedonia) produce high cassava yields. These areas have fertile soil, excellent water management or favorable rainfall patterns, good agronomic practices, and very few disease or insect problems.

The rainfed rice area of Asia shows stagnant, low yields. Tropical American savannas are not suitable for successful cassava production. Physical factors contribute to the low productivity of such areas, and multiple disease and insect problems abound. Biological factors are most numerous and severe in low-productivity environments and are most accentuated within centers of crop origin. The major biological yield restraints in low-productivity environments are numerous and the crop genotypes interact with them in an extremely complex manner. The elimination of one or two pests through breeding would not result in successful cultivars for these difficult conditions. New strategies for multiple and stable pest resistance are needed, particularly for areas within centers of crop origin.

In a review of numerous cases of crop disease interaction, Robinson (1976) carefully distinguished between vertical and horizontal pathosystems. He concluded that vertical (non-rate-reducing, monogenic) resistance, frequently present in sexually propagated annual species, often results from plant breeders disturbing evolutionarily balanced systems. Nature, and less meddling by man, favored the development of horizontal (rate-reducing, polygenic) resistance in vegetatively propagated perennials. That suggests that vegetatively propagated perennial crops such as sugarcane and cassava are more easily bred for durable disease resistance. Durable, multiple resistance in sexually propagated annuals such as rice and field bean in less favored environments must come from exploitation of the rate-reducing resistance remaining in land varieties. Alternative strategies include the pyramiding of major genes in the development of genotypically diverse cultivars.

TRADITIONAL CULTIVARS

Traditional cultivars are genotypes that have been selected and grown for many years by farmers of a given region. They have stable performance and are in balance with their total physical and biological environment.

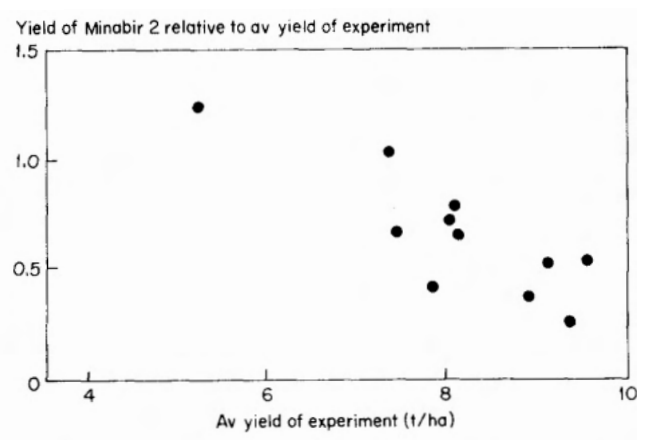
The relative productivity of traditional strains of rice and cassava was analyzed under different levels of environmental productivity. The grain yield of Minabir 2, a local rice cultivar of the northern coast of Peru, was compared with the total average yield of 25 genotypes, including many modern selections, in 11 environments. The relative yield of Minabir 2 was higher in low-yield environments (Fig. 4).

Valluna is a traditional cassava cultivar of the Valle region of Colombia; Manteca and Montero are traditional cultivars from the northern coast of Colombia. Llanera and Chirosa Yema de Huevo are traditional cultivars from the Llanos Orientales region of Colombia. Twenty-eight varietal yield trials, including the local cultivars, were conducted in these regions. The root yield of the traditional cultivars was compared with the total average yield of all varietal entries in each trial. The relative root yield of the traditional cultivars was highest in the low-yield environments (Fig. 5).

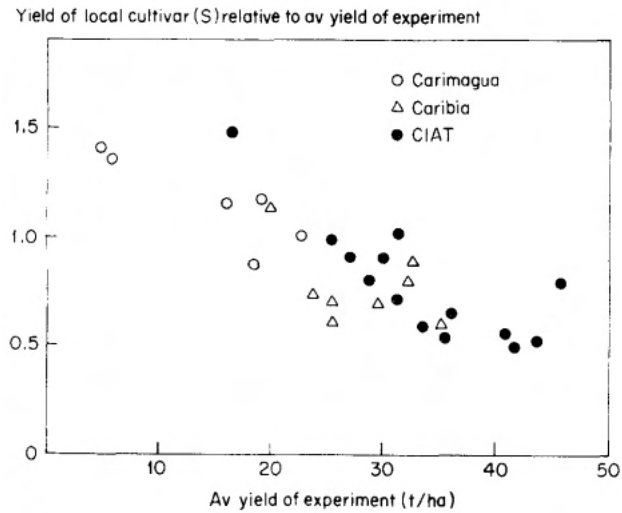
Traditional cultivars of rice and cassava (and perhaps all other crops) are successful under low-productivity conditions. In the past most farm conditions had low productivity by modern standards, and the ancient practice of bulk-population selection favored adaptation to low-productivity environments. Natural selection favored the accumulation of genetic resistance to diseases and pests and to an array of other physical stresses including soil, weeds, drought, and flooding. Thus, we confirm the direct usefulness of traditional strains under low-productivity environments and view such strains as elite sources of resistance for more modern varietal types designed for high-productivity environments.

CENTER OF ORIGIN AND PRODUCTIVITY

Man has domesticated plants and transferred them from their centers of origin to other continents. Purseglove (1968) and Jennings and Cock (1977) have shown that the principal production areas for many major economic crops are distant from the



4. Relation between yield level of cultural environment and relative yield of a traditional rice cultivar.



5. Relation between yield of cultural environment and relative yield of traditional cassava cultivars (Central International de Agricultura Tropical, Cauca Valley; Caribia, Northern Coast; Carimagua, Llanos Orientales).

regions in which they originated. The average yield figures for some important food and industrial crops show that, in general, crops yield better outside their centers of origin (Table 3).

Crops such as maize, soybean, barley, and potato, extensively cultivated in the more developed temperate countries, show the largest yield increases outside their centers of origin. All our major crops have their centers of origin in less developed areas of the world. The increase in yield of a crop that is grown outside its center of origin can be ascribed, in many cases, to the greater technology available in the developed countries.

Table 3. Yields of various crops within and outside their centers of origin (data from FAO 1977).

Crop	Center of origin	Within center of origin		Outside center of origin	
		Area planted (ha × 10^3)	Yield (t/ha)	Area planted (ha × 10^3)	Yield[a] (t/ha)
Wheat	West Asia	26,966	1.41	209,605	1.82 (129)
Rice	South Asia	84,199	1.85	58,909	3.31 (179)
Maize	Mexico through Andean region of Latin America	10,241	1.22	106,662	3.02 (248)
Barley	West Asia	6,592	1.33	87,383	2.05 (154)
Sorghum	Northeast Africa	5,841	0.70	45,894	1.33 (190)
Potato	Andean region of Latin America	615	8.20	17,869	14.41 (176)
Cassava	Northern South America	306	8.48	12,216	9.01 (106)
Groundnut	Southeast South America	124	0 94	17,872	0.96 (104)
Soybean	China	14,236	0.87	30,388	1.67 (192)
Field bean	Andean region of Latin America	6,079	0.50	21,821	0.60 (120)
Cowpea	Africa	5,035	0.20	135	0.70 (350)
Sugarcane	South Asia	4,923	47.62	7,784	58.74 (123)
Banana	South Asia	846	11.37	2,069	13.23 (116)
Coffee	Northeast Africa	656	0.27	7,266	0.48 (178)

[a]Numbers in parentheses express yield outside the center of origin as a percentage of that within.

Some tropical crop production — exemplified by sugarcane in South America, rubber in Malaysia, rice in Colombia and Peru, and cassava in Thailand — has been remarkably successful. These crops were transferred to places distant from their centers of origin. The successes, however, are limited to medium- to high-productivity environments with medium to high technology. In areas where the physical environment is extremely unfavorable (as in the case of upland rice production in Central Brazil) or where the production technology is very poor (e.g. rice in West Africa), crop production is very low even when the crop is carried far away from its center of origin.

In contrast, importation into the center of origin of specific crop technology developed outside it normally does not succeed. Importation of maize hybrids to the Andean zone and of Japanese or U.S. rice cultivars to tropical Asia are clear examples.

Crop species, including their weedy progenitors, existed within centers of origin for thousands of years before man developed agriculture and directed crop improvement toward his ends. The evolution of parasites followed a course parallel to crop evolution. Centers of crop origin are rich not only in varietal diversity, but also in variability of pathogens and pests. Jennings and Cock (1977) deduced that the principal areas of production of many important crops are located outside their places of origin mainly because crop yield losses due to insect and disease damage are greatest within such centers of crop origin.

Although crops outside their centers of origin are not free from insect and disease damage, the causal agents are fewer and the overall damage is easier to contain. However, there are several cases of massive disease attacks and crop losses to pests outside their centers of origin. They include coffee rust in Sri Lanka, the Panama disease of bananas in Central America, stem rust of wheat in North America, late blight of potato in Europe, *Sogatodes* feeding and hoja blanca virus on rice in the American tropics, and the Southern corn leaf blight epiphytotic in the United States (Jennings and Cock 1977). Most of these epidemics, however, including that in the Gros Michel banana, the Lumper potato, the rice cultivar Bluebonnet 50, and the Texas cytoplasm in maize, were induced by genetic crop uniformity. These examples of genetic vulnerability outside centers of origin resulted from human miscalculations and emphasize the importance of genetic diversity wherever crops are produced.

The massive biological. physical, and social restraints to productivity within centers of origin demand a comprehensive research program. These restraints, the inadequate capital investment for improving infrastructure, and the frequently limited research capability in these areas render difficult the task of overcoming stagnancy in food production within centers of origin.

Incomplete technological packages, inadequate within centers of origin, may dramatically increase food production outside centers of origin. This point is well illustrated by the new rice and wheat technology based on dwarfed cultivars that yield only about 0.5 additional t/ha in tropical Asia and the Middle East, but a portion of which adds 2 t/ ha to the yield of rice in tropical America and of wheat in Mexico. Although a technology related to improved yielding ability can be successfully tested outside centers of origin, a simple technological change is unlikely to succeed within centers of origin.

EXPERIMENT STATIONS VS FARMERS' FIELDS

One of the greatest difficulties in tropical agricultural research is the transfer of experiment station results to farm production. This difficulty also exists in temperate areas, but to a lesser degree.

In Japan, for example, there are 8 national agriculture experiment stations and 47 prefecture agriculture experiment stations. Each station has substations. The network covers most of the environmental variation found on farms. Scientists in developed temperate countries can aim at maximum crop productivity for most farmers. The technology thus generated often involves high input levels. Most farmers can apply the new technology and obtain yields that surpass those in experiment stations. Well-developed educational, social, and credit systems permit the farmers to respond to the recommendations by the experiment station. A yield increase of 10% is considered a significant technical advance for extension to farmers. Japan may be an overly specific case, yet the basic goal of research in temperate countries is the generation of maximum yield technology for each environment.

Brazil has about 23 times the area of Japan but it has fewer experiment stations. Yet, among the tropical countries, it has one of the most developed experiment station networks. The typical situation in the tropics involves a scattering of experiment stations over a large area and enormous environmental variability. Experiment stations tend to be located on the more fertile soils in the more favorable rainfall areas and they usually have irrigation facilities. The clients for research are the minority of influential farmers who produce high-value cash crops in favored environments. Most farmers grow traditional crops such as upland rice, beans, maize, or cassava in mixed associations on less fertile soils. They benefit little from research aimed at productive environments. Agricultural production infrastructure is normally insufficient to reach most of the farmers.

We suggest two reasons why experiment station technology is often ineffective.

1. The experiment station is not located in an environment representative of most farms.
2. The technology developed on experiment stations is unsuited to the needs of most farmers because it is generated with cultural practices atypical of most farms.

The cultivars developed with high fertilizer application and good water and weed control are inappropriate for low-productivity environments (Table 1) characterized by low soil fertility, irregular water and weed control, and complex disease and pest problems. The genotypes selected under chemical disease and pest protection are biologically unfit for low-productivity environments.

The CIAT (Centro Internacional de Agricultura Tropical) cassava program, aware of these factors, evaluates and selects genotypes in three environments:

1. The Cauca Valley fertile soil and favorable rainfall, an environment considered highly productive for cassava.
2. The tropical northern coast, a center of cassava production in Colombia that resembles many other cassava production areas, characterized by a wide range of cultural practices.

3. The Llanos Orientales, characterized by infertile Oxisols, representing a vast area of Latin American savannas.

Trials involving varieties and agronomic practices are conducted on experiment stations and farms in each of those areas.

The remarkable progress made by breeders in the Cauca Valley is indicated by the large difference in average yield between CIAT clones and local traditional cultivars (Table 4). This difference narrows considerably when the trials are conducted in farmers' fields, but CIAT clones remain superior. The decrease in the superiority of CIAT clones on farms is due partly to the excellent production systems developed for local cultivars on large farms. Yields of the newest CIAT clones now average 50 t/ha on farms and indicate the success of breeding for this highly productive environment which, however, represents only a tiny portion of cassava production in the tropics.

On the northern coast, cassava breeding progressed on the local experiment station and the CIAT clones consistently outyielded the local traditional cultivars (Table 5). The superiority of CIAT lines on farmers' fields is maintained with improved cultural practices (good land preparation. good preparation of planting stakes, and good weeding). However, it disappears totally on farms that use no improved cultural practices. There the traditional cultivars are best.

In the Llanos Orientales, breeding and selection at the experiment station progressed. The superiority of CIAT clones to traditional cultivars was greater with high-input technology (heavier lime application and irrigation) than medium-input technology (Table 6). The soils in this area are so poor that no meaningful yield can be obtained from either traditional strains or CIAT clones without soil amendments. In this low-yield environment, breeding would not advance without fertilizer application.

These data, although scanty, permit a generalization that agrees with our observation of plant breeding in the tropics: that the newly selected genotypes are superior on experiment stations using high-input technology while the improved genotypes are useless in traditional farmers' fields without any attendant improvement in technology.

Table 4. Cassava root yields of CIAT lines and traditional cultivars on experiment station and farms in the Cauca Valley of Colombia (high-yield environment).

Location	Root yield (t/ha)		Agronomic description of cultural environment
	CIAT lines[a]	Traditional cultivars	
Experiment station (CIAT-Palmera, 8-season av)	45.3	25.3	Fertile soil, favorable rainfall, good land preparation, good preparation of planting stakes, good weeding, no fertilizer application, no irrigation, no chemical application
Farms (Calcedonia, 5-yr av)	32.2	29.3	Same as above

[a] CIAT line, genotype selected or developed by the Centra Internacional de Agricultura Tropical Cassava program. Yield is av of upper 50% of all the ClAT lines tested. Data source: Agronomy and varietal improvement sections, CIAT cassava program (CIAT 1975. 1976, 1977, 1978, 1979; Kawano et al 1978a, b).

Table 5. Cassava root yields of CIAT lines and traditional cultivars on experiment station and farms in the northern coast of Colombia (low- to medium-yield environment).[a]

Location	Root yield (t/ha)		Agronomic description of cultural environment
	CIAT lines[b]	Traditional cultivars	
Experiment station (ICA-Caribia, 7-season av)	32.2	22.9	Medium fertile soil, long dry season, good land preparation, good preparation of planting stakes, good weeding, no fertilizer application, no irrigation, no chemical application
Farm fields with improved cultural practice (9-trial av)	17.6	11.6	Poor to medium soils, long dry season, good land preparation, good preparation of planting stakes, good weeding, no fertilizer application, no irrigation, no chemical application
Farms without improved cultural practice	7.3	8.4	Poor to medium soil, long dry season, poor or no land preparation, poor preparation of planting stakes, poor or no weeding, no fertilizer application, no irrigation, no chemical application

[a]Data source: Agronomy, Economics, and Varietal Improvement sections, CIAT Cassava program (CIAT 1975, 1976, 1977,1978,1979, 1980; Kawano et al 1978a, b). [b]CIAT line: genotype selected or developed by the Centro Internacional de Agricultura Tropical cassava program. Yield: average of upper 50% of all the CIAT lines tested.

Table 6. Cassava root yields of CIAT lines and traditional cultivars under high- and medium-input technologies on an experiment station in the Llanos of Colombia (low-yield environment).[a]

Location	Root yield (t/ha)		Agronomic description of cultural environment
	CIAT lines[b]	Traditional cultivars	
With high input technology (2-year av)	35.2	15.6	Infertile, acid soil, 4 months dry season, good land preparation, good preparation of planting stakes, good weeding, 2 t/ha of lime applied, 1 t/ha of 10-20-20 applied, frequent irrigation, no fungicide and pesticide applied
With medium-input technology (1 1-trial av)	20.2	14.7	Infertile acid soil, 4 months dry season, good land preparation, good preparation of planting stakes, good weeding, 0.5 t/ha of lime applied, 1 t/ha of 10-20-20 applied, no irrigation, no fungicide and pesticide applied

[a]Data source: Agronomy, Soil Science, and Varietal Improvement sections, CIAT Cassava program (CIAT 1975, 1976. 1977,1978,1979; Kawano et a1 1978a,b). [b]CIAT line: genotype selected or developed by the CIAT casava program, Yield: average of upper 50% of all the CIAT lines tested.

The data also suggest that the genotypes selected at experiment stations can be highly effective if a) the selection conditions resemble those of the target-area farms, and b) the farmers are able to upgrade their cultural practices to permit expression of genotype potential. Thus, to plant breeders, the crucial issue is the capability of

farmers to improve their cultural practices, which, in the case of cassava, include land preparation, selection of planting stakes, weeding, and fertilization for poor Oxisols as the basic requirements for the expression of higher productivity in new cultivars.

The data also raise the question: Can crop breeders improve yield in low-yield environments of traditional farms where the farmers are unable or unwilling to improve or change their cultural practices? Other studies demonstrate that the evolution of cultivars is accompanied by improvement in cultural practices, suggesting the difficulty of changing cultivars without changing crop agronomy (Oka and Chang 1964, Kawano et al 1974). Traditional strains resulted from natural and bulk selection over thousands of years. It is understandable that traditional cultivars have remained superbly adapted to their total environment for long periods with no major change. No strategy for the genetic improvement of traditional agriculture is available. Substantial change in cultivar type would require an equivalent change in crop husbandry. A minor change at minimum yield levels would be unnoticeable to both the scientist and the farmer.

Traditional farmers produce crops for their own subsistence. They are more concerned about crop failure than about a modest yield increase. Consequently, subsistence farmers are most conservative. Convincing them to adopt new cultivars necessitates demonstrating the large yield advantage of modern cultivars under their farm conditions. While the yield of new cassava materials may increase by 50-100% on farms of medium- to high-level technology, a yield gain would be extremely difficult to obtain on traditional farms. The paradox is that we can produce a quantum yield advance for rice farmers, for whom a small increase would suffice, but we cannot create a small improvement for poor farmers who theoretically would benefit most from large yield increases.

Very little scientific attention has been given to the improvement of traditional farms. Our understanding is too scanty to justify abandoning attempts to improve productivity through plant breeding. Nevertheless, improvement of the traditional low-yield agriculture in the tropics is more logically a task for production agronomists.

Large interactions between genotypes and geographical areas introduce an additional complication in tropical crop breeding. Such interactions have been the subject of much study and are relatively easy to understand. Careful description of the target area and careful location of experimental sites are the best solution to the problem. However, the interaction between genotype and technology level is difficult to quantify, less scientifically attractive, and more dependent on socioeconomic factors. Our inadequate understanding of this type of interaction prevents us from defining a comprehensive strategy of breeding and selection, particularly for low-yield environments in the traditional agricultural sector.

SUCCESS AND FAILURE

A review of modern crop breeding would indicate unquestionable Success in some areas and failure in others.

The early rice breeding work at IRRI is one of the few notable successes in tropical

crop breeding. The success stemmed from the strategy of concentrating research on high-yield environments with good water control, nitrogen fertilizer application, and selection for high-harvest-index types having short stems, erect leaves, and photoperiod insensitivity (Jennings 1964, 1974; Tanaka et al 1967; Chandler 1969). Rice genotypes with a high harvest index are productive under high-yield environments but not under low-yield environments (Table 1). Human and natural selection evolved many venerable strains well adapted to traditional low-input technology. These rices are tall, vigorous, low-harvest-index types. Selection for harvest index was not practiced by farmers. Similarly the bulk population breeding method would discriminate against genotypes with a high harvest index because of their low competitive ability. Thus, advance in rice breeding depended upon finding a plant character that would be productive in the target area but had not been uncovered in the farmers' practice of bulk selection. The character used was a simply inherited dwarfism of stems and leaves.

The great success of the wheat breeding program in Mexico may be interpreted in the same manner. The small-grain achievements, however, are largely confined to areas with good water control and high fertilizer application. Yield increases have been higher outside the center of origin than inside. The inability to increase yield under low-yield environments is readily explained by the complete difference in the physiological factors related to high yield between high- and low-yield environments (Table 1). A distinct breeding strategy for low-yield rice and wheat areas requires an assessment of the different yield restraints and a search for distinct genotypes to overcome them.

In cassava, harvest index is the critical trait for high yield in medium- to high-productivity environments where medium to high technology is available. Improved harvest index did not usually result from long-term natural and farmer selection. Thus, progress in modern cassava breeding in favored environments should result from attention to harvest index (Kawano et al 1978a, b). The process, however, would be lengthy because the crop is propagated vegetatively, and has low multiplication rate and low economic value.

Because harvest index is also important for cassava production under low-yield environments, breeders should be able to make some progress in such areas, although progress appears to be extremely difficult to achieve on farms with no improved cultural practices.

The case of tropical maize is confounded by the added complexities of genetic manipulation of populations. Increased economic yield in maize is related to an increase in total biological yield. In temperate favored environments, maize is successful as a result of vigorous single- and double-cross hybrids. These genetically uniform populations were unknown during the domestication of maize. This success cannot be repeated on small farms in the tropics because: 1) precise husbandry of genetic populations is difficult on small farms, 2) the yield restraints and agronomy in maize-growing areas differ from the cultural conditions in maize research stations, 3) open-pollinated maize in low-productivity environments was milked dry by farmers during thousands of years of bulk selection, leaving little scope for modern breeders, and 4) hybrids lack the genetic variability to tolerate the multiple stresses of low-yield environments.

Field beans were domesticated in the Andean zone and have been a major component of the human diet there for thousands of years. Variability and adaptability to diverse local environments are evident in the collections of traditional cultivars found from Mexico to Chile. In this crop total biological yield is highly correlated with competitive ability and grain yield under a wide range of environments. That suggests that breeders must work fundamentally in the same path of natural and farmer selection. Hence, modern efforts to improve the yield may represent only a fraction of what has been achieved during thousands of years. Consequently, a quantum jump in yielding ability is not likely.

We cite sugarcane, apart from the mentioned major food crops, as a superb example of breeding success. This crop is among the highest in dry matter production per unit area per unit time. Especially in the American tropics, dry matter production is highly efficient on millions of hectares, largely in the absence of major disease or pest problems. Sugarcane is managed as a plantation crop on high fertile lands with good water control, heavy fertilizer application, and good cultural practices. It appears that intelligent plant breeding successfully managed the relatively uncomplicated physical and biological yield constraints in this high-value cash crop whose main production areas are now concentrated far from the center of origin.

Progress in tropical crop breeding has been confined to medium- to high-productivity environments with medium to high technological investments. No crop breeding program has significantly contributed to the traditional farming situations in low-productivity environments. Attempts to extend technology developed in high-productivity environments to low-productivity environments have failed.

EASY AND DIFFICULT CASES

Apart from the factors already described, which control the degree of difficulty of plant breeding in the tropics, there are others that are more generally understood. Genetic materials of vegetatively propagated crops are the easiest to handle, those of sexually propagated crops are more complicated, and those of outcrossing crops are the most difficult. The physiological yield formation of root and tuber crops is the simplest because the sink-source relation is fairly straightforward and there is no danger of lodging caused by overfilling the sink. In this connection, crops such as sugarcane or oil palm have the same advantage. Cereal crops are more complex because the time factor complicates the sink-source relation and yield components are more numerous. Grain legumes are among the most difficult because of the added factor of the balance between protein and carbohydrate synthesis. Table 7 summarizes these factors according to their contributions to the difficulty of plant breeding.

THE CHALLENGE

The major research efforts in tropical crop breeding have been concerned with development of high-yielding cultivars for high-yield environments with high technology levels partly because of the tradition of agronomic research in temperate

Table 7. Schematic description of degree of difficulty in tropical crop breeding.

Factor related to breeding work	Breeding is	
	Less difficult	More difficult
Productivity level of environment	High	Low
Level of cultural practice	High	Low
Center of origin	Outside	Inside
History of production	Short	Long
Kind of crop (complexity of physiological yield factor)	Root/tuber crop	Legume grain crop
Kind of crop (possibility of further improvement)	Harvest index being yield-limiting factor	Total biological yield being yield limiting factor
Kind of crop (complexity of pest interactions)	Evergreen perennial with vegetative propagation	Annual with sexual propagation
Kind of crop (ease of cultivar replacement)	Seed propagation	Vegetative propagation

areas and also because measurable research results can be expected in a short time. In several instances, this strategy has been successful. Examples of potential success include high-technology cassava production for animal feed in Asia or cassava farming with massive inputs for alcohol production in Brazil.

In some instances, research for high-productivity environments has fulfilled its primary mission, and a continuing strategy of research priority for these environments is debatable. Most arable lands in the tropics have infertile soils and irregular water supply. The underlying philosophy in agronomic research in temperate areas has been to convert unfavored environments into highly productive ones. Low-productivity environments in the tropics may be upgraded but only with immense investment in irrigation, drainage, and fertilizer application. The capital for such investment is rarely available. Hence, more research attention is needed for moderate and stable yields under less favorable environments. Important examples include Asian rainfed rice and Andean maize and field beans.

The first requirement is a careful analysis and definition of target areas in climatic, soil, biological, and socioeconomic terms. The most critical determination is the level of cultural practices or technology within the reach of most farmers in each target area. Experiment sites within each target area are required. The research organization that assumes world responsibility for the crops should be located in the principal center of origin.

Experimental plot management should not exceed the cultural practices within the reach of average farmers. Impractical and cosmetic plot protection, including pesticides and excessive water or weed control, should be eliminated. The major selection criterion should be overall performance within a given environment.

Selection for individual traits is used to reinforcegeneral adaptability. Extensive use of land cultivars from each target area is a necessary component of the broad germplasm variation in hybridization programs.

The pedigree method of selection is falling into disfavor largely because the cost of accommodating a desired volume of segregants is prohibitive. There is renewed interest in modified bulk population breeding for specific environmental complexes as a substitute for pedigree selection.

We take issue with the belief that a widely adapted cultivar confers stable yield. A farmer is not interested in wide adaptability. His concern is stable yield on his farm. More important is stability of performance over seasons within each target area. Multilocational testing identifies tolerance for important disease and pest problems that are sporadic in any single location. The physical rotation of segregating populations among relatively similar environments may permit identification of tolerances for subtle but cumulatively massive physical and biological yield restraints.

Finally, we are confronted with the most difficult question of whether the breeder can serve those traditional farmers who cannot improve their cultural practices. That is primarily a socioeconomic issue and even among agriculturists, it is primarily a concern of agronomists. It is extremely difficult for breeders to contribute to the improvement of this situation because most of the possible improvement might have been done by farmers already. One approach that farmers may not have exhausted, however, is use of wide and multiple crosses among varied germplasm sources. Thousands of multiple crosses in one year at one location may be equivalent to natural crossing over many years at many locations. That, combined with modified bulk selection, may be our only realistic approach to the lowest yielding situations.

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GROWTH AND YIELD OF FIELD CROPS

RICE

S. Yoshida

Compared to other C-3 species, rice has a relatively high leaf photosynthetic rate, ranging from 40 to 50 mg CO_2 dm^2 per hour. Leaf orientation is closely correlated with culm length; more erect leaves are associated with shorter culm length. A rice crop can attain maximum leaf area index (LAI) values of 10 or higher when planted at close spacingand with high nitrogen levels. Crop growth rate (CGR) reaches maximum at LAI of about 6 for IR8, an improved variety. and about 4 for Peta, a tall traditional variety. No optimum LAI exists.

The maximum CGR is usually around 30-36 g m^2 per day in the Philippines and in Japan. Harvest indices of improved semidwarf indica varieties are around 0.45-0.55; those of japonica varieties are around 0.4-0.49. Maximum recorded yields of rice are 13.2 t/ha for Japan and 17.8 t/ha for India.

Using the data on harvest index and the maximum recorded grain yield, total dry matter production per crop is estimated at 22.7 t/ha for Japan and 30.6t/ha for India. Efficiency of absorbed nitrogen to produce rice grains is estimated at 50 kg rough rice/kg N absorbed, regardless of yield level and planting time. Nitrogen recovery percentages usually range from 30% to 50% in the tropics. Combining these 2 gives fertilizer efficiencies of 15 to 25 kg rough rice/kg N applied.

Under most conditions, spikelet number per square meter appears to be the major factor limiting rice yield. But when the yield potential of varieties with different grain size is to be compared, the product of spikelet number per square meter and weight per grain is a measure for agronomic sink size.

Growth and yield of rice are climatically controlled. Temperature affects rate and duration of growth and development, solar radiation largely determines productivity, and rainfall determines the rainfed rice crop period and stability in the tropics.

Potential rice yields can be estimated by a formula based on

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effective grain-filling period, photosynthetic efficiency, and incident solar radiation. For the same level of daily incident solar radiation, the temperate regions are more productive than the tropics because of a longer duration of grain filling. However, annual productivity is higher in the tropics than in the temperate regions because more crops can be harvested in the tropics if irrigation water is available.

This paper discusses selected topics of rice crop physiology as they relate to productivity.

Recent taxonomic revisions recognize 20 species for the genus *oryza* of the tribe oryzeae of the family *Gramineae,* but only two are cultivated — *Oryza sativa* and *O. glaberrima.* The dominant rice species *O. sativa* is believed to have originated in the region including northeastern India, northern Bangladesh, the triangle adjoining Burma, Thailand, Laos, Vietnam, and southern China (Chang 1976). It is cultivated today in Asia, Africa, Europe, North America, Central America, South America, and Oceania. The other cultivated species, *O. glaberrima,* originated in Africa but is being rapidly replaced by *O. sativa.* The two cultivated species show small morphological differences but hybrids between them are highly sterile. *O. sativa, O. glaberrima,* and their wild relatives are diploids (2n = 24). More than half of the wild species are tetraploids (2n = 48).

The rice plant is highly adaptable to environment. And man has succeeded in modifying the environment, so that rice can now be grown in widely different locations and under a variety of environments. Geographically, rice is grown in northeastern China at latitude 53° N, in Central Sumatra on the equator, and in New South Wales, Australia, at latitude 35° S. It is grown below sea level in Kerala, India. at sea level in many rice-growing areas, and at elevations above 2,000 m in Kashmir and Nepal. It can be grown under dryland conditions, moderately submerged conditions, and in 150 to 500 cm of water (Yoshida 1977).

Asian rice *O. sativa* is often divided into japonica, indica, and javanica ecological groups. Japonica rice, adapted to cooler areas, is widely grown in temperate countries such as central and northern China, Korea, and Japan. Indica rice is widely grown in tropical regions such as South and Southeast Asia. Both indica and japonica rices also can be grown in subtropical regions such as Taiwan. Javanica rices are the tall, large, and bold-grained bulu varieties of Indonesia. Bulu varieties have spread from Indonesia to the Philippines, Taiwan, and Japan.

The distribution of indica and japonica rices in the tropical and temperate regions is primarily determined by their different responses to temperature and day length. The northerly movement of japonica rices has been made possible by their insensitivity to day length, early maturity, and increased tolerance for low temperature. When grown in the tropics, most japonica rices flower so early and cannot have sufficient vegetative growth so that low yields result. However, ponlai rice developed in Taiwan is well adapted to tropical and subtropical climates (Huang et al 1972).

Recently, crosses between semidwarf indicas and japonicas have grown successfully in South Korea (Kim 1978). The crosses are insensitive to day length and mature early. They grow well in both temperate and tropical regions (IRRI 1980).

Even in the tropics, temperature goes down with increased altitude. In the southwest of China, indica rice is grown in low-altitude areas and japonica rice is grown in high-altitude areas. Both indica and japonica rices are grown at intermediate altitudes (IRRI 1978).

CROP PHOTOSYNTHESIS AND DRY MATTER PRODUCTION

Leaf photosynthetic rate

Rice is generally believed to have a C-3 photosynthetic pathway (Ishii et al 1977b). A report suggests, however, the operation of both C-3 and C-4 pathways in a salt-tolerant indica variety (Hegde and Joshi 1974). As a C-3 plant, rice has a high CO_2 compensation point (Ishii et al 1977c), exhibits photorespiration (Akita and Miyasaka 1969; Ishii et al 1977a, c), and lacks bundle sheath chloroplasts (Akita et al 1969). Compared to other C-3 species, rice has a relatively higher net photosynthetic rate per unit of leaf area. Within *O. sativa,* indica rices have a higher optimum temperature than japonica rices (Osada 1964).

Early studies on rice photosynthesis reported a leaf photosynthetic rate of 10-20 mg/dm^2 per hour, but recent studies indicate a rate of 40-50 mg CO_2/dm^2 per hour. This difference can be attributed primarily to improvements in the measuring technique (Yoshida and Shioya 1976). In early studies on rice photosynthesis, the CO_2 exchange rate was measured by enclosing several cut leaves in a plastic chamber. Later studies use an intact leaf.

Leaf photosynthetic rate in rice is well correlated linearly or curvilinearly with leaf nitrogen or protein content. When rice plants are subjected to nitrogen deficiency, the stomatal resistance of the leaves, particularly that of the lower leaves, increases sharply, indicating that the stomatas are closed to a considerable degree. This increased stomatal resistance is associated with a decrease in photosynthetic rate (Yoshida and Coronel 1976).

Other green tissues in rice, such as leaf sheaths and panicles, are considered nonphotosynthetic because their gross and net photosyntheses are extremely small (Tsuno et al 1975, Yoshida and Cock 1971).

Leaf orientation

Leaf orientation is an important parameter determining light environment within a crop canopy (Monsi and Saeki 1953). Leaf orientation is related to foliar absorption coefficient (K), which is defined as:

$$\ln \frac{I}{I_o} = -KF \tag{1}$$

where I_o is light intensity incident on the leaf canopy, I is light intensity in the crop stand, and F is average cumulative total leaf area per unit of ground area. F is zero at the top of canopy and takes its maximum value at ground level, a value generally referred to as leaf area index (LAI).

Measured K values for rice varieties range from 0.3 for erect leaves to 0.8 for droopy leaves (Hayashi and Ito 1962, Tanaka et al 1966). The foliar absorption coefficient is negatively correlated with specific leaf area and the average leaf angle of the upper three leaves when measured from the horizontal plane and weighted for

the area of each leaf (Hayashi and Ito 1962). Culm length is negatively correlated with the average leaf angle of the upper three leaves. As a consequence, culm length is positively correlated with the foliar absorption coefficient. In other words, leaf erectness in rice is closely correlated with culm length.

Leaf area index and dry matter production

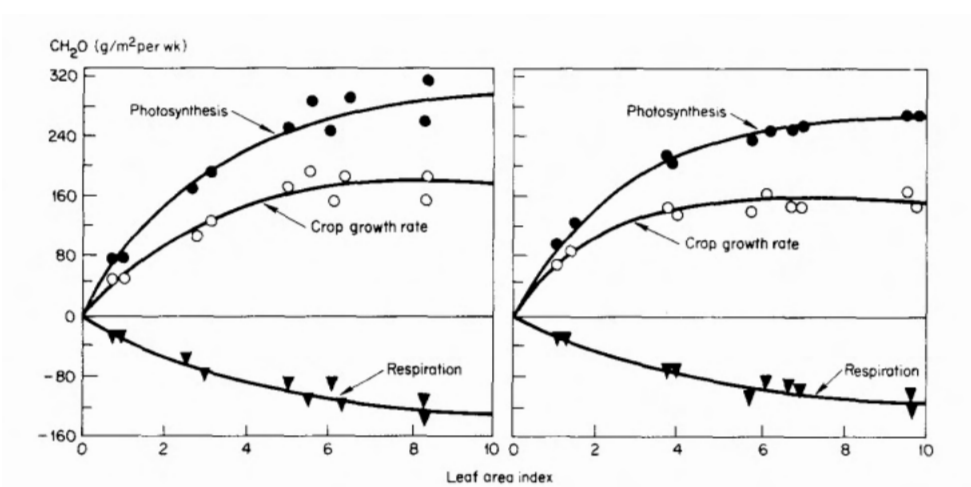
The LAI of a rice crop increases as growth advances and reaches maximum at around heading, when the rice plant has its five largest leaves. After heading, LAI declines as the lower leaves die. A rice crop planted at close spacings and with high nitrogen levels can attain maximum LAI values of 10 or greater (IRRI 1970).

Whether there is an optimum LAI for net dry matter production has been widely debated (Yoshida 1972). A reexamination of the relationship between LAI, respiration, and crop growth rate (CGR) indicates that there is no optimum LAI for CGR (Cock and Yoshida 1973). CGR reaches maximum at a LAI of about 6 for IR8 and about 4 for Peta. Beyond that the growth rate remains the same despite any further increases in LAI (Fig. 1). The LAI at which CGR reaches maximum may be called a critical LAI.

Crop respiration increases curvilinearly with increases in LAI, and is closely related to gross photosynthesis. It is about 40% of gross photosynthesis over a wide range of values for LAI and leaf area ratio until 2 weeks after flowering (Cock and Yoshida 1973).

Crop growth rate

The maximum CGR of rice is around 30-36 g/m^2 per day in the Philippines (Yoshida and Cock 1971) and in Japan (Murata 1975). An unusually high value of 55.4 g/m^2 per day has been reported by Tanaka et al (l966) for variety Fujisaka 5 grown under a solar radiation of 564 cal. cm^2 per day in the Philippines. Monteith (1978) questioned whether this value was distorted by a large sampling error.



1. Photosynthesis, crop growth rate (X 0.9) and respiration of IR8 (left) and Peta (right) during the 4 weeks before flowering (Cock and Yoshida 1973).

One way to examine reported CGR values is to use solar energy use efficiency. Solar energy use efficiency is usually defined as:

$$E_u = \frac{K \times \Delta W}{\Sigma S} = \frac{K \times \Delta W}{S \times T} \times 10^{-4} \tag{2}$$

where K= heat of combustion (cal g), ΔW= dry matter increase (g/ m^2), ΣS=total amount of incident solar radiation (cal/m^2), S = average daily incident solar radiation (cal/cm^2 per day), and T = number of days. When T is substituted for 1 in equation (2). ΔW becomes dry matter increase per m^2 per day, which is CGR. CGR can be estimated if E_u S, and K are known, as in:

$$\text{CGR (g m}^2\text{ per day)} = \frac{E_u \times S}{K} \times 10^4 \tag{3}$$

The maximum E_u value recorded in Japan is 3.75 (Murata et a1 1968). This value was not reproduced in the subsequent, more comprehensive 5-year experiment of the Japanese International Biologica1 Program (JIBP) from 1967 to 1971. In JIBP trials at 8 experiment stations, the highest recorded E_u values ranged from 2.83% to 3.32% with a mean of 3.00% (Kanda 1975). Using 3.005 for E_u and 3,750 cal g for K, we can estimate the maximum CGR for the Tanaka et a1 experiment as:

$$\text{Maximum CGR} = \frac{0.03 \times 564}{3{,}750} \times 10^4$$
$$= 45.1 \text{ g m}^2 \text{ per day} \tag{4}$$

The E_u value is expected to decrease with increasing levels of incident solar radiation. Therefore, a CGR of 55.4 g/m^2 per day is considered exceptionally high for rice.

Harvest index and total dry matter production

Economic yield can be related to total dry matter production by harvest index (HI). In rice, the HI is usually calculated as the ratio of dry grain weight to total dry matter weight (dry panicle weight plus straw weight). Root weight is usually neglected in computing total dry weight.

The HI for rice is negatively correlated with plant height (Tanaka et a1 1966) and with culm height (IRRI 1977). It is modified to some extent by nitrogen levels. Mean HI of 1 I varieties for 3 nitrogen levels ranged from 0.28 for Peta (culm length = 128 cm) to 0.57 for IR747B2-6 (culm length= 53 cm). The low HI for Peta is partly the result of lodging before maturity (IRRI 1977).

The HI of improved semidwarf indica varieties are 0.45-0.55. HI of japonica varieties ranged from 0.40 to 0.49 (calculated from Table 1.2-4, Murata 1975).

HI vary with variety and environment. HI of 5 varieties grown in South Korea, Taiwan, Philippines, and India ranged from 0.45 to 0.50 with an average value of 0.47 (IRRI 1980).

Whether the HI decreases with an increase in total dry matter production is not clear. In one example, brown rice yield *(Y)* is related to total dry matter production *(W)* as:

$$Y = 0.631\ W^{0.901} \tag{5}$$

This relationship holds up to 10 t rough rice/ha (Kiuchi et al 1966), implying that the HI decreases slowly with increasing total dry weight. However, records of high-yielding crops indicate that high rice yields are achieved by increasing total dry weight and by maintaining a high HI (Shiroshita et al 1962).

Data on total dry matter are not always available from agronomic experiments, particularly for high yielding crops. Estimated total dry weight can be obtained from the data on grain yield and HI. The maximum recorded rice yield is 13.2 t/ha in Japan and 17.8 t/ha in India. Assuming the HI is 0.50 and grain yield is measured at 14% moisture, the estimated total dry weight per crop would be 22.7 t/ha for Japan and 30.6 t/ha for India.

NITROGEN REQUIREMENTS

Under most conditions, nitrogen is the first limiting nutrient for rice. Fertilizer nitrogen applied to soil is absorbed and used for grain production. Efficiency of fertilizer nitrogen can be formulated as:

$$\text{Efficiency of fertilizer nitrogen (kg rice/ kg applied N)} = \text{efficiency of absorption (kg absorbed N/kg applied N)} \times \text{efficiency of utilization (kg rice/ kg absorbed N)} \quad (6)$$

The ability of absorbed nitrogen to produce grains or straw vanes with the growth stage at which the nitrogen is absorbed. This is called partial productive efficiency (Kimura and Chiba 1943). When total nutrient uptake is examined for field crops, the amount of grain produced per unit of nitrogen absorbed is very similar among crops with low and high yields and among crops grown in different years (Table 1).

Table 1. Removal of nutrients by rice crops in the tropics and in Japan.

Place, variety	Yield (t/ha)	Nutrient removal (kg/t rough rice)		
		N	P	K
Tropics (IRRI)				
IR8 [a]	8.7	18.9	5.2	35.5
Peta [a]	6.1	23.5	5.7	50.6
IR36 [a]	6.2	22.3	35	21.9
IR50 [b]	6.6	18.8	3.5	21.1
IR19743-25-2-2 [b]	6.2	19.0	3.2	25.2
IR9752-71-3-2 [b]	6.8	20.3	3.2	20.3
3 varieties × 4 crops average [c]	4.7	19.0	4.3	47.0
Mean		20.3	4.1	31.7
Japan [d]				
Japan No. 1 contest winner (Mr. Kitahara 1958)	12.8	1.5.2	3.4	21.7
14 agricultural experiment stations (av)	5.3	17.0	3.8	22.2
Mean		16.1	3.6	22.0

[a] 1968 dry Season crop, IRRI. [b] 1980 dry season crop, IRRI. [c] Tanaka et al (1964).
[d] Calculated from Yamazaki (1966) using a factor of 1.25 to convert brown rice yield to rough rice yield.

The amounts of nutrients absorbed to produce 1 t rough rice in the tropics are about 19-24 kg nitrogen with a mean value of 20.3 kg, 3-6 kg phosphorus with a mean value of 4.1 kg, and 20-50 kg potassium with a mean value of 31.7 kg. Similar amounts are shown for moderate and high-yielding crops in Japan.

Despite large differences in yield, removal of the three nutrients, particularly of nitrogen, by moderate- and high-yielding crops is similar. Dividing 1 t rough rice by a nutrient removal value gives the efficiency of absorbed nutrient (kg rough rice per kilogram nutrient absorbed). The nitrogen removal value for the tropics is about 20 kg; hence: nitrogen use efficiency is about 50 kg rough rice/kg absorbed N. Nitrogen use efficiency for Japan is about 62 kg rough rice/kg absorbed N.

On the other hand, efficiency of absorption or percentage of nitrogen recovery varies to a much greater extent, depending on soil properties, methods, amounts, timing of application, and other management practices. Recovery of applied nitrogen varies from 30 to 50% in the tropics (Prasad and De Datta 1979). The percent recovery of applied nitrogen tends to be high at low levels of nitrogen application and when nitrogen is topdressed at later stages of growth. Using values for efficiency of absorption and efficiency of utilization, we get

$$\begin{aligned}\text{Efficiency of fertilizer nitrogen} &= 0.3 \sim 0.5 \times 50 \text{ kg rice/kg absorbed N} \\ &= 15 \sim 25 \text{ kg rice/kg applied N}\end{aligned} \tag{7}$$

These values for efficiency of fertilizer nitrogen are common in agronomic experiments (Prasad and De Datta 1979).

Grain yield (Y) can be divided into two parts with respect to nitrogen source: yield obtained without fertilizer nitrogen (Y_o) and yield increase obtained with fertilizer application ($\mathrm{D}Y_F$).

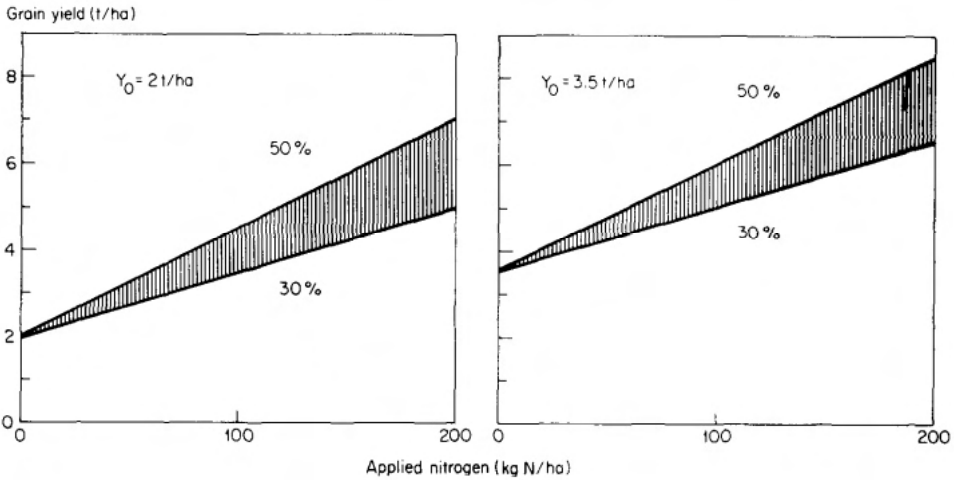
$$Y = Y_o + \Delta Y_F \tag{8}$$

$$Y = Y_o + (\text{efficiency of fertilizer nitrogen}) \times N_F \tag{9}$$

where N_F is the amount of nitrogen applied (kg/ha) and Y_o represents the nitrogen fertility level of the soil. Y_o varies with soil and perhaps with variety. To simplify the problem, we shall assign 2 values, 2 t/ha and 3.5 t/ha to Y_o • Y_o = 2 t/ha perhaps represents the average nitrogen fertility level of paddy fields and Y_o = 3.5 t/ha, a high fertility level. The yield increase obtained by fertilizer application can be computed from the second term of equation 9.

Grain yield is determined by soil fertility level, amount of nitrogen applied, and percent nitrogen recovery (Fig. 2). At Y_o = 2 t/ha, 50 kg of fertilizer nitrogen can produce yields of 2.7 to 3.2 t/ha, and a minimum of 160 kg N is needed to produce 6 t rice/ha. These computations illustrate the relationship between target yield and minimum fertilizer requirement. Long-term fertility experiments indicate that the average amount of biologically fixed nitrogen is about 50 kg N/ha (Watanabe et al 1979). This amount of nitrogen corresponds to a rice yield of 2.5 t/ha.

In actual nitrogen response, the relationship between yield and fertilizer nitrogen is not linear but curvilinear. Efficiency of absorption tends to decrease with increase in nitrogen application and a crop may bend or lodge at high levels of nitrogen



2. Simplified models of the relationship between fertilizer nitrogen and rice yield, with 30% and 50% as minimum and maximum values for nitrogen recovery.

application and hence, yield less increase per unit amount of applied nitrogen. These limitations can be eliminated by improving technology or variety.

YIELD AND YIELD COMPONENT ANALYSIS

In temperate regions. one or two rice crops can be grown annually. In the tropics, three to four crops a year are possible if irrigation is available. Productivity of rice yield can be compared three ways: on a per-crop basis, on a daily production basis. and on an annual production basis. Production per day is more meaningful than yield per crop when year-round rice cropping is practiced or when rice is one component of an annual multiple cropping system.

Yield

Yield per crop. National average rice yields range from about 1 t/ ha or less for some African countries to about 6 t/ha for Japan, Korea, and Australia.

The maximum recorded yield per crop in Japan is 10.5 t brown rice/ ha, which is equivalent to 13.2 trough rice/ha (Agricultural Policy Study Commission 1971). In the tropics, IR24 produced 11.0 t/ha at IRRI in the dry season (IRRI 1973) and IR8 yielded 10.7 t/ha at Battambang, Cambodia (Hirano et a1 1968). In India, the maximum recorded yield is 17.8 t/ha in Maharashtra State (Suetsugu 1975). Records on high rice yields in Japan and India indicate that 10 t/ ha or greater is achieved somewhere every year.

Yield per day. Yield per day is normally around 50-1 00 kg/ ha in the main field. It appears to be inversely related to growth duration: the shorter the growth duration, the higher the yield per day (IRRI 1977). A high daily production of 106 kg/ha was recorded for early-maturing selection IR747B2-6 planted at 10- × 10-cm spacing in the dry season. Apparently daily production is high when solar radiation is high (Yoshida et a1 1972).

Yield per year. In the Philippines, a total of 25.7 t / ha in 335 days was recorded for 4 crops (Yoshida et a1 1972b). However the 3-year average in the same experiment was 23.7 t ha. Year-round continuous rice cropping, called rice garden, is now under way at several sites in the Philippines. The annual rice production by rice garden was 23.6 t ha at Los Baños, Philippines (Morooka et al 1979).

Yields per year in the temperate region and the tropics ranged from 6.5 t ha for Hokkaido, Japan (43°N) to 10.9 t/ ha for Kagawa, Japan (34°N), to 15.3 t ha for Okinawa, Japan (27°N), to 23.7 t/ ha for Los Baños (14° N) (Yoshida 1977). Annual production increased with an increasing number of rice crops per year. The data indicate that potential annual productivity is much higher in the tropics than in the temperate region. In practice, continuous rice cropping may not be advisable because it can cause severe disease and insect problems. However, the tropical environment provides great flexibility in planning rice production.

Yield components

An examination of yield components for a given rice crop provides a way to analyze the components limiting yield and suggests ways to increase yield (Matsushima 1970, Murata 1969, Murata and Matsushima 1975, Yoshida 1972, Yoshida and Cock 1972a. Yoshida and Parao 1976).

The grain yield of a rice crop can be expressed as:

$$\begin{aligned}\text{Grain yield (t ha)} &= \text{panicle number/m}^2 \times \text{spikelet number/panicle} \times \text{\% filled spikelets} \times \text{1,000-grain weight (8)} \times 10\text{-}5 \\ &= \text{spikelet number m}^2 \times \text{\% filled spikelets} \times \text{1,000-grain weight (g)} \times 10\text{-}5 \qquad (10)\end{aligned}$$

The panicle number per square meter can be varied by varying plant density and tillering performance. But beyond a certain density, correlations are negative between panicle number per square meter and spikelet number per panicle. Spikelet number per square meter, the product of the two components, is determined by the potential of a variety, the environment. and nutrition.

Most rice varieties have only one floret per spikelet. Modern wheat varieties may set four or more florets per spikelet.

The yield components limiting rice yield are location-specific (Yoshida and Parao 1976). Under most conditions and with good management, spikelet number per square meter is likely to be the major limiting factor. In an experiment using IR8 at Los Baños, the percentage of filled spikelets and the 1,000- grain weight are about the same, regardless of spikelet number per square meter and crop season. Grain yield correlated linearly with spikelet number per square meter (Yoshida et a1 1972a).

When IR747B2-6 at 10- X 10-cm spacing with 100 kg N/ha was planted year-round at Los Baños, yields of 19 crops ranged from 4.6 to 7.1 t/ ha. Spikelet number per square meter alone explained 60% of the yield variation. The combination of all yield components accounted for 81% of the yield variation, and filled spikelet percentage and grain weight together accounted for 21%. If the contribution of all yield components is taken as 100, which would be true if there were no error in measurement, the contribution of spikelet number per square meter becomes 74% and the combined contribution of filled spikelet percentage and grain weight

becomes 26% (Yoshida and Parao 1976).

A close correlation between spikelet number per square meter and grain yield also is reported for very high-yielding rice crops in Japan (Tanaka 1980).

Spikelet number per square meter

Under subnormal cultural practices, spikelet number per square meter can be increased by increasing plant density. An optimum plant density or spacing that maximizes spikelet number varies with the tillering capacity and growth duration of a variety and with nitrogen application. A higher plant density is required for low-tillering, early-maturing varieties and at low nitrogen levels.

Within a moderate range, low temperature during the reproductive stage appears to favor increased spikelet numbers. In the northern regions of Japan, a larger number of spikelets can be produced per unit nitrogen absorbed or per unit weight of vegetative part than in southern Japan (Murayama 1967). The efficiency of spikelets produced per unit nitrogen or dry weight is much higher in cool regions than in warm regions.

A minicrop experiment in the phytotron indicated that number of spikelets per square meter increases as temperature decreases at a given level of nitrogen. This effect is most significant at the highest level of nitrogen. However, the efficiency of the absorbed nitrogen in producing spikelets was higher at lower temperatures and lower nitrogen levels (IRRI 1978).

Solar radiation during the reproductive stage also has a pronounced effect on spikelet number per square meter. The number of spikelets per square meter increases linearly with increasing levels of solar radiation (Yoshida and Parao 1976). A high solar radiation combined with a relatively low temperature during the reproductive stage tends to produce more spikelets.

Filled spikelet percentage

Percentage of filled spikelets of a rice crop is affected by such factors as climate, soil, variety, and nitrogen fertilization (Yoshida and Parao 1976). Filled spikelets for 77 rice crops grown at 4 sites in the tropics ranged from 60% to 97%. Under most conditions, about 85% of spikelets filled is considered normal. Low percentages of filled spikelets usually indicate adverse climates at the reduction division stage, at flowering and during the ripening period, and poor nutrition.

Grainweight

The potential size of a rice grain is physically restricted by hull size. Accordingly, the 1,000-grain weight is a quite stable varietal character. The coefficient of variation (CV) of 1,000-grain weight ranged from 2.2 to 4.4%, with a mean value of 3.3% in data collected from 9 varieties for 19 years at Konosu, Japan. The mean CV was 12.4% for panicle number and 14.1% for yield (Matsushima 1970).

Unusually adverse conditions affect the 1,000-grain weight to some degree. Heavy shading before heading changed the hull size and decreased the 1,000-grain weight from about 26 g to 21 g (Matsushima 1970). But this appears to be an extreme example. A similar shading experiment during the reproductive and ripening stages caused only a slight change in 1,000-grain weight, from 20.0 g at full sunlight to 19.1 g

at 25% full sunlight for IR747B2-6 (Yoshida and Parao 1976).

Temperature during the ripening period also affects the 1,000-grain weight. One field experiment in Japan indicated that the 1,000-grain weight varied from 24 g at a daily mean temperature of 22° C to about 21g at 28°C, a 13% reduction (Murata 1976).

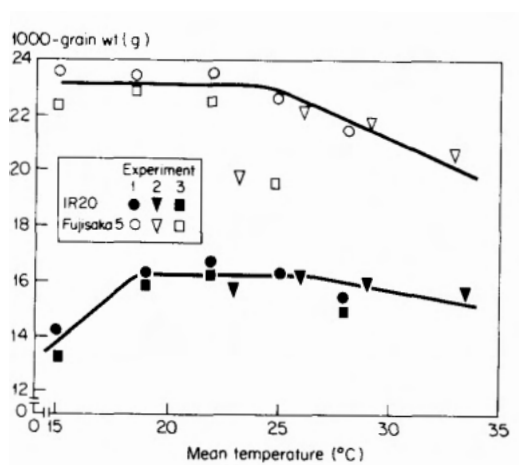
However, the effect of temperature during ripening on the 1,000-grain weight appears to differ among varieties. In a controlled-temperature experiment, the 1,000-grain weight of Fujisaka 5, a japonica variety, was affected adversely by high temperature. The 1,000-grain weight of IR20, an indica variety, was unaffected by high temperature but was affected adversely by low temperature (Fig. 3).

Sink size

When yields of different varieties are compared, the product of spikelet number per square meter and 1,000-grain weight (potential grain size) is a meaningful measure of potential yield. This quantity has been termed capacity of yield-container or yield capacity (Murata 1969, Murata and Matsushima 1975, Yoshida 1972). The 1,000-grain weight of 11 selected varieties ranged from 11.6 g to 44.4 g at 0% moisture (IRRI 1977). When these varieties were grown in the field, spikelet number per square meter correlated negatively with 1,000-grain weight, but their product increased with increasing 1,000-grain weight (IRRI 1978). Thus, it is meaningful to examine the yield potential of a variety in terms of spikelet number per square meter and 1,000-grain weight. The product of these two yield components is considered agronomic sink size.

CLIMATIC CONTROL OF GROWTH AND YIELD

Climatic factors such as temperature, solar radiation, and rainfall influence growth and yield of rice in two ways. Directly, they affect the rate and duration of growth at different growth stages. Indirectly, they affect grain yield through the incidence of diseases and insects.



3. Relationship between 1,000-grain weight and mean temperature for 2 rice varieties (Yoshida and Hara 1977).

Temperature

Germination. Germination of rice starts when seed dormancy is broken, the seed absorbs adequate water, and the seed is exposed to temperatures ranging from 10° C to 40° C. At 27° -37° C, 90-97% germination may be attained in 2 days. Rice seed may germinate even at 0° -5° C, but at such low temperatures germination proceeds very slowly and may take a month or longer.

Geographical distribution of indica and japonica rices suggests that japonica rices may germinate better at low temperatures, as in fact, some do. But other indica rices germinate better than other japonica rices.

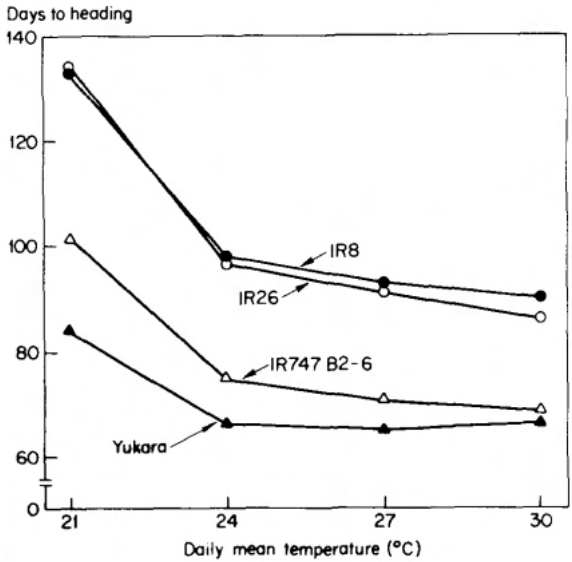
Germination at low temperature may be complicated by seed dormancy. There is evidence that when the dormancy has been broken, some indica rices can germinate at low temperatures as well as or better than japonica rices (Ikehashi 1973). Local selection pressure related to either cultural practices or local environments may have caused differential selection of varieties better adapted to low temperatures. At 15.6°C, California variety Caloro germinated and grew better than most Japanese varieties tested (Ormrod and Bunter 1961). In California, rice is sown directly into cool water irrigated fields, while in Japan, rice seedlings are grown in protected nursery beds where high temperatures are maintained. At low temperatures, traditional varieties in Japan quite often germinate better than improved varieties. Before the use of protected nursery beds, the traditional varieties were raised in unprotected beds and were inadvertently selected for low temperatures (Toriyama 1962).

Duration from germination to flowering. The duration from germination to flowering of photoperiod-insensitive varieties mostly is determined by water and air temperatures. Until the elongation of culm, the growing points of leaves, tillers, and panicles are under water where water temperature affects growth and development. However, leaf elongation and plant height are affected by both air and water temperatures, presumably because they are completed in an aerial environment. As the growing panicles reach above the water surface at around the reduction-division stage, the effect of water temperature decreases. Eventually air temperature becomes dominant in controlling panicle growth and ripening (Tsunoda and Matsushima 1962).

Temperature summation varies with the maturity of a variety; early-maturing varieties have smaller temperature summations than late-maturing ones. Temperature summation from sowing to heading for selected Japanese varieties ranges from 1,000 to 3,000 degree-days, depending on varieties, latitudes, and planting season (Toriyama et al 1969). Ripening requires an additional 700-800 degree-days (Ishizuka et al 1973, Komoda 1958). Consequently, a rice crop requires about 2,000-4,000 degree-days from sowing to maturity, which corresponds to 80-160 days at a mean temperature of 25° C.

The relationship between temperature and growth duration can be examined experimentally by growing photoperiod-insensitive varieties in controlled-temperature facilities (Fig. 4).

In terms of temperature summation, varieties differ in number of days to heading for each temperature. Yukara from northern Japan has a much lower temperature summation value than tropical varieties IR8 and IR26. The shape of the response curves is basically the same and typical of many other crops. Within a daily mean



4. Relationship between temperature and days to heading for 4 photoperiod-insensitive varieties grown in controlled temperature glasshouses (IRRI 1975).

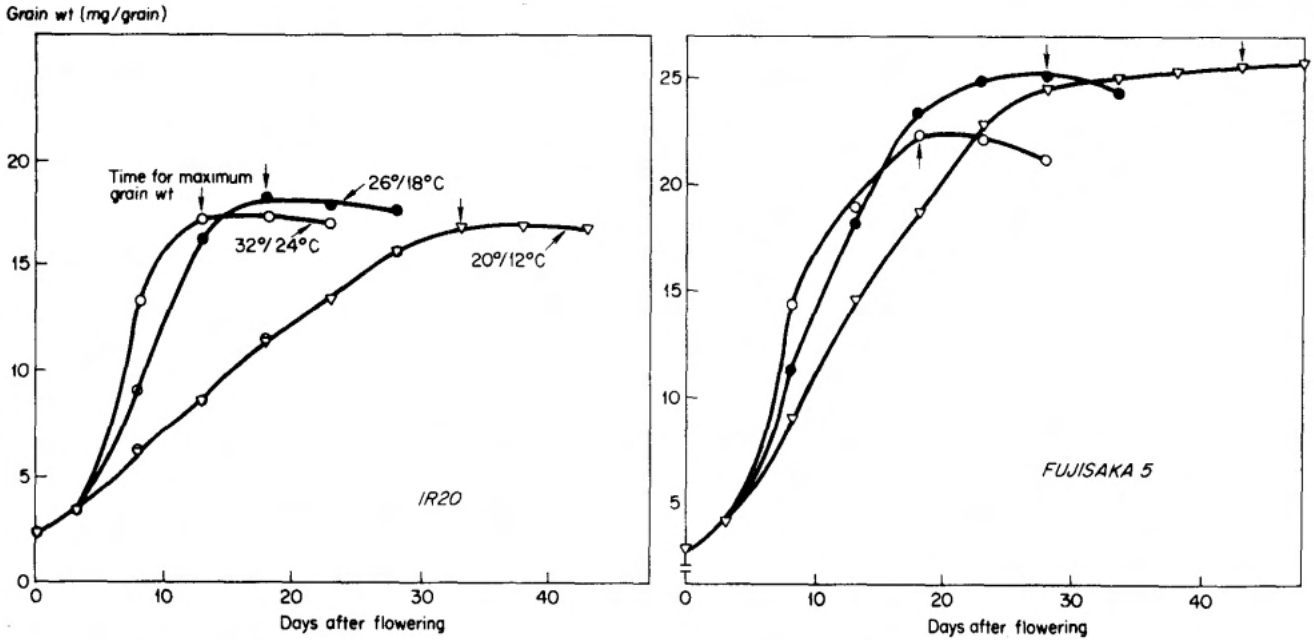
temperature range of 24° to 30° C, the number of days to heading is not linearly related to temperature.

When temperature drops from 24° to 21° C, there is a sharp increase in days to heading. For example, the number of days to heading for IR26 increases from 96 days at 24° C to 134 days at 21° C. A temperature drop of 1° C causes a 13-day delay in heading. When the temperature increases above 24° C, days to heading decreases to 91 days at 27° C and 86 days at 30° C. A temperature rise of 1° C shortens the number of days to heading by less than 2 days. These results indicate that temperatures above 24° C are much less effective than temperatures below 24° C, and suggest the existence of a ceiling temperature.

This idling effect of high temperature on growth duration is similar to that observed in the field. IR747B2-6 grown throughout the year at Los Baños, where the monthly mean temperature changes from 25.3° C in January to 29.4° C in May, matures in about 95 days regardless of planting time.

Grain-filling period. The duration from anthesis to maturity of a spikelet and a panicle is controlled mostly by air temperature. The rate of grain filling of a spikelet is faster and the grain-filling period is shorter at higher temperatures for both an indica and a japonica variety (Fig. 5). For IR20, the duration of the grain-filling period, defined as number of days required to reach maximum weight, is 13 days at a daily mean temperature of 28° C and 33 days at 16° C. For Fujisaka 5, it is 18 days at 28° C and 43 days at 16° C. Temperature appears to markedly affect the grain-filling period.

The duration of the grain-filling period of a field crop is longer than that of a spikelet or a panicle because it includes variations in the date of anthesis among different spikelets of the same panicle and in the date of panicle emergence within the same field. Ripening of a field rice crop persists for 30 days at a daily mean



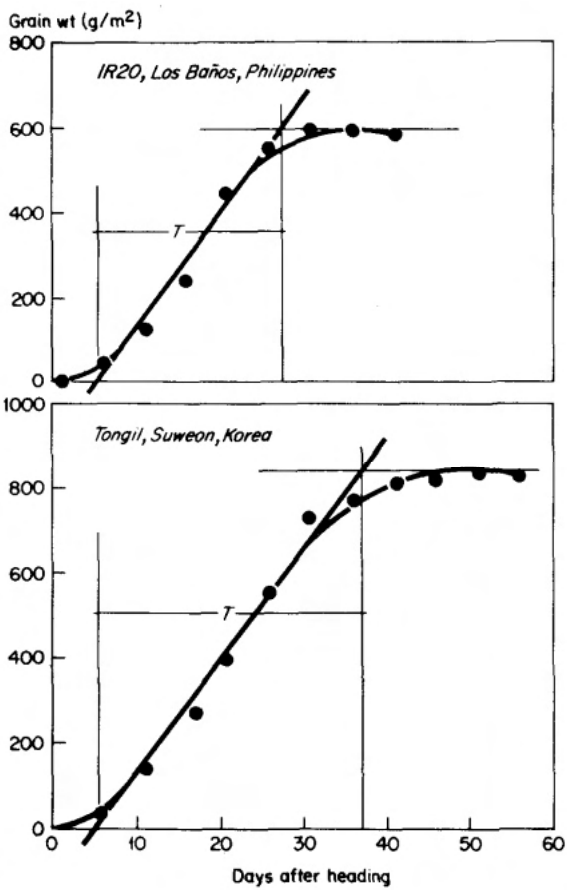
5. Growth of single grains of IR20 and Fujisaka 5 at different temperatures (Yoshida and Hara 1977).

temperature of about 29° C and for 53 days at a daily mean temperature of 18° C (Yamakawa 1962). In terms of temperature summation, these figures correspond to 870 and 954 degree-days.

In other studies, ripening required 700-800 degree-days (lshizuka et al 1973. Komoda 1958). The length of the ripening period varies from 64-66 days in cool regions such as Hokkaido (Japan) and Yanko (Australia), to 30 days in warm regions such as Los Baños (Philippines) and Taichung (Taiwan) (Tanaka and Vergara 1967).

In the field, crop maturity is usually determined by visual examination. There are two slow development phases, at the initial stage of grain filling and toward maturity. But most grain increase takes place during the period of linear growth between the two phases. The duration of such a linear phase is termed the effective filling period and is considered more meaningful than the agronomic ripening period in determining grain yield (Daynard et al 1971).

The effective grain-filling period is 23 days for IR20 rice at Los Baños, Philippines, and 33 dags for Tongil rice at Suweon, Korea (Fig. 6). Other measurements on the effective grain-filling period of indica rices at Los Baños indicated a range of 23 to 25 days.



6. Gram growth of rice at 2 sites
T = effective grain-filling period

Grain weight. Temperature affects the final grain weights of an indica and a japonica rice in different ways (Fig. 3). Indica rice IR20 is better adapted to higher temperatures while japonica variety Fujisaka 5 is better adapted to lower temperatures.

Low temperature stress. Depending on growth stages, injury to rice may occur when the daily mean temperature drops below 20°C. Common cool injuries are failure to germinate, delayed seedling emergence, stunting, leaf discoloration, panicle tip degeneration, incomplete panicle exsertion, delayed flowering, high spikelet sterility, and irregular maturity.

Rice is most sensitive to low temperatures at the young microspore stage after reduction division. It is less sensitive just before and at the leptotene stage of reduction division about 10-11 days before anthesis (Satake 1976). For practical purposes, 14 to 7 days before heading is considered the stage most sensitive to low temperatures, depending on variety and weather conditions (Sasaki and Wada 1973). The second most sensitive stage is flowering. Low temperature at these critical stages causes high percentages of spikelet sterility.

Spikelet sterility appears to be affected by both night and day temperatures. This can be demonstrated by the cooling index concept (Uchijima 1976). Cooling index (Q) is defined as:

$$Q = (20 - \bar{\Theta}_o)N \text{ (degree-day)} \qquad (11)$$

where 20 = critical low temperature limit (°C),
$\bar{\Theta}$ = weighted daily mean temperature (°C)
N = number of days when $\bar{\Theta}_o$ £ 20.

The cooling index correlates closely and positively with percentage of spikelet sterility attributed to low temperatures at the reduction division stage. That implies that the day and night temperatures affect the incidence of spikelet sterility equally and that both the magnitude and the duration of low temperatures affect spikelet sterility.

Clear varietal differences exist for rice tolerance for low temperature-induced sterility. In general, japonica varieties are more tolerant of low temperatures than indica varieties. But when 6 cold-tolerant indica varieties were screened from 12,200 varieties and selections (IRRI 1977), some varieties were shown to be as tolerant as, or even more tolerant of low temperatures than. some of the most cold-tolerant japonica varieties (Satake and Toriyama 1979).

High temperature stress. When rice is exposed to temperatures higher than 35° C, different types of heat injury occur according to growth stages (IRRI 1975). Rice is most sensitive to high temperatures at flowering and next most sensitive at about 9 days before flowering (Satake and Yoshida 1978). One or two hours of high temperature at anthesis have a decisive effect on the incidence of spikelet sterility. High temperatures before or after anthesis have much less effect on sterility.

Clear varietal differences exist in the resistance of rice to high temperature-induced sterility. At 35° C, N22 dryland rice from India has higher than 80% spikelet fertility, whereas the BKN6624-46-2 wetland selection from Thailand has only about 10%.

Solar radiation

The solar radiation requirements of a rice crop differ from one growth stage to another (Stansel et a1 1965, Yoshida and Parao 1976). Shading during the vegetative stage affects yield and yield components only slightly (Table 2). During the reproductive stage, however, shading has a very pronounced effect on spikelet number and yield. Shading during the ripening period also decreases the percentage of filled spikelets and reduces grain yield considerably.

A quantitative relationship between yield and solar radiation at different growth stages is shown in Figure 7. Solar radiation at the reproductive stage has the greatest effect on grain yield; that at the vegetative stage has an extremely small effect.

Solar radiation of 300 cal cm^2 per day during the reproductive stage makes possible yields of 5 t/ ha. Less solar radiation during ripening is required to achieve the same yield level. Thus, the effect of solar radiation is apparent only when grain yield is higher than 5 t/ ha. When grain yield is below 5 t/ ha, sunlight per se may not have any direct significance.

That conclusion was obtained with a 95-day variety. Yield of a medium-growth-duration variety could be even higher with the same level of solar radiation. The right variety and good management could achieve a yield of 5 or 6 t/ ha during the tropical wet season. In fact, the grain yield of IR8 is stabilized at about 6 t/ha in the wet season when leaf area index at flowering is larger than 5.

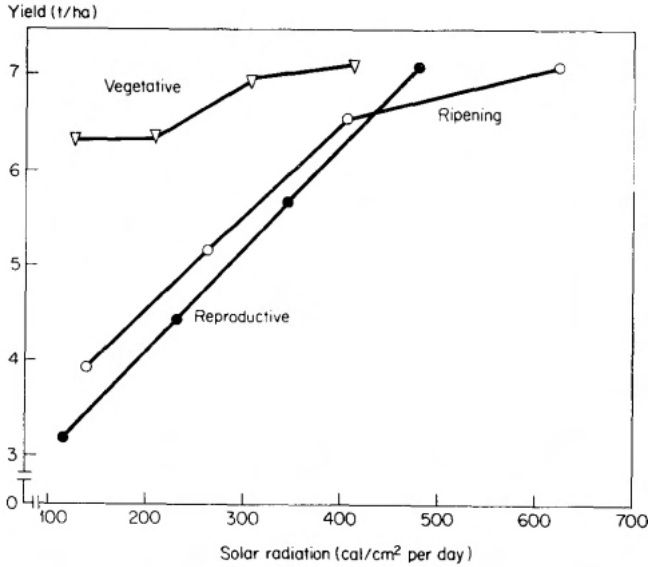
Day length

Rice is basically a short-day plant. Traditional tropical varieties usually are photoperiod sensitive and varieties in northern Japan usually are photoperiod insensitive. Improved varieties released by the International Rice Research Institute (IR8, IR5. IR20, IR22) and the University of the Philippines College of Agriculture (C4-63) are

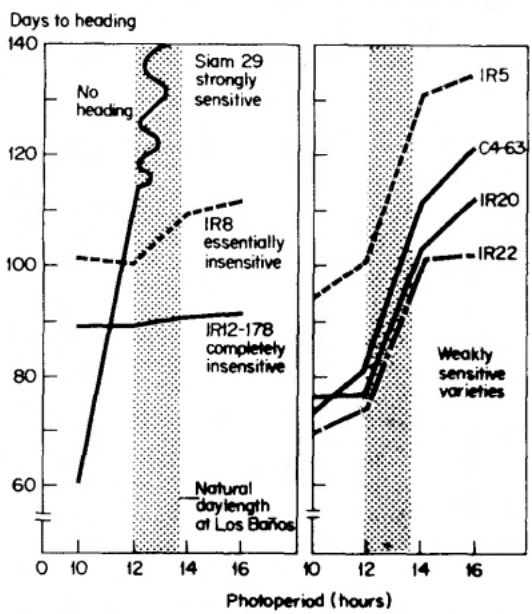
Table 2. Effect of shading at different growth stages on yield and yield components of IR747B2-6.[a]

Sunlight (%)	Grain yield (t/ha)	Harvest index[b]	Spikelets (no./m^2)	Filled spikelets (%)	1000-grain wt (g)
		Vegetative stage			
100	7.11	0.49	41.6	88.9	20.0
75	6.94	0.48	40.6	89.9	19.9
50	6.36	0.51	38.3	89.5	19.9
25	6.33	0.51	38.1	84.3	19.8
		Peproductive stage			
100	7.11	0.49	41.6	88.9	20.0
75	5.71	0.47	30.3	87.8	20.3
50	4.45	0.40	24.4	89.4	19.5
25	3.21	0.36	16.5	89.4	19.1
		Ripening stage			
100	7.11	0.49	41.6	88.9	20.0
75	6.53	0.49	41.1	81.1	20.0
50	5.16	0.44	40.6	64.5	19.5
25	3.93	0.38	41.7	54.9	19.1

[a]Yoshida and Parao (1976). [b]Ratio of dry grain weight to total dry matter weight.



7. Effect of solar radiation at different growth stages on grain yield of IR747B2-6 (Yoshida and Parao 1976).



8. Effect of 4 photoperiod treatments on the seeding-to-heading period of 7 rice varieties.

weakly photoperiod sensitive. Variety IR12-178 is completely photoperiod insensitive and hence even under different day lengths flowers in the same number of days after sowing (Fig. 8).

The use of photoperiod-insensitive varieties makes planning rice cultivation more flexible and more suitable for the multiple cropping systems characteristic of progressive agriculture.

On the other hand, photoperiod sensitivity continues to be a useful characteristic under certain environments.

Sensitivity to photoperiod is an important characteristic for survival in the

deepwater areas. Floating rice varieties are highly photoperiod sensitive. They are planted early in the season, when the soil can still be worked, and usually harvested when floodwaters have receded. This may be 150 to 270 days after sowing. Such a long growth duration requires a photoperiod-sensitive variety. So far, there is no known tropical variety that has a long growth duration and is not sensitive to photoperiod (Vergara and Chang 1976).

Photoperiod sensitivity may function as a safety mechanism when the onset of the rainy season is considerably delayed (Oka 1958). In most areas of tropical Asia, the onset of the rainy season is unpredictable, with year to year variation. The end of the rainy season is fairly fixed. When planting is delayed because of a delayed onset of the rainy season, a photoperiod-sensitive variety may still mature at its usual time, regardless of shortened growing periods. On the other hand, a photoperiod-insensitive variety requires a specified length of growing time for flowering, and hence for maturity. Such a variety will suffer from drought at later growth stages after rains cease.

Rainfall and water requirements

When irrigation is provided, as it is in temperate areas, growth and yield of rice are determined largely by temperature and solar radiation. In the tropics, where temperatures are favorable for rice growth throughout the year, where irrigation is not available in most places, and where a wet season is clearly separated from a dry season, rice cultivation starts with the rainy season. In equatorial monsoon climates, where monthly rainfall is evenly distributed throughout the year and where no regular dry season occurs, rice cultivation may be started any time of the year (Yoshida 1978).

The water requirement of a rice crop is affected by both climate and soil. Climatic factors such as solar radiation, temperature, wind speed, and air humidity primarily determine evapotranspiration. Soil factors such as texture, depth of water table, and topography determine seepage, percolation, and runoff. The average water requirement of irrigated rice at 43 sites in China, Japan, Korea, Philippines, Vietnam, Thailand, and Bangladesh is 1,240 mm crop (Kung 1971). Consequently, rice cultivation appears to be limited to areas where the annual rainfall exceeds 1,000 mm.

But during the rainy season, uneven distribution of rainfall, droughts, and floods can cause partial or total crop failure. In Thailand, more than 15% of the cropped area was affected by either drought or flood in 8 of the years from 1907 to 1965 and more than 10% of the cropped area was damaged in 24 of the 58 years (Israankura 1966). In both the tropics and the temperate region, typhoons are unavoidable hazards.

The most critical water deficit stage is the period from about 10 days before flowering to flowering (Matsushima 1962). Severe water stress then causes high percentages of sterility, thereby reducing grain yield. Since sterility is irreversible, an adequate supply of water at later stages is totally ineffective. On the other hand. while water stress during the vegetative stage may reduce plant height, tiller number, and leaf area, the plant can recover from this retarded growth if water is supplied to permit sufficient time for recovery before flowering.

Use of photoperiod-sensitive varieties is one way to avoid drought damage during ripening period if the onset of the rainy season is delayed.

ESTIMATION OF POTENTIAL RICE YIELD

Estimation of potential rice yield is risky because several unavoidable assumptions may or may not be true. But it is useful in that it gives some idea of the limit beyond which rice yield cannot be increased even with additional inputs.

The method proposed is a solar energy use efficiency formula much simpler and more empirical than those previously reported (Evans 1972, Murata and Matsushima 1975).

Equation 2 can be converted into:

$$DW = \frac{E_u \times T \times S}{K} \times 104 \qquad (12)$$

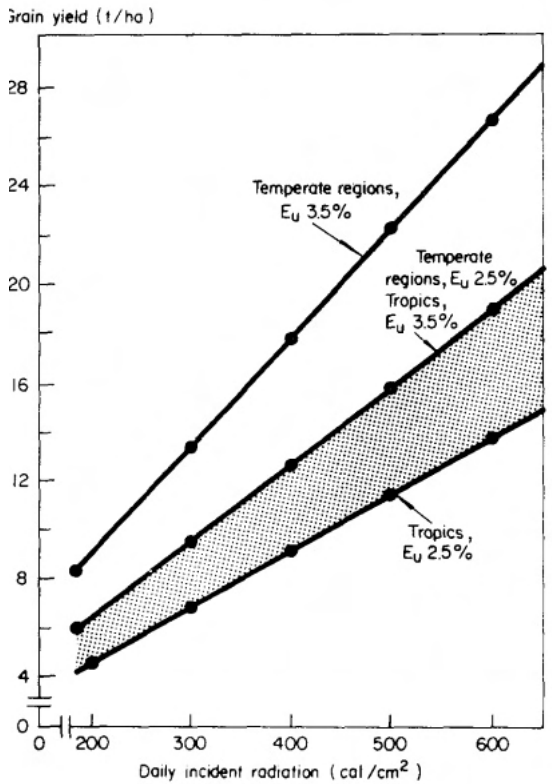
where T represents the effective grain-filling period. For convenience, T is assumed to be 25 days for the tropics and 35 days for the temperate region. The dry matter produced during the ripening period is assumed to be used for grain production, Hence, 4,000 cal/g was used for the K value.

Dry weight increase (DW) can be converted to rice yield through appropriate conversion factors for husk weight and moisture content. The 2 E_u values used at all levels of incident solar radiation are 3.5% representing high efficiency, and 2.5% representing moderately high efficiency.

Equation 12 gives a linear relationship between incident solar radiation and potential yield. The E_u value is expected to decrease with increasing levels of incident solar radiation. As a consequence, the relationship between incident solar radiation and potential yield would probably be curvilinear, not linear. However, information currently is lacking on how E_u relates to incident solar radiation in rice. Considering this, the potential yield calculated by equation 12 is likely to be underestimated at lower levels of incident solar radiation and overestimated at higher levels of incident solar radiation.

The contribution to maximum grain yield of the carbohydrate accumulated before flowering was not taken into account. The contribution of accumulated carbohydrate has been estimated at about 2 t/ha (Cock and Yoshida 1972, Evans 1972). However, it is not certain that a similar amount of carbohydrate would come from the carbohydrate accumulated before flowering when the maximum potential yield is to be achieved. The contribution of accumulated carbohydrate tends to decrease when the application of nitrogen is increased (Murayama et al 1955, Yoshida and Ahn 1968). The maximum potential yield probably would be achieved with high nitrogen application.

The estimated potential yield (Fig. 9) indicates that the temperate region, where the effective grain-filling period is longer, is more productive than the tropics on a per crop yield basis. These estimated maximum yields may be compared with recorded maximum yields: 13.2 t/ha in Japan with an estimated solar radiation of



9. Relation between potential yield and incident radiation during the grain-filling period of rice (IRRI 1977).

400 cal/cm^2 per day and 11.0 t/ha at IRRI with an estimated solar radiation of 550 cal/cm^2 per day. With good management, about 6 t ha is normally obtained at IRRI in the wet season when incident solar radiation is about 300 cal/cm^2 per day during the ripening period. When the rice crop was given carbon dioxide enrichment before flowering to increase spikelet number per square meter but was kept under normal atmospheric conditions after flowering, the yield was 7.7 t/ha (Cock and Yoshida 1973). The recorded maximum yields mentioned above are close to estimated potential yields.

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WHEAT

R. A. Fischer

I attempt to cover fully, but briefly, the determination of yield potential in wheat, with emphasis on the overriding importance of radiation, temperature, and photoperiod, and on recent genetic progress with spring wheats. Much evidence suggests the situation is not very different for winter wheats, or even durum wheats, triticales, and other temperate cereals. More importantly, the effects I describe operate, although less strongly, at the suboptimal levels of fertility and water typical of many wheat production regions, and the higher yield potential cultivars have generally proved superior in such situations.

Experience favors cautious optimism regarding the realization of more yield potential, and I indicate some areas more likely to reward the breeder-physiologist's scrutiny. For example, further improvement in sink through greater allocation to the growing spike seems feasible. Attention to leaf angle and A_{max} variation could raise stagnant crop growth rates and E values. The number and potential size of kernels obtained from a given dry matter investment in inflorescence have received virtually no attention, yet it is in my analysis directly related to sink size. Genetic differences in thermal adaptation, so evident in rice, sorghum and cowpea, have yet to be seriously sought in wheat.

I believe progress in raising potential yields is likely to be harder than in the past, and less likely to lead to automatic yield increases at low levels of input. We are reaching the point where breeding for specific adaptation to less favorable physical environments needs more attention. In particular, I refer to exploitation of the elusive, but undoubtedly real, genotypic differences in adaptation to moisture stress, high and low temperature stress, nutrient toxicity, and certain nutrient deficiencies. IRRI experience with rice is also stimulating wheat scientists to look more closely for such specific adaptations, in this postdwarfing gene era of wheat improvement.

Wheat comprises bread wheat (*Triticum aestivum* L. 2n = 42), durum wheat (*T. turgidum* L. 2n = 28), and their wild and cultivated hexaploid, tetraploid, and diploid relatives. It is a temperate cereal that originated in western Asia, but is now cultivated in all regions of the world with the exception of the lowland humid tropics.

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Wheat is the world's most important food crop in quantity of grain (about 420 million t in 1979-80, 95% being bread wheat) and protein produced (about 45 million t), but is surpassed by rice as a food crop in developing nations (150 million t vs 200 million t).

The key ecological characteristics of wheat are 1) the general adaptation of' its photosynthetic and growth processes to daily mean temperatures in the range 10 to 20°C, and 2) the interactions between genotype and environment, principally temperature and day length, which determine crop phenology. A major but not complete phenological separation exists between spring wheats (with small or nil responses in time to floral initiation with vernalizing temperatures) and winter wheats (often, but not always, showing an obligate requirement for vernalization). At high latitudes (about 35 to 55°N) winter wheats with genotypic resistance to frozen soil (winter kill) in the vegetative stage are sown in autumn, and spring wheats in spring. Autumn-to-winter sowing of spring or semiwinter wheats predominates at lower latitudes and in the southern hemisphere, although spring wheat is sown in early summer at the onset of the wet season in tropical highlands (e.g. Mexico, Kenya, Ethiopia).

Of the major crops, wheat is relatively drought resistant and moderately frost resistant, except from the stage of rapid stem elongation until flowering when frost (plant temperatures < about -3° C) can cause major yield losses. The flowering date of wheat in many ecological situations is a compromise between the need, on one hand, for time to develop a large enough plant structure or yield potential and to avoid late spring frost, and on the other, to avoid the high temperatures and poor water relations of summer. In high-latitude (> about 50° N) continental situations where only spring wheat can be grown (e.g. Canadian and USSR steppe regions), the completion of grain filling before the onset of autumn frost and snow is also a consideration. Wheat is not well adapted to saline or acid soils, although useful genetic resistance to the acid soils exists. Foliar disease, insect attack, and high mean temperatures that cause excessively rapid and abnormal development now presently exclude wheat from the humid lowland tropics (<about 25° latitude), although some wheat is grown in lowland areas below this latitude (e.g. parts of India, Mexico, Peru) where the winter is dry.

The remainder of this paper examines the physiology of yield potential in wheat, i.e. environmental and genotypic factors controlling yield, not at the extremes of adaptation, but in generally favorable environments in the absence ofdisease, weeds, drought, or nutrient stress. Under such conditions. maximum yields in relatively cool regions presently reach about 13 t/ ha (winter wheat) and 9 t ha (spring wheat). The view presented is much influenced by the results of field research on yield potential of spring wheat in northwest Mexico, and by similar European work on winter wheat. Good general reviews of wheat physiology can be found elsewhere (Thorne 1974, Wardlaw 1975, Austin and Jones 1975, Evans et al 1975).

PHENOLOGY AND ALLOCATION

Phenological characteristics establish the temporal framework within which dry matter is allocated. The widely recognized cardinal points for wheat are sowing,

floral initiation, anthesis and maturity, delineating the vegetative (or sometimes tillering), reproductive and grain filling periods. Within the reproductive period, workers often separate the relatively short interval from floral initiation until terminal spikelet appearance (spikelet formation). Its duration as a response to environment is closely tied to that of the vegetative period. I believe it is vital to also distinguish the latter half of the reproductive period (specifically the interval from emergence of the penultimate leaf on the main shoot until anthesis), when the spike accumulates more than 95% of its nongrain dry weight. I define this as the spike growth period. Finally, the postanthesis or grain-filling period has been separated into an initial lag period, and a longer grain growth period of linear increase in kernel weight.

Environmental control

The duration of these phenological periods is related almost exclusively to mean temperature, day length, and, sometimes, vernalizing cold; the last two interact markedly with genotype (Table 1). In addition to the main effects of Table 1, minor effects are caused by interactions between the listed environmental factors, subtleties associated with certain subperiods (Aitken 1974), and drought and nutrient stress.

Vernalization responsiveness usually refers to the acceleration of rate of development in the vegetative and spikelet formation periods following exposure of imbibed seeds or young seedlings to an artificial period of cold in the range 2-8° C. In the most responsive winter cultivars. vernalization sensitivity is usually under simple genetic control, insensitivity being dominant. In the field, vernalization begins with daily minima below about 13° C. For weakly sensitive spring cultivars, the optimum daily minimum for faster floral initiation was about 10° C (Midmore 1976). Once vernalization requirements are satisfied, rate of development is closely and linearly related to the temperature above a basal threshold of 1-5° C. Genotypic differences in this universal sensitivity to temperature have not yet been demonstrated,

Wheat is a long-day plant. The acceleration of development by longer days is especially high in the region of 9 to 13 hours photoperiod (Levy and Peterson 1972), but the response persists even above 16 hours. Day length sensitivity is under

Table 1. Acceleration of development[a] due to influence of environmental factors.

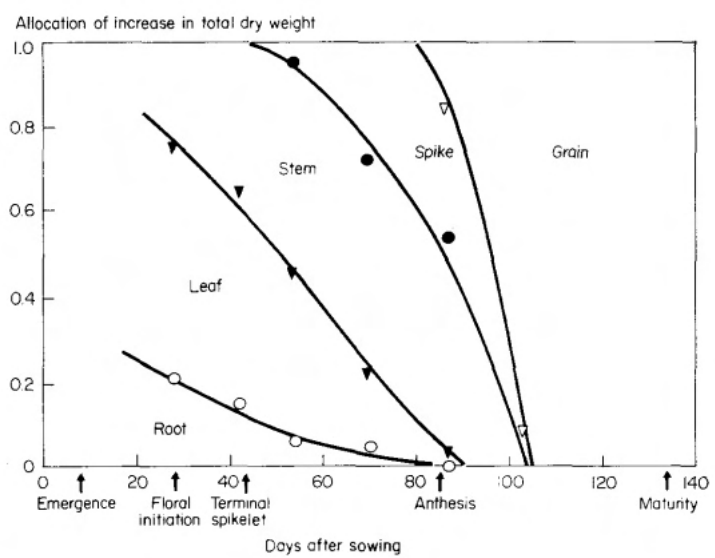
Developmental period	Acceleration due to		
	More vernalizing cold	Increased mean temperature	Longer day length
Vegetative	0-3	3	1-3
Reproductive	0-1	3	1-2
Spikelet formation	0-1	3	1-2
Spike growth	0	3	0-1?
Grain-filling	0	3	0
Lag	0	2-3?	0
Grain growth	0	2-3?	0

[a]Arbitrary scale from 0 (nil influence) lo 3 (substantial influence); range shown indicates recognized or possible (?)genotypic variation.

substantial and often simple genetic control: earliness or insensitivity genes, which are dominant, have played a major role in the adaptation of wheat to low and intermediate latitudes (Borlaug 1968, Pugsley 1980). Reproductive period responsiveness may show some genetic independence from responsiveness evident in the vegetative period (Pinthus 1963, Wall 1979). Artificial photoperiod manipulation shows the spike growth period to be moderately responsive (Cries et a1 1956; Fischer, unpubl.); at 14-hour photoperiod its duration is about 350-400 day degrees above zero (Fischer and Stockman 1980). Genotypic effects on the duration of grain-filling appear to be small (Marcellos and Single 1972. Sofield et a1 1977). Considerable progress has been made in predictive modeling of wheat phenology, especially in the case of vernalization-insensitive genotypes (e.g. Robertson 1968), and useful advances in such modeling can be expected.

Assimilate allocation

The pattern of allocation of dry matter in the wheat crop (Fig. 1, 2) is tied closely to the phenological framework and reflects the determinate nature of wheat development and the high degree of synchrony between tillers at later stages of development. Environmental influences on the gross allocation pattern, other than through effects on phenology, appear to be small, with the exception perhaps of effects on root-to-top ratio. Genotypic effects may also operate through differences in phenology, although at least one major effect of genotype — reduced stature — has an independent influence, favoring allocation to spike at the expense of stem during the spike growth period. Figure 1 ignores the allocation of carbon to the rhizosphere,



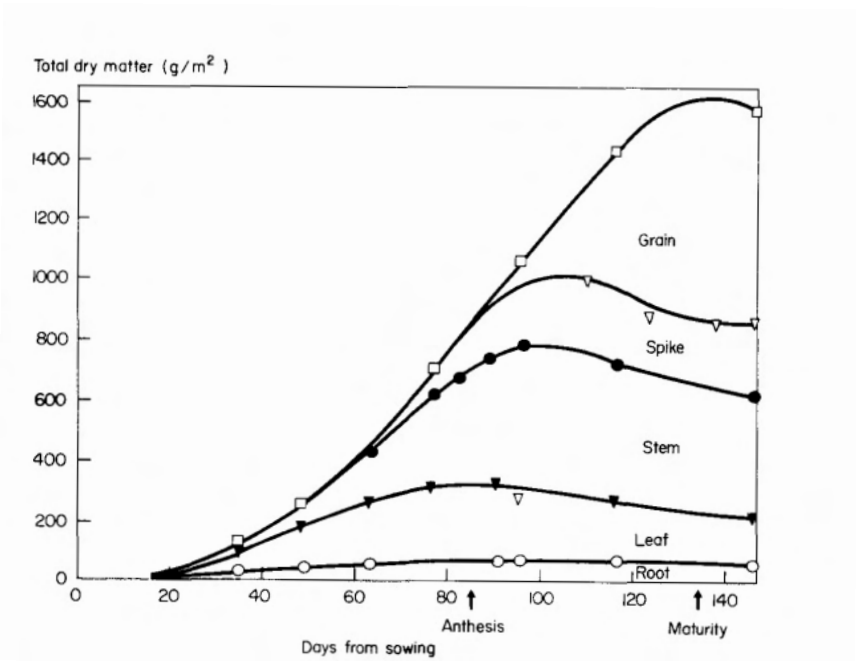
1. Stages of development and the allocation of accumulating dry matter to roots, leaves, stems, spikes, and grain in a typical spring wheat crop. Yecora 70, sown Nov 23, 1973 under irrigation and high nitrogen, northwest Mexico.

which some results suggest is substantial (Sauerbeck and Johnen 1976), and retranslocation of modest portions of leaf and stem carbon to grain, thereby permitting grain to grow at higher rates than crop dry matter accumulation during late grain-filling.

DRY MATTER ACCUMULATION

Leaf photosynthesis

This subject has been thoroughly reviewed by Austin and Jones (1975). Generally hexaploid wheats show maximum light-saturated rates of assimilation (A_{max}) in the range of 25-40 mg CO_2/dm^2 per hour at optimum temperatures of 20-25° C, but rates vary little over the temperature range 15-30° C (Stoy 1965, Downes 1970, Vong and Murata 1977). Ninety percent of A_{max} is reached at about 200 W/m^2 photosynthetically active radiation (PAR) (Stoy 1965, Downes 1970, Dunstone et al 1973) or slightly more (Winzeler 1979). Differences between species and genotypes are complicated by ontogenetic rank and age of the leaf chosen, light conditions during leaf growth, and possible sink strength effects (Austin and Jones 1975, Evans and Wardlaw 1976). Nevertheless, it appears that primitive wheat species have substantially higher A_{max} values than cultivated wheats (Evans and Dunstone 1970, Khan and Tsunoda 1970); leaves of *T. boeoticum* grown under high light exceeded 60 mg CO_2/dm^2 per hour (Dunstone et al 1973). Shimshi and Ephrat (1975) and Fischer et



2. Dry matter accumulation in crop parts, Same crop as Figure 1.

al (1981) have detected small but consistent leaf photosynthetic activity differences between cultivars of hexaploid wheat in field crop situations: however, the latter authors suggest the differences may reflect differences in sink strength.

Leaf and canopy structure

Depending on phenological conditions, each main shoot axis of the wheat plant normally forms 6 to 15 leaves (Aitken 1974). Leaf size increases progressively until the flag leaf if final leaf number is low, or peaks with the second or third to the last leaf if it is higher. Flag leaf area varied from 22 to 54 cm^2 in typical spring wheat genotypes in one study (Fischer et al 1981). Tiller production in the vegetative stage multiplies the number of shoot axes in the crop: at typical plant densities of 100-300/m^2, maximum shoot numbers ranged from 500 to 1,500 m^2 (Watson et al 1963, Evans et al 1975).

Leaf angle varies with genotype, especially after the vegetative period. Although all later leaves are erect when emerging from the subtending leafsheath at the top of the canopy, in most cultivars the leaf lamina soon bends, with the central portion in particular adopting a more horizontal position. In dense stands this often leads to a marked planophile canopy. However, leaves of some genotypes, usually ones with small leaves, resist bending and produce erectophile canopies like those seen with IR8 rice. These considerations mean that predicted leaf area indices (LAI) for 5% transmission of incident PAR (full interception) vary with genotype and stage of development. Measured values reported include: 4 (at LAI = 2) to 8 (at LAI = 9) (Osman 1971), 6 (Puckridge and Donald 1967), and 6 (relatively planophile cultivar Yecora 70, Fischer et al 1976). Usually LAI values include the vertically oriented green leaf sheaths and green stems; their equivalent lamina areas are assumed to equal from 0.3 to 1.0 of their surface area, depending on the author. In any case this component is small before flowering; using an equivalent area ratio of 0.5, stem sheath area increased from < 10% at 40 days before flowering to 20% of green area index at flowering (Fischer, unpubl.). After flowering green stem, sheath, and spike tissues are often of substantial importance as sites of photosynthesis.

The area ratio of flag leaf lamina varied from 130 to 217 cm^2/g across 48 irrigated spring wheat genotypes (Fischer et al 1981). Leaf area ratio for the whole canopy varied less in the vegetative and early reproductive stages, averaging 224 cm^2/g, but it fell from then on to average around 100 cm^2/g at anthesis (Fischer, unpubl.). Thus a LAI of 6 for full light interception implies an aboveground crop dry weight of around 250-300 g/m^2 in an early stage of development (see also Fig. 3). Beyond this point of growth and in the absence of stress, leaf area should not limit light interception or crop growth rate (CGR) until senescence sets in, late in grain filling. Nevertheless LAI usually rises further, peaking at about flag leaf emergence and declining only gradually under well-watered fertile conditions (Fig. 3, also Watson et al 1963).

Canopy photosynthesis and crop growth rate

The relation of canopy net photosynthesis and CGR to LAI in wheat appears to be asymptotic, reaching a maximum at LAI values of about 6 and not declining at least up to values of 8-12 (Stoy 1965, King and Evans 1966, Puckridge 1971, Fischer et al

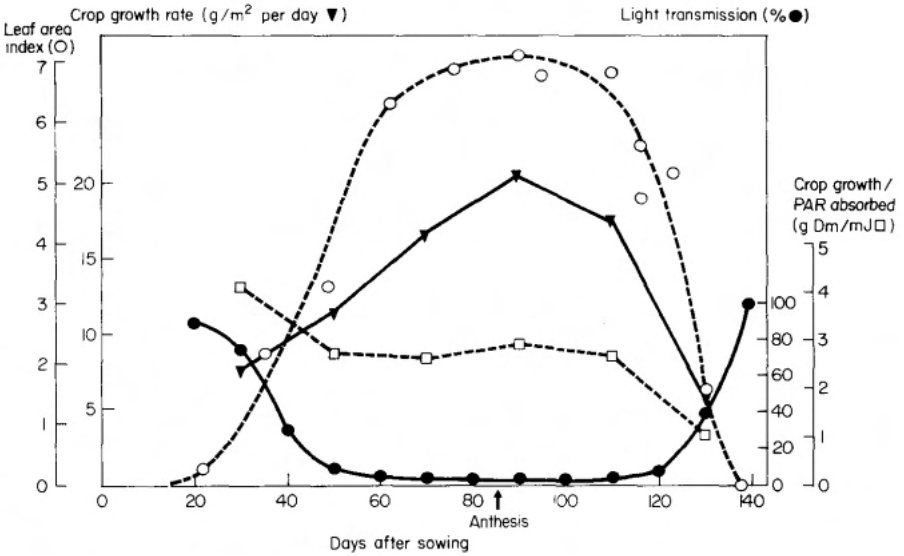
1976, Watson et al 1976). Crop respiration also varies asymptotically with LAI throughout this range (King and Evans 1966). The demonstration of optimum LAI. above which CGR declines, appears to be associated with unusual conditiond, namely artificially dense communities and very low radiation regimes, or both (Puckridge and Donald 1967).

The photosynthesis of wheat canopies with LAI values greater than about 2 responds almost linearly to irradiance (Puckridge 1971, de Vos 1975, Walcott and Laing 1976), with peak photosynthesis rates around 7 g CO_2/m^2 per hour. The effects of LAI and irradiance are largely explained by linear relations between the quantity of radiation intercepted by the canopy and canopy net photosynthesis (Puckridge 1971) or CGR (Puckridge and Donald 1967; Fischer et al 1976, Gallagher and Biscoe 1978). Independent effects on canopy photosynthesis have been demonstrated in certain situations, e.g., the effect of low day temperature and the after-effect of low night temperature (Koh et al 1978). Nevertheless the slope of the relation of CGR to absorbed PAR (intercepted PAR × 0.9. Gallagher and Biscoe 1978) is remarkably stable in normal field situations before spike emergence (Gallagher and Biscoe 1978, Fig. 4). The slope in Figure 4 is 3 g dry matter (DM) per MJ of PAR absorbed (at 17 kJ/g DM this represents 5% growth efficiency [E] with respect to absorbed PAR). Decreases in E with nitrogen deficiency and water stress have been detected by this approach but effects were surprisingly small (Gallagher and Biscoe 1978). The major part of variation in CGR due to these factors is ascribed to variation in LAI. Reasons for the comparative stability of E discussed by Gallagher and Biscoe (1978) include the approximately linear response of canopy photosynthesis to irradiance and the constancy of the fraction of photosynthate which is respired. Also theory suggests that canopy photosynthesis is relatively insensitive to changes in A_{max} (Monteith 1977).

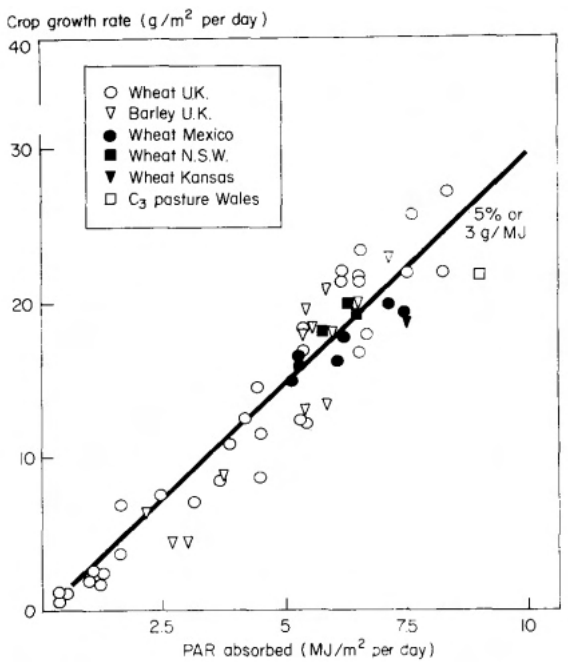
Theoretically erect leaves should increase canopy photosynthesis, hence CGR, under favorable conditions (LAI > 4, high sun angle), and results with related C_3 grasses support this (e.g. uppermost point in Figure 4, an erect *Lolium,* of Sheehy and Cooper 1973): as does the only wheat study I know of on this issue (Austin et al 1976). Perhaps because there were no clear-cut effects on yield in wheat (e.g. Austin et al 1976, Carvalho and Qualset 1978, Fischer et al unpubl.), the important question of leaf angle in wheat has not received adequate attention.

Several workers have reported that E declines during postanthesis (Gallagher and Biscoe 1978, Doyle and Fischer 1979, Hodges and Kanernasu 1977), but that is not always the case (de Vos 1975, also see Fig. 3). Possible causes of decline are the rising proportion of maintenance respiration and dechning A_{max} as leaves age. The persistence of high E values after anthesis is associated with situations where A_{max} values remain high (de Vos 1975). A_{max} values of flag leaves for semidwarf wheats did not fall noticeably until at least 35 days after anthesis under conditions similar to those of Figure 3 (Fischer et al 1981) an effect possibly due to good nitrogen nutrition and a strong sink (high number of kernels/m^2).

Because errors in determining light interception are high, CGR (aboveground DM) was only measured after full interception had been reached in a 5-year comparison of genotypes in irrigated field trials in northwest Mexico. Results revealed that CGR before anthesis was consistently related positively to canopy



3. Variation in leaf area index, % incident photosynthetically active radiation (PAR) transmitted by the canopy, crop growth rate (CGR), and CGR per unit of absorbed radiation. Same crop as in Figure 1.



4. The relation of crop growth rate to absorbed photosynthetically active radiation (PAR) for wheat and related species. Data of Gallagher and Biscoe (1978, UK). R. A. Fischer unpublished (Mexico), Doyle and Fischer (1979, NSW), Hodges and Kanemasu (1977. Kansas). The 2 points from Sheehy and Cooper (1973, Wales) refer to an erect (uppermost point) and nonerect (lowermost point) genotypes.

height and to mature plant height (Table 2; also Table 4), a 1-cm increase in mature plant height giving about 0.5% increase in CGR. In a 1-year study, CGR was also positively correlated with estimated A_{max} (Table 2), but at constant height the partial correlation was zero. At constant A_{max}, the association of CGR with height remained (r = 0.59); this may be due to excessive mutual shading in dense short canopies. On the other hand, the shorter high yielding genotypes consistently showed higher (CGR) values after flowering than taller lower yielding ones (see Table 4). E values fell after flowering only in the taller cultivars. E was remarkably stable in the face of normal environmental variation (largely temperature and radiation) when averaged over genotypes. E, now corrected for below ground DM, averaged 4.9 ± 0.1% of absorbed PAR across seven 3-week preanthesis growth periods which were measured over the 5 years. One growth period was excluded from this sample because it included the only frosts encountered (7 consecutive screen minima below zero) and E fell to 4.0%.

In conclusion, much of the CGR variation in wheat is explained by variation in PAR absorbed by the canopy, the ratio E between these variables being remarkably stable. E appears to be depressed by freezing cold, and slightly by nitrogen and moisture stress, and may show some genotypic variation due to positive associations with plant height before flowering, and with sink strength after flowering. Measured E values of 5% are well below most, but not all (e.g. Monteith 1977), theoretical calculations of its upper limit (e.g. 7-10%, Nichiporovich 1971; 7.5%, Evans 1973). Curiously, E has not been determined for canopies of the wild diploid wheat species having very high values of A_{max}.

KERNEL NUMBER DETERMINATION

I have suggested that there are reasonably predictable quantitative relations governing phenology, and assimilate production and partitioning in the wheat crop. Figure 2 illustrates the outcome of these relations. What then are the problems with understanding grain yield? They lie with the precise determination of kernel number in the interval up to and around anthesis, and in the interactions between assimilate supply and the kernel sinks, which govern grain filling.

Numerical components

In the typical wheat crop, each of the successive numerical components, which together describe kernel number variation (Table 3), reaches an early peak from which subsequently there may be a considerable drop or mortality (Fig. 5, also Gallagher 1979). However, because of a lack of explicit studies, this pattern can only be inferred for the last component in the series — kernels per competent floret. Figure 5 shows that the total number of florets initiated (tiller number × spikelet number × floret number) per unit area in the crop climbs to a value much greater than the final number at anthesis, a potential kernel number which is never realized because of competition for resources in the crop.

Thinning studies and the behavior of components in isolated plants confirms that, in the absence of competition, the maximum values of the components, seen early in their development in Figure 5, are expressed in actual terms at anthesis. Vast effort

has been expended in studying these numerical components; their initiation and rise to peak values is reasonably well understood (e.g. Evans et al 1975), However, their survival (very dependent on levels of competition) is so poorly understood that this whole approach to kernel number determination is ineffective.

Table 2. Phenotypic correlations between aboveground crop growth rate (period 22 Jan to 12 Feb)[a] and physiological traits.

Trait	Genotype range	Simple correlation with crop growth rate
A_{max} [b]	12-21 mg CO_2/dm^2 per hour	0.417
Ht of canopy, 12 Feb	34-69 cm	0.683
Ht at maturity	50-112 cm	0.532
LAI, 22 Jan	2.6-5.3	0.051
Sowing to anthesis	83-104 days	–0.230

$r > 0.349$. $P < 0.05$: $r > 0.449$.$P < 0.01$.

[a] 33 Norin 10 dwarf spring bread wheat genotypes grown under high fertility and irrigation in northwest Mexico, 1974-75 (Fischer et a1 1981). Sown 29 Nov, mean anthesis date 5 Mar. [b]From $^{14}CO_2$ uptake, adaxial surface only, uppermost expanded leaf, 5-8 Feb.

Table 3. Determination of kernel number in the wheat crop.[a]

Components (range of values for typical crops)	Subcomponent	Major factors affecting component
	Numerial component approach	
Plant density (50-300/m²)		
Spikes per plant (1-10)	Tillers per plant Tiller survival	Plant density, genotypes, radiation, nutrition, water stress.
Spikelets per spike (10-25)	Spikelet primordia initiation Primordia survival	
Competent florets per spikelet (1.5-5.0)	Floret primordia initiation Primordia survival	
Kernels per competent floret (0.6-0.99)	(= grain set)	Genotype?
	Assimilate-based approach	
Spike dry wt at anthesis (100-250 g/m²)	Duration spike growth period	Temperature, photoperiod.
	Crop growth rate in period	LAI, radiation.
	Ratio of allocation to spike	Genotype
Kernels per unit spike dry wt (70-140/g)	Competent florets per unit spike weight	Genotype, water stress.
	Kernels per competent floret	Genotype?

[a]Components multiply to give values of kernel number from 10,000 to 25,000/m^2.

Assimilate-based approach

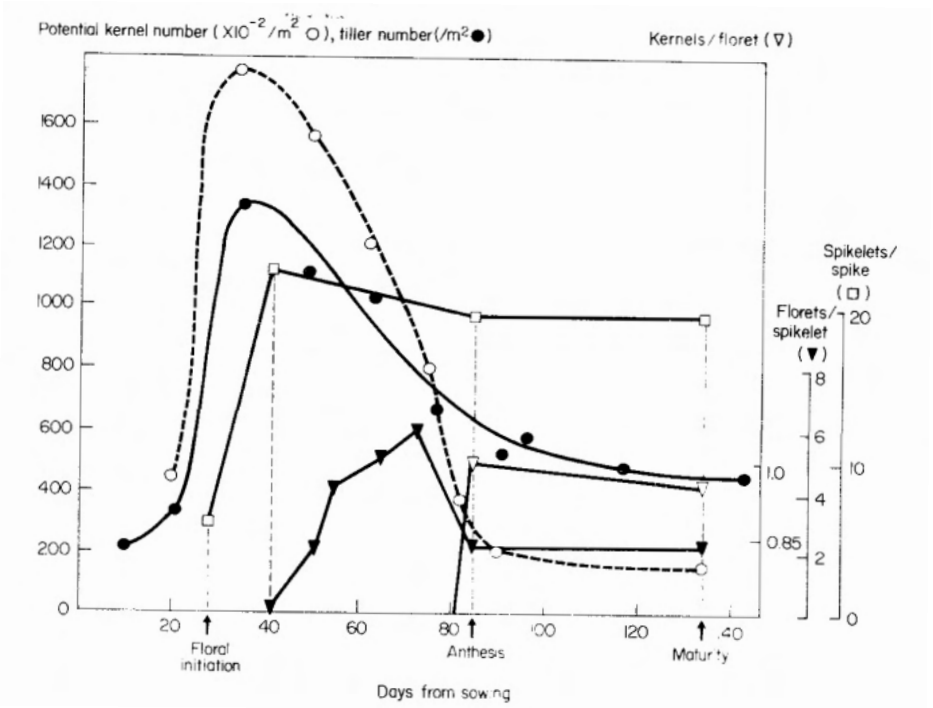
In many crop situations, especially those in which high yields are sought, competition for assimilate appears to determine component survival. However, before the spike growth period, assimilate investment in the spikelets and florets is minor relative to other sinks in the crop (<1%). It is proposed that assimilate competition becomes critical for component survival only when the plant enters the spike growth phase, for then a substantial allocation of dry matter is needed to build the inflorescence or spike (Fig. 1, 2). Thus, there is never enough assimilate in the crop to build all initiated florets into competent ones at anthesis. As a rough guide, each competent floret at anthesis requires 10 mg of spike dry weight in an awned cultivar; 20,000 florets m^2 would require a spike dry weight at anthesis of about 200 g/m^2. These considerations lead me to the approach to kernel number as outlined in the lower portion of Table 3. This replaces the interdependent numerical components with relatively independent durations, quantities, and ratios of assimilate (see also Gallagher 1979. Fischer and Stockman 1980).

Spike dry weight. There have been few studies on the determination of spike dry weight or kernels per unit spike weight, therefore my listing of influential factors in

Table 4. Mean of grain yield and associated traits in short spring wheat genotypes and the changes in each trait relative to the mean for tall genotypes.[a]

Trait	Short wheats mean[b]	Change relative to tall genotypes[c] (%)
Final plant ht (cm)	86	-31
Grain dry wt (g/m^2)	641	+22
Crop growth and development		
Leaf area index (LAI) at 51 days	3.9	-9
Crop growth rate (g/m^2 per day)[d]	14.1	-14
Days to anthesis	93	- 1
Total dry weight (TDW) (g/m^2) at anthesis	810	-10
Kernel number determination		
Spike dry wt/total dry wt at anthesis	0.24	+55
Spike dry wt (g/m^2) at anthesis	216	+39
Kernels/spike dry wt (g)	83	- 7
Kernel no./m^2	18,000	+32
Grain-filling period		
LAI at anthesis	7.1	- 2
TDW at maturity (g/m^2)	1,494	0
DTDW anthesis to maturity (g/m^2)	684	+14
Yield/DTDW	0.94	+ 7
Kernel wt (mg)	37	-7
Kernel wt/potential kernel wt	0.82	-19

[a]Mean of 3 years trials in northwest Mexico under conditions of irrigation and high fertility, with lodging protection for the tall genotypes. [b]6-30 genotypes containing Norin 10 dwarfing genes tested each year. [c]2-4 genotypes without dwarfing genes tested each year. After full cover.



5. Tiller numbers per unit area, spikelets per spike, florets per spikelet, kernels per floret and their product (potential kernel number) for the wheat crop of Figures 1, 2, and 4 Potential kernel number refers to tiller number multiplied by either the peak value (at or before its attainment) or the actual value (post-peak) of each of the other components. The initiation of florets in spikelets was estimates from growth cabinet studies of Fischer and Stockman (1980).

Table 3 may be incomplete. Nevertheless, it is clear that these factors dominate the processes against which they are listed. Kernel number is reduced drastically by higher temperature (Fischer and Maurer 1976, and by longer photoperiod (Wall 1979) in the spike growth period; both effects are ascribed to curtailment of the period. For example, artificial photoperiod extension for 14 days within the period 45 to 18 days before anthesis, advanced anthesis date 4 days and reduced kernel number significantly (13,870 vs 18,120/m^2, sign difference = 1,260) in a crop of Yecora 70 in northwest Mexico (Fischer unpubl.). Earlier photoperiod extension, in the interval 73 to 44 days prior to anthesis, advanced anthesis more (10 days) but did not reduce kernel number any further (14,820 vs 13,870/m^2), presumably because the extra acceleration of development occurred before the spike growth period. Altered radiation affects kernel number most when it coincides with the spike growth period (Willey and Holliday 1971, Fischer 1975, Evans 1978; see also Table 5). The effects appear to be approximately proportional to those on the overall rate of dry matter accumulation (Fischer 1975, Fischer and Stockman 1980). The net effect of radiation and temperature appears to be well summarized in the ratio of daily radiation to mean temperature during the spike growth period, as used later (see Table 5).

Table 5. Grain yield, crop characteristics, and weather for crops of Yecora 70 grown under irrigation and high fertility in each of 5 years in northwest Mexico.[a]

	1970-71	1971-72	1972-73	1973-74	1914-75
Gram yield (g/m^2)	724	605	588	707	863
Standard error (g/m^2)	4	4	24	26	29
Preanthesis period (A-30 days to A)					
Kernel number ($10^2/m^{-2}$)	190	157	129	165	186
Mean radiation (MJ/m^2 per day)	18.6	16.9	14.2	16.4	18.2
Mean temp (°C)	14.7	16.4	16.0	13.8	14.0
Photothermal quotient[b]	1.82	1.42	1.24	1.76	1.92
Postanthesis period[c]					
Kernel wt (mg)	38.3	39.5	45.6	42.5	45.1
Duration (days)	39	39	55	45	48
Mean radiation (MJ/m^2 per day)	24.0	22.7	23.1	21.1	22.1
Mean temp (°C)	19.6	20.3	16.8	17.8	16.9
Σ rad/kernel (MJ x 10^{-2})	4.9	5.8	7.4	5.8	5.7
Reduction KW with shade[d] (%)	18	18	2	20	20
Increase KW with thinning[e] (%)	32	28	12	23	18

[a]Sown Nov-Dec. anthesis late Feb-early Mar. [b]MJ/m^2 per day degree > 4.5°C. [c]From 50% anthesis to 50% spikes without green. [d]Fifty percent shade cloth over crop from anthesis to maturity. [e]Removal of all light competition from side rows at anthesis (see Fischer and Laing 1976).

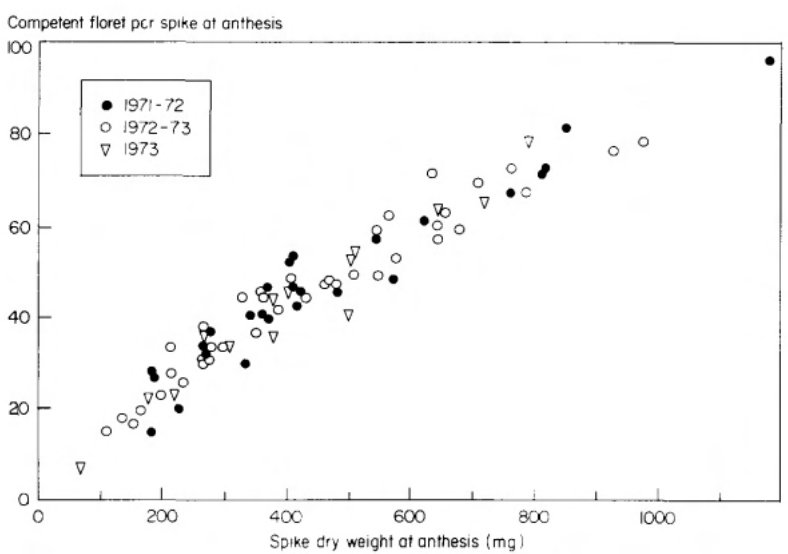
The proportion of assimilate allocated to the spike is not constant but rises to a plateau some 10 days before anthesis. The proportion does not appear to be greatly influenced by radiation environment, but is influenced by genotype and is greater in short cultivars. Because it is difficult to measure these ratios precisely over short periods, I use the ratio spike dry weight to total dry weight at anthesis as an indirect guide to allocation. In a comparison of a near isogenic pair of awnless genotyes differing only in stature, the portion was 0.21 for the short member with 2 major dwarfing genes, and 0.16 tor the tall (Fischer unpubl., see also Table 4).

This approach to spike dry weight determination ignores entirely any possible direct influence of the number of floret primordia a spike or crop may initiate, on the spike's final size or the crops' kernel number. This may seem ridiculous; I can only suggest that final average spike size in the crop is usually so far below potential (<50%) that this potential is irrelevant. For example, Evans (1978) reported for microcrops that short days in the vegetative stage, increasing the duration from about 20 to 50 days with corresponding increases in tiller and spikelet number, did not produce any more kernels per square meter for a given reproductive period radiation level. In tall and short wheats, the key to the allocation difference lies not in more floret primordia per spike or a stronger spike sink, but rather in less competition from the growing stem which is the major alternative sink (Bingham 1969. Brooking and Kirby 1981, Fischer unpubl.). I admit, however, that it is difficult to design unequivocal experiments and much remains to be resolved. The approach does lead to the suggestion that differences in early crop growth are important only if LAI is so limited that full light interception is not attained by the onset of the spike growth period (Fischer et al 1976).

Kernels per unit spike dry weight. The second component of kernel number, namely kernels per unit spike dry weight, is usefully divided into competent florets

per unit spike weight and kernel set (commonly known as grain set). Because competent florets are generally defined as those with complete floral parts at anthesis (having plump green anthers and capable of self-fertilization and bearing a kernel), this division refers to processes operating either *before* anthesis or at *or soon after* anthesis. Small problems arise because anthesis lasts several days in a spike and because spike structural dry matter continues to increase for several days after first anthesis. Nevertheless, I choose first anthesis as the sampling point.

The value of considering florets per unit dry weight or its reciprocal weight per floret, is that in a given genotype subject to environmental variation there is a close relation between floret number per spike and spike dry weight at anthesis (Fig. 6). It has been drawn that sudden or severe stress, either due to shading or water shortage, can by damaging developing anthers, in particular, reduce the number of competent florets per unit spike weight (Bingham 1966, Fischer and Stockman 1980, Morgan 1980). Reduced concentrations of water-soluble carbohydrate in the developing spike accompanied the shading effect (Fischer and Stockman 1980). The results may be exaggerated by the suddenness of stress in artificial environments because male sterility is rarely so clearly evident in the field, except as a result of late frost. Genotypic effects on the ratio measured in crops of 15 spring cultivars range from 85 to 124/g (Fischer unpubl.). I have always included the awns in spike dry weight; they can account for as much as 30% of the spike weight (60% in durum wheats) at anthesis. The inference then is that awns tend to reduce the number of competent florets expected per unit of investment in spike dry weight. However in one study there was no difference in kernels per spike between a pair of closely related lines with and without awns (Evans et al 1972a).



6. The relation of competent floret number per spike to spike dry weight at anthesis. Individual spikes are of Yecora 70 grown under a range of densities over several seasons in central and northwest Mexico.

The ratio of developed kernels per competent floret falls below its maximum value of one, because of failure in pollination or fertilization, or because of abortion and reabsorption of the young kernels. That is why the ratio is often called grain set and is expressed as a percentage. There have been few measurements of grain set as I define it, but evidence suggests that grain set is not particularly sensitive to normal variation in radiation level around anthesis (Fischer 1975, Wall 1979, Fischer and Stockman I980 cf. severe reduction in radiation in Wardlaw 1970, Jenner 1979), but there may be genotypic differences in this respect (Wall 1979, Jenner 1979, Fischer unpubl.). Grain set is not sensitive to moisture stress at anthesis (Fischer 1973). The damaging effects of moisture stress occur at a slightly earlier stage and the number of competent florets is more affected. Other indirect evidence points to detrimental effects of low (Kolderup 1975, 1979) and high temperature (Wardlaw 1970; Kolderup 1975, 1979), and effects of relative humidity (Kolderup 1975) and cultivar (Kolderup 1979, Bremner and Davidson 1978). In some cultivars grain set is substantially below maximum because fertilization of the more advanced basal florets inhibits grain setting in distal florets although they are also competent (Rawson and Evans 1970, Evans et al 1972b). Hormonal factors emanating from the fertilized florets may cause this inhibition. Notwithstanding these reports of environmental and genotypic effects, measurement of grain set (% kernels per competent floret) across 13 spring wheat cultivars grown under irrigation in northwest Mexico was close to 100% (mean 92%, range 82-99%). However a triticale cultivar gave a value low enough (67%) to suggest substantial loss of potential kernels due to poor grain set.

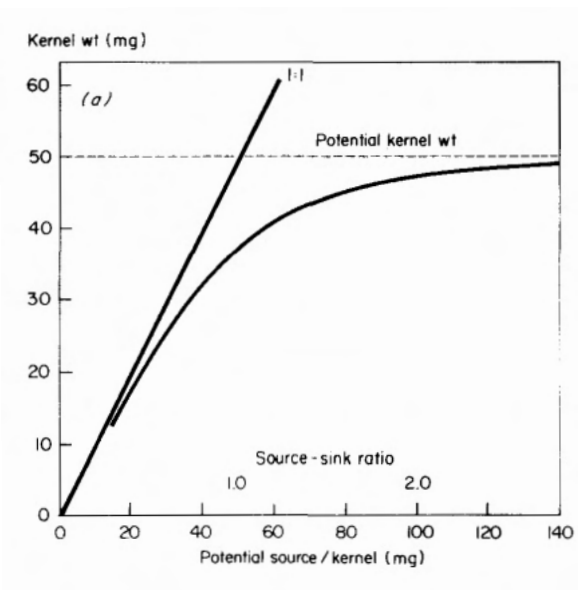
Why do short wheats have more kernels per square meter? The major genetic advance in the yield potential of wheat achieved in this century has been largely associated with reduction in plant height and is evident even in the absence of lodging. In spring wheats and where Norin 10 major dwarfing genes are involved, this advance has been most spectacular and has been entirely the result of more kernels per square meter (Aguilar and Fischer 1975, Jain and Kulshrestha 1976, Table 4). This arises from a more favorable partitioning of dry matter between spike and remainder as mentioned earlier, and is reflected in a higher ratio of spike to total dry weight at anthesis. Again there is no evidence in these data that the number of kernels per unit of dry weight invested in spike tissue is improved in the short wheats (cf. Bremner and Davidson 1978). Enough short genotypes were tested in one of the Mexican experiments to measure individual effects of the two nonallelic Norin 10 dwarfing genes (*Rht 1* and *Rht 2*). Either gene alone increased partitioning to the spike by 25%, kernel number 32%, and yield 20%. *Rht 1* tended to be more effective than *Rht 2,* while both genes together reduced stature further and increased partitioning to the spike by 56%, kernel number by 54%, and yield by 40% over the mean of these components for tall genotypes (Fischer et al 1981). These results confirm those of Jain and Kulshrestha (1976) with tall and Norin 10 dwarf spring wheats in India. Norin 10 dwarf winter wheats show yield advantages for similar reasons (e.g. Spiertz and van de Haar 1978). One question now is whether the relation between reduced stature and increased yield is in fact general, regardless of the genetic mechanism that reduces stature. Yield increases through polygenic dwarfing effects in Australian wheat (Davidson and Birch 1980) and UK wheats (Austin et al 1980), and non-Norin 10 major dwarfing genes as in Yugoslavian winter wheats (Borejevic

et al 1971), suggest to me that the relation is general, but some results suggest otherwise (e.g. "tall dwarf" hypothesis of Gale and Law 1977). A corollary question, whether reductions in stature and, more particularly improvements in partitioning to the spike structure, hair been exploited to their physiological limit, is also of great importance.

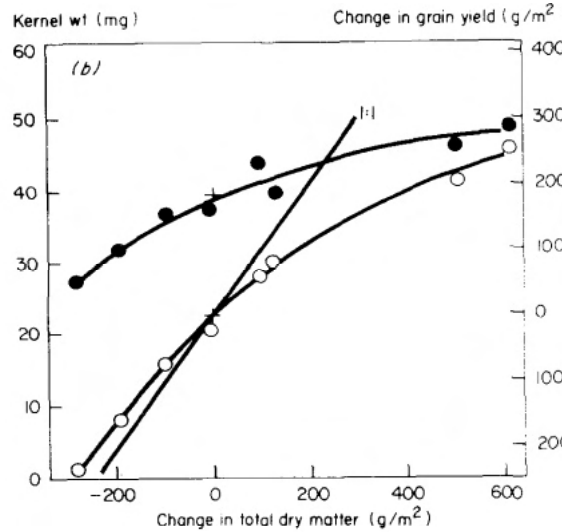
SOURCE-SINK INTERACTIONS IN GRAIN FILLING

Crop physiologists now favor the idea that yield can be limited by either the supply of assimilates (source) during grain filling, or by the number and capacity of kernels to be filled (*sink*), or by source and sink simultaneously. Experiments in which kernel number or source was artificially manipulated (Bingham 1966. Fischer and Hille-RisLambers 1978) suggest that in wheat the response of final kernel weight to the supply of assimilates resembles the response of reaction rate to substrate concentration (Fig. 7a). As source per kernel increases, final kernel weight falls below the initial linear relation with assimilate supply, and at higher levels of supply approaches asymptotically an upper limit which I define as the *potential kernel* weight of the genotype. Thornley (1979) has recently formalired a similar approach.

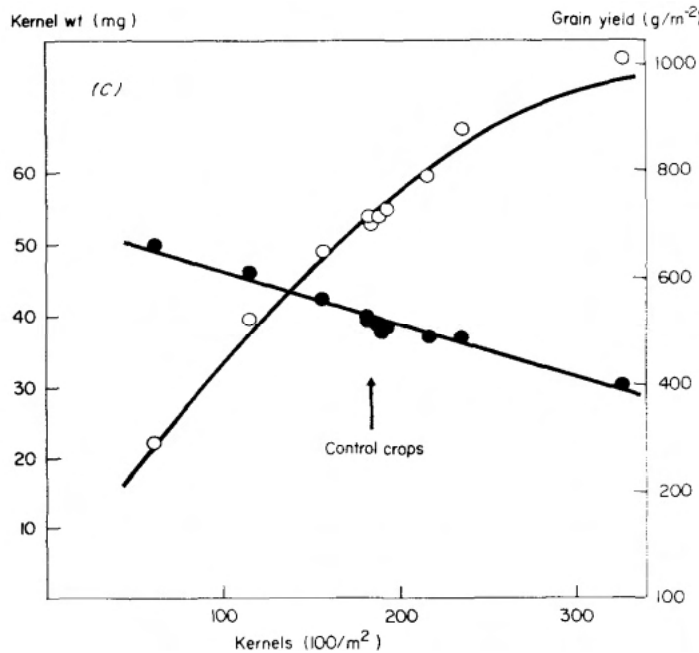
Multiplying both axes of Figure 7a by any given kernel number per square meter gives the response of grain yield to total source for that kernel number. The response was measured in crops of a given variety grown identically until anthesis, after which assimilation levels were manipulated through shading, thinning, and CO_2 fertilization (Fig. 7b). Yield responded to change in source (net total dry matter production from anthesis to maturity), thus indicating source limitation. However, the response was less than the 1:1 line especially at higher source levels. suggesting some sink limitation as well (see also Gifford et al 1973). Alternatively yield can be plotted as a



7a. Relation between kernel weight and potential source per kernel for a hypothetical cultivar with a potential kernel weight of 50 mg.



7b. Change in grain yield (open symbols) and actual kernel weight (clod symbols) vs change in total dry matter (DM) at maturity. Crosses represent the mean of control crops (total DM = 1,376 g m^2; grain yield = 594 g/m^2). Source (total dry matter) was reduced by postanthesis shading and increased by CO_2 fertilization and crop thinning. Yecora 70, northwest Mexico, 1971-72.



7c. Grain yield (open sysmbols) and kernel weight (closed symbols) as a function of Link size in terms of kernels m^2. Crops of Yecora 70 in northwest Mexico in 1970-71 having identical grain filling environments (see text and Fischer et al 1977).

function of sink size, with source held constant. Thinning and crowding at around anthesis, preanthesis shading, and early CO_2 fertilization treatments were used to vary sink size through change in kernel number in other experiments with the same cultivar as in Figure 7b (Fischer et al 1977). Grain filling radiation, temperature, and

moisture were identical for all crops; hence potential source remained approximately constant. Again the control crop fell in the region of curvilinear response, indicating both sink and source limitation of yield (Fig. 7c).

Sources of-assimilate for grain filling

Current assimilate has traditionally been considered the main source of reduced carbon for grain filling in wheat (Thorne 1974, Evans et al 1975). Total crop photosynthesis after anthesis can again be considered in terms of radiation intercepted by green tissue and its efficiency of utilization, E. Most well-grown crops would intercept all the radiation at anthesis (1 estimated 600-800 g/m^2 DM at anthesis is sufficient growth to give 95% interception in a typical crop). Nevertheless certain conditions such as high temperatures and moisture stress lead to rapid senescence of green tissue, especially leaf lamina; interception can be substantially less than 95% soon after anthesis, with essentially zero interception at or even before maturity. Only irrigated well-fertilized crops can be expected to show full radiation interception for the major part of grain filling (as in Fig. 3); maturity in these crops is characterized by spike senescence *before* flag leaf lamina senescence.

E values after anthesis have already been discussed. It is sufficient to reemphasize that the size of the spike sink relative to the green area may influence photosynthetic activity during grain filling. Under artificial conditions a decrease in relative sink size reduced activity, and an increase increased it (King et a1 1967, Rawson et a1 1976). Such control by sink probably operates in the field also, although it is not easy to demonstrate (e.g. Austin and Edrich 1975). Sink control superimposed upon the general decline in leaf nitrogen content as maturity is approached probably explains much of the variation in E seen during grain filling in field crops. In other words, the sustained high E values seen in Figure 3 probably require both the high kernel number of the 2-gene dwarf cultivar (18,000/m^2), and the high leaf nitrogen content resulting from the heavy fertilization (flag lamina contained 4.4% nitrogen 1 week after anthesis, 3.4% 3 weeks later).

The contribution of preanthesis assimilate reserves to postanthesis supply for grain filling has received renewed attention since it was reported that this contribution in wheat is substantial, especially under stress. It can amount to more than 50% of grain yield or up to 35% of dry matter at anthesis (Gallagher et a1 1976). However, studies using frequent in situ labeling of the whole crop canopy with $^{14}CO_2$ did not confirm such high contributions, even under grain filling stress (Lupton 1969, Bidinger et a1 1977, Austin et a1 1978, Stoy 1979). The data of Bidinger et a1 (1977) suggest a maximum contribution of around 10% (8% without drought, 13% with drought) of total dry weight at anthesis. At anthesis this stored assimilate appears to be divided approximately equally between water-soluble carbohydrate in stem tissue, and leaf protein. The cause of the large decreases in nongrain DM, often seen in crops between anthesis and maturity, remains unclear.

Sinks during grain filling

Before considering the obviously dominant sink represented by the kernels, it should be mentioned that the upper part of the wheat stem (peduncle) continues to grow

after anthesis and is one minor permanent sink for assimilate during the first part of grain filling (the lower stem is a major but temporary sink). Maintenance respiration is a substantial and probably essential sink throughout, being strongly influenced by temperature (Biscoe et al 1975). Other minor sinks may include lignin formation (Stoy 1965) and wasteful respiration.

Kernel sink. Kernel number was discussed when I suggested it is largely independent of postanthesis events. On the other hand, potential kernel weight, although by definition independent of factors operating solely upon assimilate supply (see Fig. 7a), appears to be influenced weakly by temperature. In one cultivar potential kernel weight decreased 0.6 mg or about 3% 1° C increase in mean grain filling temperature (Fischer and HilleRisLambers 1978). The same study suggests that potential kernel weight is independent of the preanthesis assimilation environment, but was strongly influenced by genotype. The effect that seems to be related directly (by a factor of about 4) to spike weight per competent floret (Fischer and HilleRisLambers 1978). Thus 10-mg spike weight per floret corresponds to a potential kernel weight of around 40 mg. or 2 t/ha of spike tissue at anthesis to a yield potential of 8 t ha. This relation indicates a hitherto unrecognized reason for negative phenotypic correlations between kernel weight and kernel number.

Problems of source/sink approach

1 have presented a simple view of the grain-filling period whereby the potential yield is essentially fixed at anthesis, and the grain-filling environment only affects the quantity of assimilate available to fill the kernels. Kernel size relative to potential responds, in turn, in a quantitative manner to the total assimilate supply, regardless of the temporal or spatial distribution of source. Many possible weaknesses in this gross approach to grain-filling can be identified.

Much work points to major changes occurring within the grain-filling period. In particular, large amounts of surplus assimilate build up in the stem during early grain filling but subsequently disappear due largely to retranslocation to the grain. Adequate time to permit the growing kernels to fully exploit these reserves may be an important consideration.

Another problem is that grain morphogenesis can be divided into several distinct phases, e.g. coenocytic (0-4 days after anthesis), cell division (0-14 days), and cell expansion (14+ days) (Brocklehurst 1979). There are possible separate environmental influences on each phase, and there is good evidence that early in grain filling the rate of cell division and hence final endosperm cell number is influenced by temperature (Wardlaw 1970) and the level of available carbohydrate (Brocklehurst 1979). Thus a second potential kernel size or weight would be defined that is probably governed by total endosperm cell number and determined in the first 10-14 days after anthesis (Brocklehurst 1979, Jenner 1979). This potential weight will be necessarily equal to or less than the one I define.

Quite independently of morphogenetic stages, dry weight accumulation by kernels shows the lag period, lasting for several days after anthesis, followed by a long period of linear growth. Curiously, the rate of linear growth, while showing a strong positive dependence on temperature in the range 10 to 20° C (Sofield et al 1977). is relatively independent of current rates of assimilation (Evans and Wardlaw 1976.

Evans 1978). While assimilate reserves probably play an important buffering role in this context, the stability of growth rate and hence linear growth in weight is still surprising. It suggests subtle control mechanisms and perhaps a degree of conservatism in the plant in setting kernel growth capacity and kernel number. These mechanisms have probably arisen in response to natural and human selection against shriveled kernels, i.e. ones whose final weights fall substantially below their early potential.

Many other aspects of the physiology of grain growth have received detailed study, because of the general but often uncritical belief that increasing gram size represents a direct route to yield increase. Aspects include the influence of environment upon size gradients in spikelets and spikes, and sucrose and nitrogen levels in growing grains. Some evidence suggests that kernel size does not respond solely to assimilate level (e.g Jenner 1980) and that other growth factors. perhaps hormones, can be limiting (Brocklehurst 1979). However, until such results are related to crops growing in the field, where source-sink ratios are often much less extreme than those used in physiological studies, their relevance is uncertain.

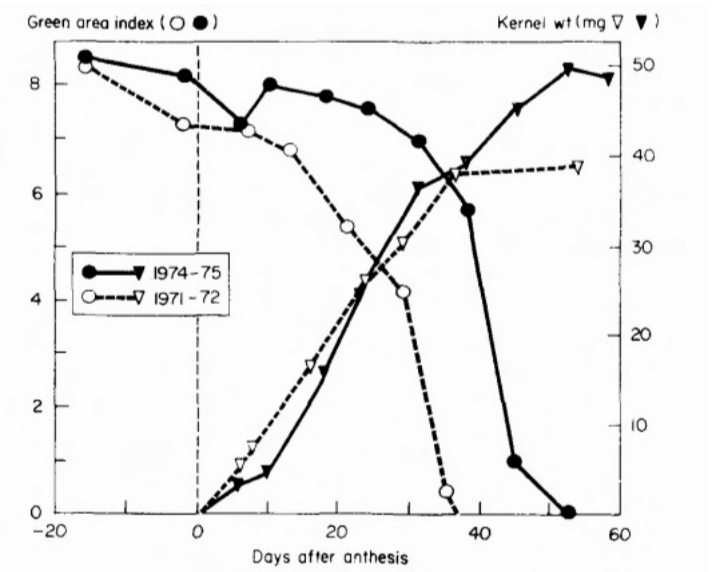
Examples of source-sink interactions

In contrast to experiments in which source and sink are manipulated artificially (thinning or shading, grain removal, etc), it is more difficult to demonstrate source-sink ratio differences in normal field crops in which growth, development, and weather interact to maintain a high degree of balance between source and sink. Nevertheless some effects have been identified. For example, the tall and short cultivar groups in Table 4 appear to differ in the direction one would expect because of the higher kernel number in the short wheats. Short wheats have a lower mean kernel weight (37 vs 40 mg), but higher potential kernel weight (45 vs 40 mg). Grain yield averaged 94% of total dry weight increase from anthesis to maturity, cf. 88% in tall wheats. All these results suggest that in this environment kernel filling in tall wheats was less limited by postanthesis assimilate supply. The higher yielding short wheats were limited to the extent that kernel weight was about 18% below potential. As a consequence yield in tall wheats might be better buffered against late stress and there is some evidence for this (Evans and Wardlaw 1976, Fischer and Wood 1979).

Environmental effects on source-sink balance can also be shown (Table 5). For a high-yielding short cultivar sown at the same time in each of 5 years in northwest Mexico, yield varied substantially. Much of the variation was due to kernel number variation which was closely correlated with preanthesis photothermal quotient. However, there was kernel weight variation and in 1 year with a high kernel weight (1973-73) the crop was almost entirely sink-limited (e.g. unresponsive to shading), presumably this was because of the very high ratio of postanthesis radiation to kernel number due to the low kernel number resulting from an unfavorable spike growth period. Other years showed moderate source limitation; it was probably greatest in the two hottest years 1970-71 and 1971-72.

It is obvious in Table 5 that postanthesis temperature had a major effect on kernel weight (simple cor·relation with mean postanthesis temperature was -0.952*, $P < 0.01$). The temperature effect is shown by time changes in green area and kernel weight during grain filling for the hottest (1971-72) and coolest (1974-75) years

(Fig. 8). The responses are as expected from controlled environment studies (e.g. Sofield et al 1977, Spiertz 1977), but do suggest that thecalculation of anthesis-to-maturity radiation per kernel (Table 5) probably overestimates source available in the hot year relative to the cooler one. The overestimate is probably explained by the more rapid senescence of green tissue in the hot year (green area index exceeded 2 for 32 days in 1971-72, about 43 days in 1974-75 for a 34% difference). Other evidence suggests that much of the effect of higher temperature on kernel filling is due to reduced source (e.g. Fischer and Laing 1976), undoubtedly through a reduction in green area (Fig. 8) and probably also through greater maintenance respiration losses. Whatever the nature of the effects involved, the strength of the negative relation between kernel weight and mean grain-filling temperature is always impressive (e.g. Midmore 1976). For 26 irrigated crops of Yecora 70 in northwest Mexico (including those in Table 5) and others sown over the October to January period, kernel weight was closely correlated with mean grain-filling temperature (r = -0.88. P <0.001, temperature range 15.5-20.9°C, slope - 1.8 mg ° C). The negative effect of higher temperature, both during the spike growth phase and during grain filling, is undoubtedly the major weather variable reducing the yield potential of wheat.



8. Changes in green area index (leaf + 0.5 surface area of green stern and sheath) and kernel weight during grain filling in hot (1971-72) and cool (1974-75) years. Yecora 70 under irrigation and high fertility in northwest Mexico.

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MAIZE

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Average grain yields of maize vary substantially among the temperate, subtropical, and tropical regions. Although the level of agronomic and economic inputs could explain much of the lower yield in the tropics, there appear to be regional differences in maximum grain yields for crops grown under nonlimiting conditions. These yield differences seem associated with partitioning of total dry matter to grain: efficiency of total biomass production appears similar for the regions.

At higher latitudes, grain yield tends to be limited by processes that influence the supply of assimilates for grain filling; in the lower latitudes (tropical) yield tends to be limited by processes that control grain sink development.

Factors that influence crop growth rate (CGR), partitioning of dry matter to the developing ear, spikelet fertility, and kernel abortion may influence grain number in tropical maize. Weight of individual grains is considered in terms of factors that might influence the size of the individual kernel sink and the supply of assimilates for grain filling.

This review briefly describes the maize plant and notes a few special characteristics of the crop as a cereal. The primary focus, however, is on limitations to grain yields in tropical maize (from lower elevations), with description of some physiological factors involved and suggestions for genetic avenues to improve grain yield. Emphasis is on improvement of yield efficiency through dry-matter partitioning.

SOME PHYSIOLOGICAL AND ECOLOGICAL CHARACTERISTICS

Flowering habit

Maize (*Zea mays* L,.) is of the family Gramineae. It is thought to have originated in the tropics of Latin America. It is normally monoecious, with staminate flowers in the terminal inflorescence (tassel) and with pistillate flowers on lateral shoots (ears).

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Thus, unlike other major cereals, maize produces its economic yield (grain) on a lateral shoot. Because of this separation of ear and tassel, plus the protandry of flowering, maize is primarily a cross-pollinated species. The separate development of the male and female inflorescences suggests unique implications for studies of grain yield limitations in the maize crop.

Photosynthetic pathway

Maize was one of the first species shown to possess the C-4 photosynthetic pathway (Hatch and Slack 1970), thus its photosynthetic metabolism differs from that of the two other major cereals, wheat and rice. Associated with C-4 photosynthesis are extremely low rates of photorespiration and the distinctive leaf anatomy, including the prominent bundle sheath cells (Hesketh and Baker 1970). Discovery of the C-4 photosynthetic pathway explained high leaf photosynthetic rates, low CO_2 compensation points, and the absence of photosynthetic light saturation up to full sunlight (Hesketh and Musgrave 1962, Hesketh 1963, Hesketh and Moss 1963). The C-4 photosynthetic pathway also is associated with different chloroplast morphology, more rapid translocation of photosynthate from the leaf, and greater water-use efficiency. These characteristics may give C-4 plants a great productive advantage over C-3 plants. However, a review of research, ranging from the microscopic laboratory level to macroscopic field experiments, suggests that the advantages of the highly productive C-4 photosynthetic mechanism over that of the C-3 diminish progressively (Gifford 1974). Monteith (1978) questioned some of Gifford's conclusions. Evans (1975b) suggested that the advantage of the C-4 photosynthetic pathway does not lie in maximizing crop growth and yields, but in better adaptation to high-temperature, high-insolation conditions (provided the nights are not cold).

Adaptation

Maize varies widely in length of growing season and in plant morphology. Characteristics such as plant height; leaf number, size, and angle; tiller number; tassel size; ear number; root morphology; grain shape, color, and texture vary tremendously. Survival of this morphological variability has depended on selection by man, without whose husbandry maize cannot survive.

Because of its variability, maize as a species shows extremely wide adaptation. It is grown as a commercial grain crop from about lat. 55° N to 40° S and from sea level to 4,000-m altitude (Goldsworthy 1974a). However, maize cultivars are generally much more restricted in their range of adaptation. The environmental factors that can be overcome by the plasticity within the species — but which so limit the range of adaptation of individual cultivars — are temperature, day length, diseases, and, to a lesser extent, insects.

LIMITATIONS TO GRAIN YIELDS IN TROPICAL MAIZE

Regional yield averages

Goldsworthy (l974b) estimated from world production figures (FAO 1970) mean maize yields in the 3 climatic regions of the world as follows: 1) temperate regions, 3.5 t/ ha; 2) subtropical regions, 1.8 t/ ha; and 3) tropical regions, 1.0 t/ ha. Most of

these yield differences may reflect the level of agronomic practices in the regions. Often, there are severe problems of soil fertility, plant diseases, insects, weeds and other pests, moisture supply, and a tendency to extremes of weather in the tropics. Furthermore, in the developing countries, maize is generally grown by subsistence farmers, frequently under poorer conditions than are other crops in the same area. It seems likely that significant yield increases will be achieved through improved agronomic and economic (market) management, with some yield increases through genetic improvement for pest resistance.

Comparison of maximum grain yields

This review emphasizes maximum maize productivity in tropical environments. Even under experimental conditions of nonlimiting nutrients (including moisture) and freedom from harmful pests, differences in the yield potential of maize would be expected for the different regions mentioned. In the temperate region, maximum yields of 19 t ha have been reported by Cuany et al (1970). More recently, a yield of 22 t/ha for a 5-ha field has been reported in Michigan, USA. Certainly yields of 10 t/ha at the commercial level are common (Frey 1971). In the tropics, most of the high yields reported are confined to intermediate- or high-altitude areas having long rainy seasons. Yields of 12 t/ha have been reported from Salisbury, Rhodesia (Zimbabwe) — lat. 18°S, alt. 1,500 m — by Allison (1969), and yields of 10 t/ha have been reported from Kitale, Kenya — lat. 2° N, alt. 1,890 m — by Harrison (1970). In the lowland tropics, yields may range from 5 to 8 t ha with good management.

However, it is misleading to compare these maximum yields without considering growth duration. High yields are obtained in temperate latitudes by careful matching of varietal characteristics with temperature, photoperiod, and radiation to use all the available growing season. By contrast, the maize-growing seasons in the tropics are often determined by moisture supply or peak incidences of insects and diseases or both. Thus, yield per crop may be less important than yield per day in the field. Productivity per unit of land per year from multiple crops may be more important than yield per crop.

Nevertheless, grain yield differences are not always caused by differences in crop duration, measured either in days or in accumulation of heat units (Table 1). Thus, grain yield and grain yield per day of crop duration are higher for temperate maize, even when tropical material is grown in a subtropical environment such as Tlaltizapan in Mexico (lat. 18° N, alt. 940 m) (Table 1).

Yield as a function of biomass partitioning

The differences in grain yield between tropical and temperate materials can be examined in terms of differences in total biological production and in the partitioning of this dry matter to the grain (harvest index).

Evans (1975b) reported that the photosynthetic pathway of crops such as maize provides growth advantages in tropical environments because of the higher optimum temperature for photosynthesis, the absence of photorespiration, and a favorable transpiration ratio. Stewart (1970) concluded that, by innovative agronomy (including careful matching of genotypes to various tropical environments), many tropical areas could outproduce temperate areas by judicious use of monocropping,

Table 1. Comparison of some growth, yield, and environmental factors between tropical and temperate maize.[a]

	Total dry matter (t/ha)	Grain yield (t/ha)	Harvest index	Parti-tioning index	Kernels (no./m^2)	Peak CGR[b] (g/m^2 per day)	Crop duration (days)	Crop duration (Ontario heat units)	Radiation receipts (g cal/cm^2)	LAI[b]
Tropical										
Yamaguchi (1974a)	15.5	5.9	0.38	0.79	2,590	35	112			4.5
Goldsworthy et al (1974)	19.7	7.5	0.35	0.86	3,000	35	145			4.8
Tuxpeño Cycle 6										
Poza Rica	12.4	4.3	0.35	0.93[c]	2,005		108	3,384	44,838	3.1
Tuxpeño Cycle 6										
Tlaltizapan	19.1	7.8	0.41	0.92[c]	2,760		135	3,891	62,217	4.4
Kowal and Kassam (1973)	18.6	6.8	0.36	0.61		53	117		60,304	3.7
Intermediate temperate										
Fritton et al (1977)	14.9	7.1	0.47				130			4.0
Duncan et al (1973)		10.7					160		84,600	
		8.1					136		93,500	
		7.6					127		63,000	
Stewart (1970)						2849				
High latitude temperate										
Daynard et al (1969)	12.0	6.5	0.54	1.16			154			
Bunting (1977)	13.5	6.8	0.50	0.91			184	2,700		
Tanaka and Yamaguchi (1972)	15.9	9.2	0.58	0.98	3,360	26	158			4.4

[a]Construction of this table involved considerable difficulty because of the dearth of such a range of data on a single crop. Some of the numbers were extracted from figures in the publications and 50 are only approximations. [b]CGR = crop growth rate, LAI = leaf area index. [c]Estimates based on total dry matter at black layer stage, below maximum.

multiple cropping, or relay cropping. Because temperatures in much of the tropics are suitable for year-round crop growth, with good management crops and pastures can produce more per unit area per day in tropical areas than in temperate areas. Stewart concluded that production of total biomass in tropical environments is not a limiting factor to yield as did Goldsworthy et al (1974) and others. Biomass production (excluding roots) was approximately 24 t/ ha, achieved in 130 days. Peak CGR in these experiments was approximately 35 g/m^2 per day compared with a peak CGR of 49, 40, 32, and 28 g/m^2 per day for maize grown in the US (Stewart 1970). This represents a conversion efficiency of visible radiation into dry matter (assuming 4 kcal/g dry matter, visible radiation 45% of total) of 5.1-7.2% in the tropical environments (Goldsworthy 1974b) compared with 4.6-6.4% in the US Corn Belt (Stewart 1970). A number of studies have shown varietal differences for photosynthetic rates in maize but there is no evidence that the genetic potential is different in tropical and temperate genotypes. Duncan and Hesketh (1968) evaluated 22 maize races and found photosynthetic rates from 36 to 59 mg CO_2/dm^2 per hour at 30° C. Races from low altitudes had higher photosynthetic rates at high temperatures than did races from high altitudes. Ancient races possessed variability for photosynthetic rates similar to that of modern races. Heichel and Musgrave (1969) studied 7 maize varieties in a temperate region and found leaf photosynthetic rates ranging from 21 to 59 mg CO_2/dm^2 per hour. Rates for temperate materials in a tropical environment ranged from 28 to 85 mg CO_2/ dm^2 per hour; those for some tropical materials in the same study, from 34 to 74 mg CO_2/dm^2 per hour.

Respiration rates of maize in the field have not received as much attention as photosynthetic rates. In recent years, photorespiration has been investigated to a greater extent than dark respiration. Yamaguchi (1978) reviewed respiration and growth efficiency in relation to crop productivity. Growth efficiency (GE) is defined as the fraction of assimilation fixed into new plant tissue. The respiratory rate for the whole maize plant was about 4-9 mg CO_2, g dry weight per hour in the early growth stages, decreasing to 2-4 mg CO_2/g per hour at flowering. This resulted in an overall GE of about 65% for the period up to flowering. After flowering, the respiration rate declined to 0.5 mg CO_4/g per hour at maturity while GE was maintained at about 70% during the grain-filling period. Thus, photosynthesis and the accumulation of total biomass in tropical materials grown in tropical environments are comparable to those of temperate materials in temperate environments.

Goldsworthy and Colegrove (1974), Goldsworthy et a1 (1974), Goldsworthy (1974b), and Yamaguchi (I974 a, b, c) attributed the low grain yields in the tropics to poor partitioning of total dry matter to grain. The materials used in the studies included a range of maturity groups and some hybrids. Plant densities were also varied. The harvest indices obtained (0.3 to 0.4) contrasted with values of 0.5 to 0.55 reported for the temperate area (Daynard et a1 1969, Tanaka and Yamaguchi 1972).

Differences in patterns of dry matter accumulation and partitioning after flowering, which may be closely associated with harvest index, appear to be associated with the three climatic zones where the crop is grown. These three zones and associated accumulation and partitioning patterns are as follows.

Zone 1: High latitude temperate areas that are fringe areas of maize cultivation; e.g., the northern fringe of the US Corn Belt, Canada, northern Europe, northern

Japan. Evidence indicates considerable late translocation to the grain of dry matter previously stored in the stem, including leaf sheaths (Daynard et al 1969, Tollenaar and Daynard 1978a, Bunting 1977, and Tanaka and Yamaguchi 1972). Low temperatures limit the length of the growing season, growth duration is short, and the varieties appear to be very efficient — the ratio of grain yield to dry matter produced after flowering (partitioning index) is high (about 1.1) and the harvest index is high (about 0.55). Maize scientists in this zone consider the crop to be limited by the *source* during grain filling. The varieties have short plant height, small tassels, and low apical dominance.

Zone 2: Intermediate temperate areas exemplified by the Corn Belt of the US, southern Europe, and much of Japan. The most productive varieties in this zone have an almost constant stover weight after maximum weight is achieved a few days after flowering. Thus, the partitioning index is about 1.0 and the harvest index, usually about 0.5. Growth duration is relatively long. Goldsworthy (1975) considered such a dry matter accumulation and partitioning pattern, where grain growth almost parallels crop growth after flowering, to be ideal for a grain crop. Maize scientists consider yields to be equally limited by *sink* and *source.*

Zone 3: Lowland tropical areas (below 1,000 m). Maize accumulates considerable dry matter in the stem, leaf sheaths, cob, and husk after flowering. Some of this dry matter is translocated to the grain late in the grain-filling period (Palmer et al 1973). Varieties are inefficient, having a low partitioning index (0.8) and low harvest indices (0.3 to 0.4) (Goldsworthy 1974b). Maize scientists consider yields to be limited mainly by the size of the grain *sink,* although under some environments loss of leaf area (source) near maturity may reduce grain yields (Goldsworthy et al 1974).

Tropical maizes generally are late maturing, tall, leafy, and large tasseled. They show a greater level of apical dominance, a low harvest index, and are less efficient in retranslocating to the grains dry matter previously deposited in the stem. Such characters presumably were important to the adaptation of maize to the tropical environment. Tall, leafy genotypes would compete with rapid weed growth, and the effect of loss of leaf due to insects would be minimized. Reserves of stem sugars may have provided drought tolerance and may have been associated with resistance to stalk rot. The relatively large vegetative growth of tropical maize also may be important in the nitrogen nutrition of the crop (Evans 1975b).

The types of maize in the highland tropical zone (above 1,000 m) are intermediate between those of the lowland tropical and the intermediate temperate areas; the growth duration is longer than in the lowland tropics and is limited at either end by low temperatures and by moisture available for planting. Varieties grown in highland tropical areas of Mexico and lowland tropical varieties exhibited similar dry matter accumulation and distribution patterns (Goldsworthy and Colegrove 1974; Yamaguchi 1974a,c). Although yields in the highland tropics were higher than those in the lowland tropics, the authors concluded that yields in both areas were limited by the capacity of the grain sink to use assimilates.

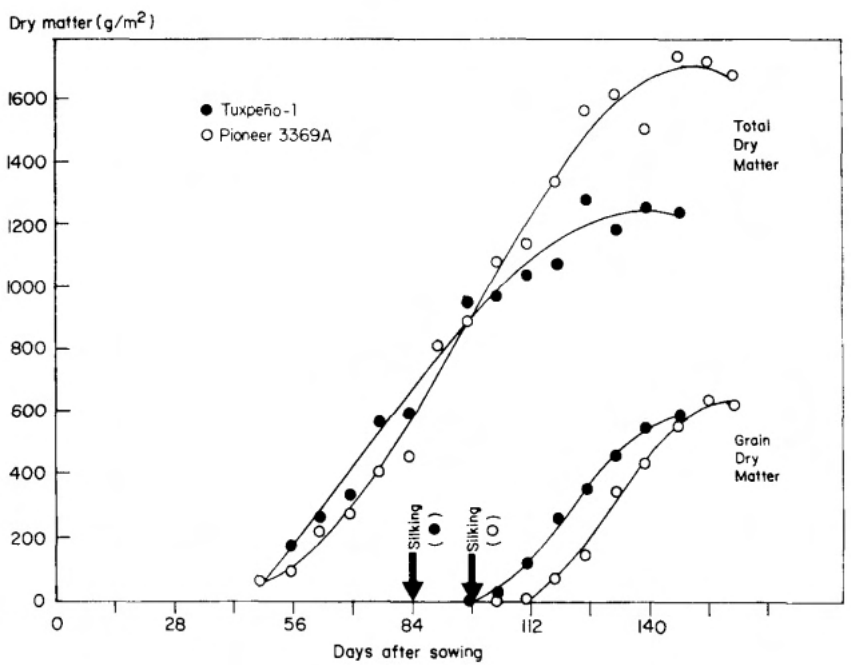
Although some of these differences in partitioning undoubtedly are due to environment and genotype × environment interactions, there are considerable genotypic variations per se when different genotypes are grown in the same environment. Because of the photoperiod sensitivity of tropical genotypes, such a com-

parison cannot be made in a temperate environment. On the other hand, temperate genotypes are susceptible to tropical pests and cannot be grown satisfactorily in the tropics. However, at a medium altitude site in Mexico (Tlaltizapan 940 m), both groups of genotypes grow well. Figure 1 compares the growth curves for a tropical maize Tuxpeño-1 and a temperate material Pioneer 3369A grown at the site. Total dry matter production for Tuxpeño-1 was higher because of 1) a larger leaf area index (LAI), 4.5 for Tuxpeño-1 and 2.3 for Pioneer 3369A, and 2) a longer growth duration.

Similarity in grain yields, however, resulted in a large difference in harvest index (0.40 for Tuxpeño-1 compared with 0.50 for Pioneer 3369A), and partitioning indices 0.80 for Tuxpeño-1 and 1.0 for Pioneer 3369A. Total soluble sugars in the stem at grain maturity were 1,250 kg/ ha for Tuxpeño-1 and 250 kg/ ha for Pioneer 3369A. In the tropical material, sugar content, measured as a percentage of stem dry weight, increased from 16% at flowering to 22% at maturity (CIMMYT 1975).

The more efficient partitioning of dry matter to grain, previously noted in the Corn Belt zone, may be a genetic characteristic, because it is expressed under tropical conditions as well. Thus, it should be possible to improve grain yields of tropical material through genetic improvement of the distribution to the grain of photosynthates already produced.

Using the example in Figure 1, if the pattern of partitioning of the Tuxpeño material was modified to that shown for Pioneer 3369A, the grain yield would be 8.25 t/ ha, an increase of 32%. In other terms, if those sugars currently stored in the



1. Total crop and grain dry matter accumulation in Tuxpeño-1 and Pioneer 3369A grown at Tlaltizapan, winter cycle 1974, at 80,000 p/ha (silking date indicated).

stem of the tropical material could be used in grain production, they would account for a considerable yield increase. This might be at the expense of adaptation to some previously mentioned tropical stress conditions.

For maize grown in the higher latitudes, yield improvement may depend more on factors that are involved in total biological production. The maximum reported grain yield of 22 ti ha at the northern fringe of the US Corn Belt approaches the biological maximum grain yield (28-31 t/ ha), from a total aboveground crop production of 60 t/ ha (US National Academy of Sciences 1975).

PHYSIOLOGICAL CONCEPTS FOR INCREASING GRAIN YIELD

Maize is discussed here as a crop grown under conditions of nonlimiting nutrients (including moisture) and free from harmful diseases and pests. Thus, suggestions for changes in some characters to improve productivity under these conditions would not apply to performance under more limiting conditions. Some possible adverse interactions have been noted.

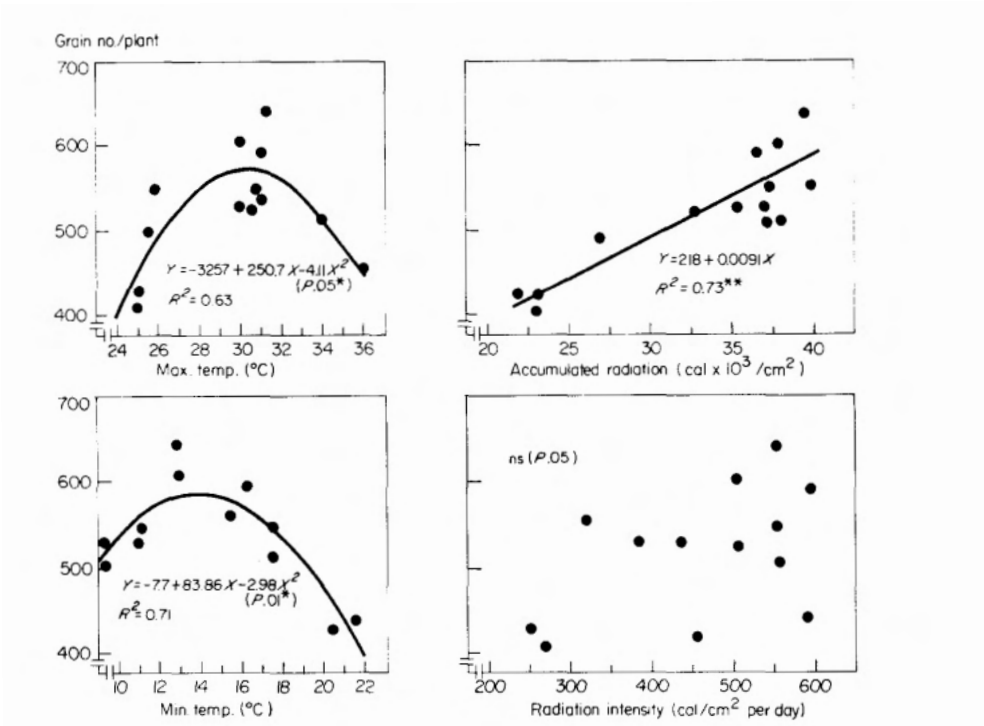
Basically, the crop is considered a system for harvesting solar energy by converting it to grain dry matter. (This focus on increasing grain yield could neglect other economically important plant parts.) The genotype influences the amount of energy fixed, as well as its distribution to various plant parts. Grain yield on an area basis is considered in its simplest components of grain number per unit area X kernel size, Some physiological processes involved in the determination of these two components, and which are amenable to genetic change, are described.

Grainnumber

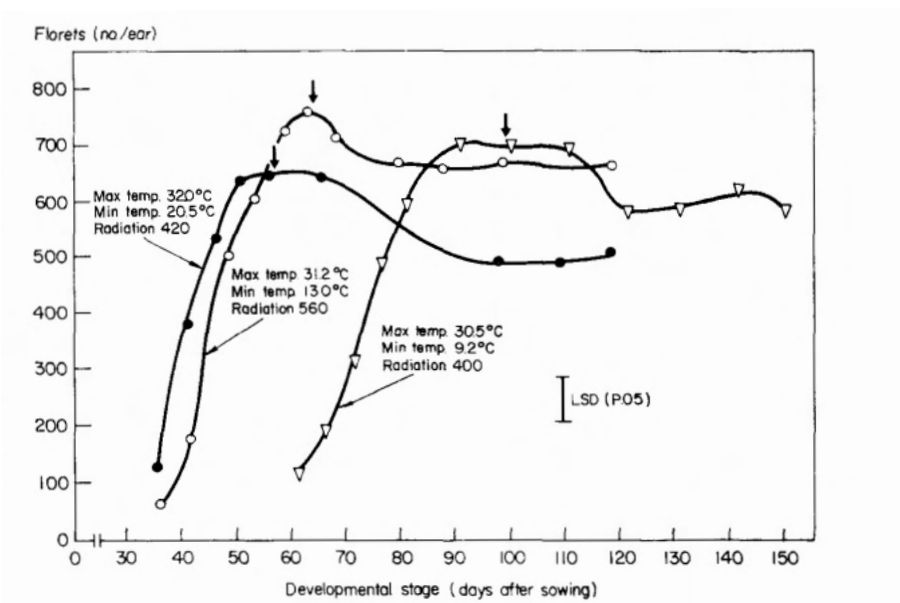
Grain number per unit area depends largely on events before and around flowering. In the tropics, it is the yield component that usually accounts for most of the yield variation between genotypes (Yamaguchi 1974d). Variation in the grain yield of 12 tropical populations, grown at 15 sites in Mexico to provide different environments and planting dates, was linearly related to changes in grain number ($Y = 482.4 + 13.6x$; $R^2 = 0.7$) and rate of grain growth ($Y = 310 + 959x$; $R^2 = 0.36$); but not to duration of grain growth.

The maximum final grain number per plant was achieved in environments where the mean temperatures were 30° C maximum and 13.5° minimum during the development stage from floral initiation to flowering. This effect was probably due to the influence of temperature on rate of crop development. There was a strong relation between grain number at harvest and the total radiation accumulated during the development stage from initiation to flowering; grain number was relatively independent of radiation intensity during the period (Fig. 2).

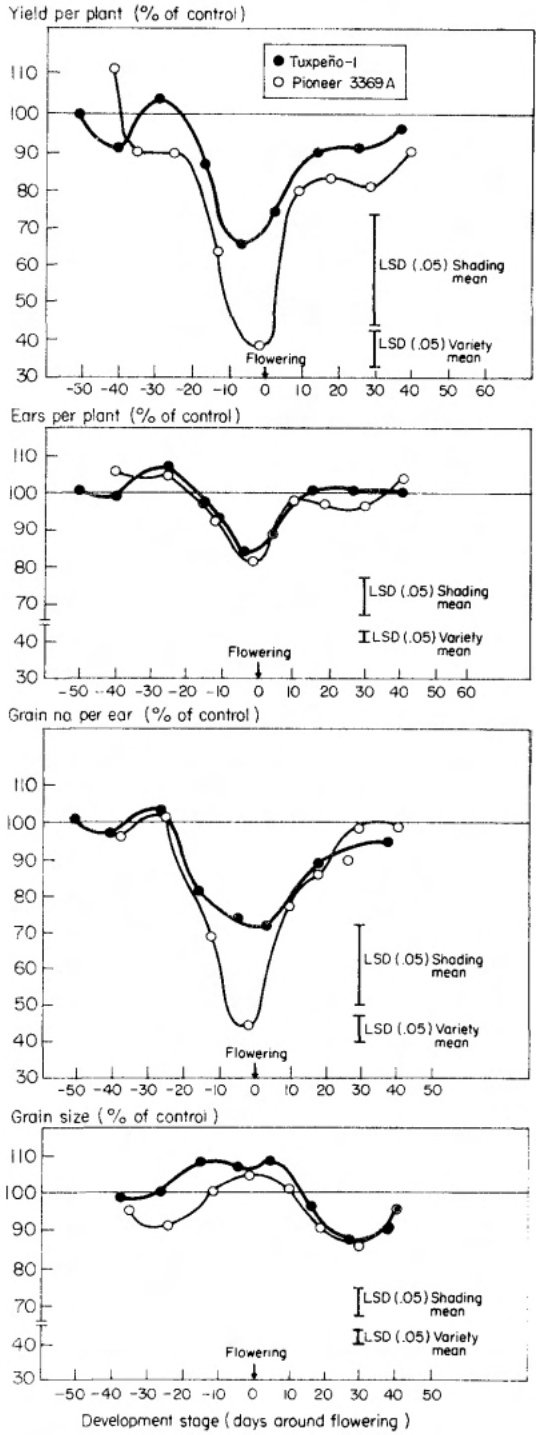
The effect of environmental conditions on spikelet number (potential grains) before flowering, and the influence of conditions on spikelet and grain abortion at and after flowering have not been studied closely. However, the pattern of spikelet development on the primary ear of one tropical variety (Tuxpeño-1) (cycle 9), grown under contrasting environments, has been examined (Fig. 3). The fewer kernels at harvest under higher temperature and lower radiation conditions are partly due to floret abortion after flowering. Tollenaar (1977) recently reviewed the control of



2. Effects of mean maximum and minimum temperatures and daily total radiation and total accumulated radiation during the period from initiation to flowering on final grain number in tropical maize.



3. Pattern of primordia development on the primary ear of tropical maize grown at 3 sites in Mexico.



4. Effect of a single period of 22 days with 54% shading of the crop at different stages of development on the grain yield and its components in a tropical lowland variety (Tuxpeño-1) and in a temperate hybrid (Pioneer 3369A) grown at Tlaltizapan, Mexico, during the winter season.

source and sink development in maize and concluded that the intercepted irradiance per plant during flowering was the dominant factor determining grain number. Grain number is considered here to be influenced by 1) crop growth rate at a critical stage, 2) the partitioning of dry matter to the ear, and 3) a *spikelet fertility,* factor.

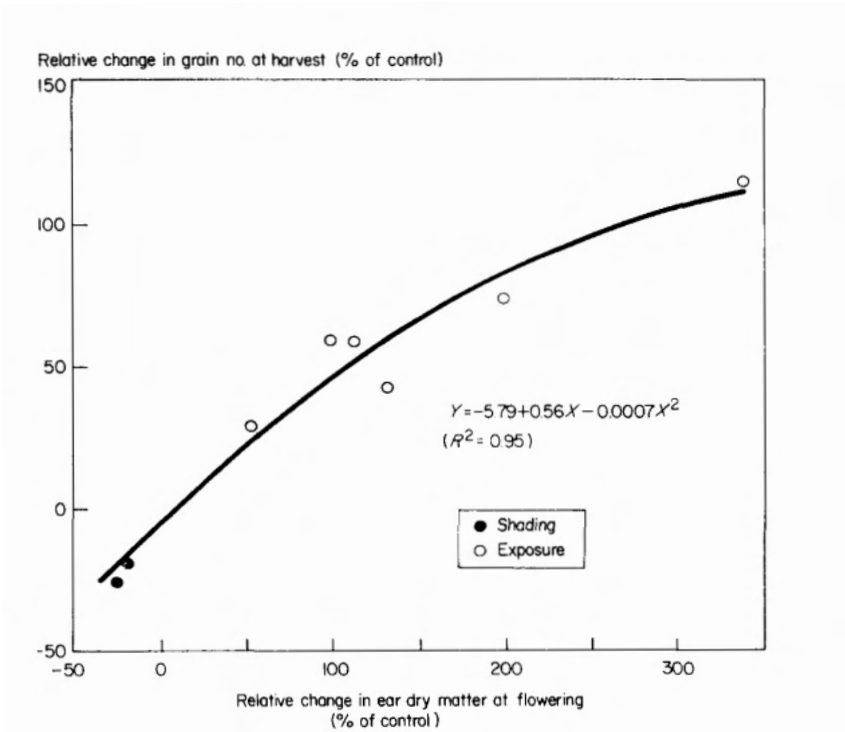
Crop growth rate

The effects of artificially reduced light for short durations during all stages of crop development have been examined for two materials, Tuxpeño-1 and Pioneer 3369A at Tlaltizapan, Mexico (elevation 940 m). Reducing the light by shade cloth with 45% transmission around flowering reduced grain yield substantially in both materials, but more markedly in Pioneer 3369A, the temperate material (Fig. 4). Most of the yield reduction and the difference in genetic response was due to effects that ultimately reduced kernel number per plant as measured at harvest. Shading during the 15 days before flowering reduced spikelet number at flowering by 7.0%. Thus, at harvest most of the effects on kernel number were due to spikelet and kernel abortion occurring after silking. Data from treatments in which neighboring plants were artificially thinned to increase irradiance per plant at successive developmental phases supported the data from shading treatments (CIMMYT 1975). Less interplant competition during the period of 10 days before and after flowering seems to account for increases in grain yield per plant after thinning. There was a significant increase in ears per plant and a nonsignificant, but large, increase in grain number per ear (CIMMYT 1975). Both shading and thinning treatments during the preinitiation stage of development did not significantly affect grain yield. The evidence suggests that efforts to increase grain yield through increased assimilate production should focus on the period around flowering (about 10-15 days before and after). Prine (1971) identified this growth stage as a critical period for ear development for temperate maize. In a subsequent discussion, this will be called the critical growth period for determining grain number.

Shading and thinning during the 15-day period before flowering altered the amount of ear dry weight at flowering. Figure 5 shows an approximate relation between ear dry weight at flowering and grain number at harvest at Tlaltizapan. Ear dry weight and grain number are expressed as percentage changes relative to their value in the control treatments. This relation suggests that a 10% increase in ear dry weight at flowering could result in a 5.5% increase in grain number at harvest. For example, a typical crop at Tlaltizapan produced 250 kg ear dry weight/ha at flowering and a grain yield of 6.25 t/ha. Hypothetically, an increase of 1 kg ear dry weight/ha at flowering could produce a grain yield increase of 14 kg/ha at harvest. Data presented in the following section appear to support this hypothetical relation.

Dry matter partitioning

During the critical growth period there is simultaneous growth of other plant parts. Shading for 14 days before flowering reduced the total crop dry weight at flowering by 14%. The dry matter was reduced by 14% in the stem, 20% in the leaf, 15% in the tassel, and 32% in the ear. Thus, at this stage, dry matter of the ear was affected more than other plant parts by a reduction in photosynthesis. Reducing the size of some of the other organs may allow for greater partitioning of dry matter to the ear.



5. Relation between relative change in ear dry matter at flowering and grain number at harvest due to shading or exposure of tropical maize plants 15 to 20 days before flowering. Data based on area and are the mean for 2 varieties. The relation is based on untransformed data; thus it is an approximation.

Table 2 shows the effect of selection for reduced plant height on the percentage of total dry matter as stem and ear at flowering in Tuxpeño Crema I. The percentage of stem was reduced from 59.5 for cycle 0 to 49.0% for cycle 15. The percentage of ear was increased from 2.02% for cycle 0 to 3.16% for cycle 15. At plant densities for optimum yields, there was progressively more ear dry matter (on an area basis) at flowering in successive cycles of selection for shorter plant height. This was associated with a higher grain number (per unit area) at harvest (Fig. 6).

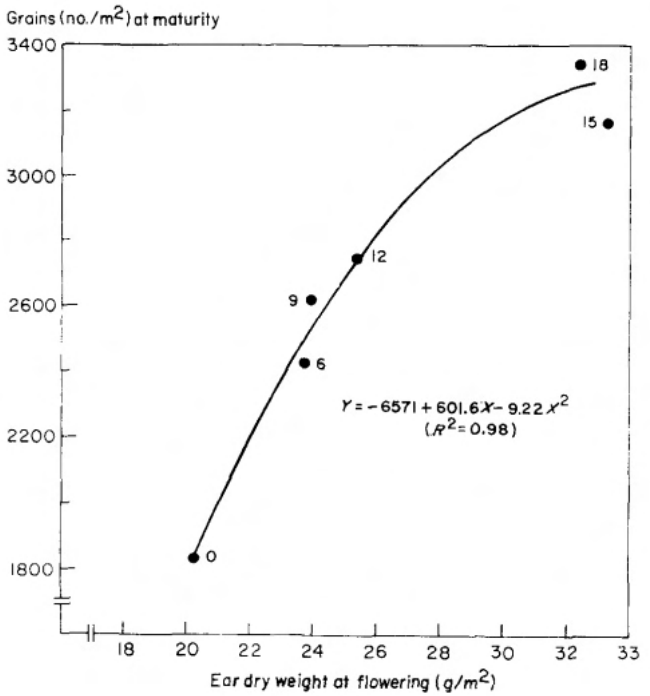
In the hypothetical example previously presented, a 1 kg/ ha increase of ear dry matter at flowering would provide a 14 kg/ ha grain yield increase. Using the relation shown in Figure 6, a 1 kg /ha increase in ear dry weight at flowering would provide a 34 kg/ ha increase in grain yield.

Detasseling of maize increases grain yields (Grogan 1956, Duncan et a1 1967, Hunter et a1 1969). In tropical maize grown under stress levels of nitrogen, water, and plant density, careful removal of the tassel before flowering increased grain yield by 9.5, 21.0, and 17.9%, respectively (Poey et a1 1977). Most of the difference in grain yields was explained by differences in grain number per plant with small differences in grain size. Although some effects of detasseling might be due to improved irradiance of the crop leaf canopy (Duncan et a1 1967, Hunter et a1 1969, Lambert and Johnson 1978), Muleba (1980) suggested that much of the effect may be through a reduction of apical dominance by the tassel. Messiaen (1963) demonstrated that

Table 2. Plant height and total dry matter (aboveground) at flowering, and its distribution to stem and ear for various cycles of selection for reduced plant height in Tuxpeño Crema 1 grown at near optimum density. (Data are the means for 2 years at Tlaltizapan and 1 year at Poza Ria, Mexico.)

Selection cycle	Plant ht (cm)	TDM[a] at flowering (t/ha)	Distribution of dry matter	
			Stem (%)	Ear (%)
0	298	10.5	59.5	2.02
6	232	9.5	53.8	2.59
9	218	10.2	52.2	2.85
12	213	10.1	51.2	2.91
15	186	8.5	49.0	3.16
LSD P.05	11	1.5	1.7	0.99

[a] TDM = total dry matter.



6. Relation between ear dry weight at flowering and grain number at maturity in various cycles of selection for reduced plant height in Tuxpeño Crema 1. Data are means of 2 locations.

maize differed from other cereals in that the ear grows from an axillary bud and is subject to apical dominance. Experiments involving male-fertile and male-sterile hybrids (Chinwuba et al 1961) support the concept that low tassel metabolic activity before anthesis may enhance ear growth.

Leaf growth continues until silking, or soon after (Hanway 1962), but there is no evidence that leaf growth influences ear growth during the critical growth period. Certainly there is considerable evidence that grain yields (and therefore grain

number) increase with LAI up to values ranging from approximately 3 to 5 under both US Corn Belt (Eik and Hanway 1966) and tropical conditions (Yamaguchi 1974d). Studies of the effects of leaf removal on grain yield in temperate maize have usually focused on the postflowering grain-filling period. Grain yield reduction tends to be proportional to loss of leaf area (Hoyt and Bradfield 1962. Egharevba et al 1976). However, with the SR52 hybrid grown in Rhodesia, defoliation about 30 days before flowering reduced leaf area approximately 30% at flowering, and reduced grain yield and grain number 6-17% (Allison et al 1975). Most of the reduction in leaf area was in leaves below the ear, and leaf growth after treatment was somewhat similar in defoliated and control treatments. The treatment, therefore, did not alter the competition for dry matter accumulation between new leaf production and other plant parts during the critical growth period. However, the study indicates that, in SR52, a reduction in overall leaf area of the individual plant may not be detrimental to yield. In tropical materials, some reduction in leaf size of those leaves growing during the critical growth period might be beneficial because cereal leaves rely on an extraneous source of assimilates during much of their ontogeny (Kirby 1973, Allison et al 1975).

Leaves of tropical maize are generally larger than those of temperate materials. In a comparison of tropical (Tuxpeño) and temperate (Pioneer 3369A) materials grown in Mexico, the temperate material had 20% less leaf area above the ear mainly because of its shorter leaves, and a 34% smaller leaf area density because the leaves were smaller and there was greater vertical separation between them.

Eastin (1969) studied the relative importance of leaves at different positions on the plant in providing assimilates for ear growth in Corn Belt maize. Of particular interest is the specific relation between leaf position and its contribution to ear growth around silking. The leaves around the ear leaf dominate contributions to ear growth at this stage. The pattern varies between genotypes. The effects of illumination of specific leaves on grain number determination during the critical growth period need more study. Photosynthate supply for the developing ear, and nitrogen nutrition and hormone balance may influence the effects. For example, the change in spectral composition of radiation in maize canopy profiles can be quite large (Sinclair and Lemon 1973). Changes in the ratio of far-red to red radiation influence phytochrome activity, which may be important in controlling plant development (Hendricks and Borthwick 1963).

Spikelet fertility

Maize has the morphological potential to produce many ears. The development of the first and second ears is similar up to a critical period near flowering, after which the second ear aborts (Hallauer and Troy. 1972). The mechanisms that control *prolificacy* (the development of more than one ear) are probably closely related to those involved in "barrenness." Cessation of ear growth during flowering can be caused by low amounts of intercepted irradiance per plant (Tollenaar 1977). Nishikawa and Kudo (1973) reported that 60% of the plants that become barren have normal ear development until silk emergence. Recent evidence suggests that ear abortion is related to intraplant competition for photosynthate during the critical growth period. Edmeades and Daynard (1979) suggested that the relation between

grain number and assimilation rate at flowering may be curvilinear with the grain yield level reaching zero (barrenness) at a small threshold net assimilation rate.

Growth substances other than photosynthates also may play an important role in controlling ear abortion. Hageman et al (1967) related ear abortion to nitrogen metabolism, whereas others emphasized the role of growth hormones (Lyons 1952). There are many examples of differences between genotypes and the degree of barren plants under stress conditions such as light competition (Stinson and Moss 1960). These differences appear to be associated with prolificacy (Hallauer and Troyer 1972). Anderson (1967) showed that the balance of indoleacetic acid (IAA) in the tassel and gibberellic acid (GA) in the leaves may be an important determinant of tolerance to high plant density.

There may also be considerable reduction in grain number per plant due to the abortion of kernels after silking. Kernels that abort then are usually the youngest ones at the tip of the cob. Tollenaar and Daynard (1978b) showed that these kernels had been fertilized and begun normal growth. However, at the onset of rapid dry matter accumulation by the older kernels lower on the cobs, the upper kernels aborted. Abortion occurred despite the relatively high soluble sugar concentrations in both stem and kernels (Tollenaar and Daynard 1978c).

The period from fertilization until rapid dry matter accumulation in the grain (the lag phase) may vary from approximately 12 to 20 days in tropical maize in contrast to small grain cereals such as wheat which has a lag phase of less than 7 days (Evans et al 1975). The mechanisms controlling kernel abortion after fertilization and the importance of the duration of the lag phase are not well understood.

Individual grain weight

The individual grain weight depends almost entirely on factors that control the supply of assimilates for grain filling (source) relative to the total number of grains (sink) and on the genetic limit of individual kernel growth (individual grain sink). Grain weight is the product of the duration of the effective grain-filling period and the rate of grain growth. The interaction of these two components with the availability of assimilates, and their combined effects on the yield of tropical maize are not understood. Mean yield variation was related to changes in the rate of dry matter accumulation by the kernels, but not the duration of the effective grain-filling period.

Mean temperature during the grain-filling period influenced both rate of kernel growth, $Y = -16.2 + 1.73\ t - 0.032\ t^2$ ($R^2 = 0.88$), and duration of effective grain filling, $Y = -82.3 - 3.93\ t + 0.075\ t^2$ ($R^2 = 0.82$). Maximum grain size was achieved at a mean temperature of 24.8°C through a kernel growth rate of 6.84 mg/day and an effective grain-filling of 30.9 days (CIMMYT, unpubl. data). Duncan (1975) considered maize grain yields as a product of the amount of assimilates available for grain-filling (photosynthesis and the change in labile reserves) multiplied by the duration of the grain-filling period; the individual grain sink capacity established the upper limit. The degree to which the parameters of rate, time, and kernel capacity limit grain size may vary between genotypes and environments. The ratio of actual to potential grain size for a given genotype may indicate the degree to which yield is limited by supply of assimilates during grain filling. Thinning and shading treatments provided a wide range of source-sink ratios. (Source was measured by the

increase in total dry matter from flowering to grain maturity and sink was measured by grain number per plant.) Under control conditions and a normal plant density of 6.6 plants m^2, kernel weight is approximately 15% less than the maximum size for the genotype. Increasing the supply of assimilate per grain increased the kernel weight, but the rate of grain increase per unit of total dry matter increase was 0.41, Other workers (Fischer and Wilson 1975, Gifford et al 1973) used this rate as an index of the relative limitation of source or sink for a crop. In the example given here for tropical maize, final grain weight is only partly dependent on assimilate supply during grain filling.

Other studies of tropical maize suggest that the duration of effective grain filling may be important in determining yield. The variation in grain yield between a number of families from five tropical populations was associated with variation in the duration of the effective grain-filling period ($y = -126 + 11.65x - 0.155x2$; $R^2 = 0.33$), but there was little variation between genotypes in the rate of grain filling. The variations in duration of effective grain filling and days to silking were not correlated, suggesting that the relative duration of these two crop development phases may be modified genetically (CIMMYT, unpubl. data).

In a similar analysis, Cross (1975) used inbred lines from the US Corn Belt and reported significant correlations between yield and effective filling period, whereas the correlation between rate of kernel growth and grain yield was nonsignificant. Carter and Poneleit (1973) recorded differences between inbreds in duration of effective filling and rate of kernel growth. Both characters were correlated with grain dry weight at the black-layer stage (physiological maturity). The effective filling period was not correlated with rate of dry matter accumulation and only poorly correlated with days to silking, suggesting that these characters might be modified independently. Kernel growth rates ranged from 6.2 to 9.7 mg/kernel per day compared with values of 6.8 to 9.0 measured for tropical materials and 8.6 for the temperate hybrid Pioneer 3369A grown in Mexico.

Some yield differences between inbred lines and their hybrids might be explained by differences in effective filling period and rate of kernel growth (Johnson and Tanner 1972). When inbreds and hybrids were grown at similar LAI, grain yield differences were not explained by differences in total vegetative production nor by number of *potential* kernels *produced* per unit area. The inbred lines had more aborted kernels after flowering, lower kernel growth rates, and a shorter grain-filling period. Neither kernel growth rate nor duration consistently explained grain size differences. The percent of soluble solids in the stalks during grain filling was higher in the inbreds, suggesting that the reduced grain size was not caused by shortage of assimilates for grain filling.

Factors that affect rate of kernel dry weight accumulation are essentially unknown. Duncan et al (I 965) and Palmer (1969) demonstrated that the rate of accumulation of kernel dry weight is not directly related to the photosynthetic rate during grain filling. Plant parts such as the stem can function as a temporary storage organ for assimilates (Palmer et a1 1973). Shannon (1972) showed that photosynthetically fixed ^{14}C in maize leaves rapidly accumulated in the pedicel tissue of the kernel and then more slowly diffused into and throughout the endosperm. Subsequent work by Shannon (1974) indicated that the number and size of starch granules may

be the limiting factor for rate of kernel growth during the linear phase.

Duvick (1951) suggested that potential grain size in maize may be influenced by the number of endosperm cells formed, and this may be determined soon after pollination. In wheat, when competition was decreased among newly formed grains by reducing floret number, the number of endosperm cells at 15 days after pollination increased and final grain size was larger (Brocklehurst 1977). Fischer and Wilson (1975) recorded larger sorghum grains at harvest due to plant thinning or grain removal at anthesis, compared with similar treatments 10 days after anthesis. There was a 6.5% increase in final grain size between treatments in tropical maize in which neighboring plants were removed at 10 and 22 days after flowering (CIMMYT, unpubl. data). Wilson and Allison (1978) achieved a similar effect in SR52 maize grown in Rhodesia by thinning plants at flowering and 14-20 days after flowering.

As mentioned in the discussion on kernel abortion. a better understanding of the importance of the duration of the lag phase as it relates to potential kernel size is needed. Cytokinin activity in the endosperm of maize kernels is at a maximum 2 weeks after pollination (Crane 1964). In barley, manipulations that depressed the cytokinin concentration in developing kernels resulted in a smaller grain size (Michael and Seiler-Kelbitch 1972). Tollenaar (1977) suggested that the role of hormones during grain filling needs further study.

GENETIC IMPROVEMENT OF YIELD EFFICIENCY

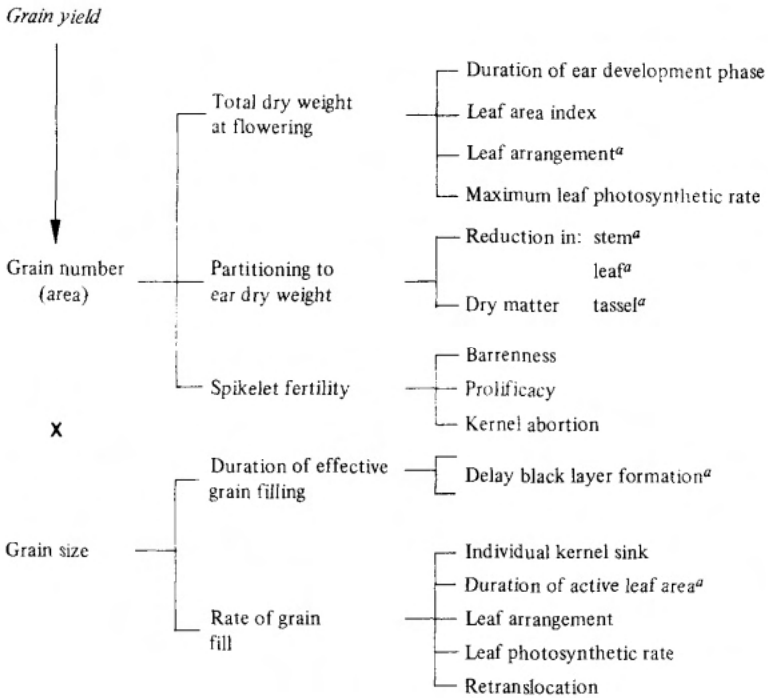
Table 3 provides a framework for discussing research areas relevant to improving grain yield of tropical maize.

The concept of analyzing grain yield in terms of source or sink limitations has not always led to a better understanding of the factors that control grain yield, The concept, however, may be useful in identifying those characters more likely to improve grain yield through genetic modification. Selection of plant traits for improvement of source or sink should be done with selection for yield *per se.*

Crop growth rate

If CGR during the ear development phase is crucial, what are the possibilities for increasing it? Leaf area must be adequate to intercept all the incoming radiation; it can be adjusted to some extent by changing plant population density and leaf area per plant. In many unimproved tropical materials. attempts to increase LAI through increased plant density or better nutrient availability have resulted in considerable yield losses caused by lodging. Extensive breeding efforts have gone into reducing plant height to reduce lodging (Johnson 1976). When selection was made for plant height reduction through quantitative effects, yields were improved over 15 cycles of short-plant selection (Table 4). The yield increases were achieved at higher *optimum plant densities.* In the earlier selections, there was significant improvement in lodging resistance. The short-plant selections had less leaf area per plant, and the higher planting density compensated for this leaf area loss. At optimum densities, LAI and total dry matter production were similar to those of the taller, leafier material of the original cycle (Table 5).

Table 3. Framework for improvement of yield efficiency in tropical maize.



[a] Character being evaluated in CIMMYT maize program.

Table 4. Plant height, lodging, optimum planting density, and grain yield of various cycles of selection for reduced plant height in Tuxpeño Crema I grown at optimum density and at 50,000 plants/ha. (Data are the means of 2 years testing at 3 sites. Poza Rica, Obregon, and Tlaltizapan, Mexico.)

Selection cycle	Plant ht (cm)	Grain yield (t/ha)		Lodging (%)	Optimum density (plants/m^2)
		Optimum density	Plants (50,000/ha)		
0	282	3.17	3.13	49	4.6
6	218	4.29	4.24	9	54
9	210	4.48	4.31	10	5.6
12	202	4.93	4.71	6	5.6
15	179	5.40	5.03	5	6.5
LSD (P.05)	7	0.32	0.36	12	1.2

Increased plant density and the improvement of genotypes to tolerate higher plant density have accounted for approximately 60% of the grain yield increases of the US Corn Belt maize over the last 40 years (Duvick 1977, Russell 1974). The newer genotypes showed some advantage in yield when grown at low densities of 32,000 plants/ha, but showed a much larger advantage when grown at densities of 44,000

Table 5. Plant height, leaf area index, harvest index, total dry matter (aboveground), and grain yield of various cycles of selection for reduced plant height in Tuxpeño Crema I when grown at or near their optimum densities. (Data are means for 2 years testing at 2 sites: Poza Rica and Tlaltizapan, Mexico.)

Selection cycle	Plant ht (cm)	Gram yield (t/ha)	LAI[a]	TDM[a] (t/ha)	Harvest index
0	273	4.05	4.67	14.94	0.30
6	211	5.54	4.49	14.75	0.38
9	203	5.67	4.41	15.32	0.39
12	196	6.1 8	4.49	15.37	0.41
15	173	6.73	4.26	15.12	0.46
LSD (P.05)	10	0.41	0.45	1.84	0.05

[a]LAI = leaf area index, TDM = total dry matter.

plants/ha and more. They attributed the yield increases to better root and stalk qualities that improved resistance to lodging, and to more resistance to barrenness at the higher plant density.

Because the optimum LAI for total biological yield is greater than that for grain yield in both temperate (Iwata 1973) and tropical maize (Rodriguez 1977), there seems to be an opportunity to increase CGR through increased LAI. Increases in grain yield from increased LAI will be achieved only if there is a corresponding improvement in *density tolerance,* a concept to be discussed later.

With increased optimum LAI, leaf arrangement and canopy illumination might become more important in CGR increase. Several workers have suggested an *ideeotype* for maize with upright leaf orientation above the ear and horizontal leaf orientation below it (Fakorede and Mock 1978), a concept based on the understanding of photosynthetic response to illumination and light penetration through the canopy. Mechanical manipulation of the plant to conform with this ideotype has resulted in grain yield increases (Pendleton et al 1968), while genetic modification of leaf angle through liguleless genes has given various results (Pendleton et al 1968. Whigham and Woolley 1974, Frolich et al 1977, Lambert and Johnson 1978). Nevertheless, increased canopy erectness was associated with recurrent selection for grain yield (Fakorede and Mock 1978) in a number of Corn Belt populations.

Leaf size, shape, and spatial arrangement may also be important factors, especially for broadleaved tropical materials that are being shortened. Genetic manipulations of leaf size, leaf shape, and density of leaf area above the ear are being made in three maize populations at CIMMYT. Preliminary analysis of this work indicates that selections made for reduced leaf area per plant have resulted in grain yield increases when the selections are grown at *higher plant densities* (CIMMYT 1978-79).

Models of canopy photosynthesis indicate that increasing maximum photosynthetic rates of leaves will lead to increases in CGR. To date, there has been some indication of genetic differences in maximum photosynthetic rates (Duncan and Hesketh 1968, Heichel and Musgrave 1969) and that, through recurrent selection, this trait can beimproved (Crosbie et al 1977. Musgrave 1971). But the association of this trait with yields has been unsuccessful. Techniques for the assessment of leaf photosynthetic rates in the field are slow and not suitable for genetic screening. Recent studies (CIMMYT 1978) suggest that stomatal resistance. as measured with

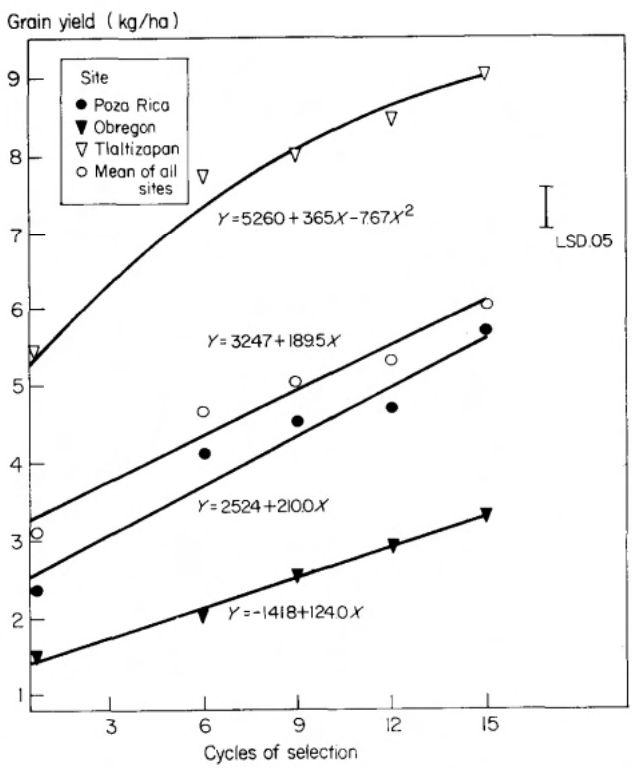
a mass-flow porometer, is a useful predictor of potential grain yield in wheat. This technique is rapid and amenable to field screening of genotypes.

Dry matter partitioning

For cereals in general most grain yield increases have come from an improvement in the distribution of dry matter, rather than from an increase in total photosynthetic production. For tropical maize, which appears more sink limited than maize from other latitudes, there should be considerable opportunity for yield increases through changes in the storage and distribution of photosynthates. However, such a redistribution should not be detrimental to the processes that improve adaptation to adverse conditions. In the selection for short plants in Tuxpeño Crema I the probable effect of reduced stem growth on ear dry weight at flowering, and the accompanying improvement in grain yield have been taken into account. Grain yields have increased with selection for short plants and this is associated with a higher harvest index (Table 5).

Short selections of Tuxpeño Crema I have been evaluated at 3 sites in Mexico (Johnson and Fischer 1979). Plant height was reduced almost linearly with cycle of selection ($y = 295.8 - 10.5x + 0.20x^2$). and grain yield at optimum densities increased linearly with cycle of selection (Fig. 7). This study was in cycle 19 of selection in the summer of 1980.

Selection for reduced tassel is being made in three tropical populations. After six cycles of selection, preliminary evaluation shows an increase in grain yield when the



7. Relation between grain yield and cycles of selection for reduced plant height in Tuxpeño Crema 1 at 3 sites and at optimum plant densities.

smaller tasseled selections are grown at higher plant densities. This yield is associated with an increase in harvest index (CIMMYT 1978-79).

Spikelet fertility

Buren et a1 (1974) identified a number of morphological and physiological traits associated with barrenness, particularly at high densities. Density-tolerant hybrids were associated with rapid completion of silk extrusion, rapid growth of the first ear and first ear silk, prolificacy, reduced tassel size, and efficient production of grain per unit leaf area. These characters may in part reflect differences in hormonal relations controlling apical dominance. A better knowledge of this control mechanism and direct selection for less apical dominance could further increase grain number during the critical growth period.

Hallauer and Troyer (1972) reviewed the performance of prolific (two-eared) maizes and concluded that this character contributes to reducing genotype X environment interactions through its ability to adjust to environmental stresses. Breeding for prolificacy could reduce the risks of production due to stress. Lonnquist (1 967) and Paterniani (1978) reported progress in the selection for prolificacy and yield in the Corn Belt and tropical materials.

Individual grain weight

Where grain size is limited by the supply of assimilates for grain filling, characters that can be considered for improvement include: 1) an increase in current assimilates through higher CGR and a longer leaf area duration, and 2) an increased contribution from labile assimilates stored in other plant parts. Factors that increase CGR at the earlier critical stage should also be useful for increasing CGR during grain filling. In maize and other cereals, the rate of photosynthesis may in part be influenced by the demand for leaf assimilates (Evans 1975a). Moss (1962), and Tanaka and Yamaguchi (1972) measured the decrease in leaf photosynthetic rate of barren plants in maize. Factors that increase the demand for assimilates during grain filling (larger sink) may in turn increase the photosynthetic rate of the leaves.

In tropical environments, there may be a loss of leaf area before grain maturation (Goldsworthy et al 1974); assimilates stored in the stem can compensate for this loss. When there is an improvement in grain sink through increased grain number (as in cycle 15 of the short plant selection in Tuxpeño Crema I), there may be a greater demand for stem reserves for grain filling. However, a reduction in stalk sugar concentration may lead to greater stalk deterioration and lodging. Improvement in the leaf area duration appears useful for both grain assimilates and stalk quality. Although some of the reduction in leaf area duration in the tropics is due to disease, this trait varies considerably in apparently healthy plants (E. C. Johnson, CIMMYT, pers. comm.). It would be useful to improve leaf area duration provided that delayed leaf senescence is independent of the grain demand for assimilate.

There is more than a fiftyfold variation in potential grain size between extreme genotypes in maize (Duncan 1975). Breeding programs to combine the genetic variation in grain components to improve yield usually fail because of negative correlations among the components (Geadelman and Peterson 1978). Failure may have been caused by the suboptimal agronomic regimes used (Evans 1975a), or

because the populations were already limited by the supply of assimilates during grain filling. There may be more potential for improvement through combinations of genotypes with favorable grain components in tropical genotypes because there is less limitation to grain yield through assimilates for grain filling. Harrison (IITA, pers. comm.) suggests that some of the grain yield increases of Kitale materials in Kenya have come from incorporating the large kernel character from Ecuadorian highland maize.

CONCLUSION

This review has suggested that a number of characters might influence productivity of tropical maize. Their relevance might be best assessed by the separate development of these traits from elite materials previously selected for desirable agronomic traits. Further incorporation of those desirable traits into one plant type requires information on genetic variability, genetic correlations between traits, and their heritability. The combined inputs of breeders and physiologists in obtaining needed information, and in the continued selection for these traits, should enhance the breeding process for increasing yields.

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SORGHUM

J. D. Eastin

Sorghum ranks among the top five grains in world importance. Improving the crop depends partly on increasing our knowledge of its physiological and developmental characteristics to permit more effective cultural and genetic manipulation.

Sorghum is a C-4 photosynthetic crop with a high CO_2 assimilation capacity and requires full sunlight levels for maximum production. Optimum temperatures for photosynthesis are close to 40° C, but optimum growth temperatures are generally 30-35° C. The adaptation range is immense — some cultivars do well near 40° C and some at less than 25° C. Yield level is positively correlated with seed number per unit land area. Where yield stability is critical, seed size becomes relatively more important. Seed number potential is set during the inflorescence development period where elevated night temperatures are probably more subtly damaging. At night 5° C above optimum during differentiation and expansion of pistil and stamen primordia can reduce yield 25-35% because of seed number reduction. Elevated night temperatures during grain fill are similarly deleterious. Elevated day temperatures can be critical because they shorten both panicle development and grain fill periods. Many problems can be potentially avoided by selecting plants that fit a given temperature environment. Sorghum has a wide range of temperature response levels, which suggests that fitting a genotype to an environment is a reasonable approach. Likewise, testing for heat tolerance at well above 5° C above optimum is possible.

Length of grain fill is a limiting factor because assimilate supply is probably limiting. Seed size capacity is easily 35% greater than commonly realized, and sorghum leaves are usually green long after grain physiological maturity. Another problem during grain fill is the substantial postbloom loss of stomatal control and its influence on CO_2 exchange and transpiration.

Water deficit effects during panicle development and grain fill are harder to define than temperature, but they also force yield reductions by altering yield components. Studies on water X temperature interaction are needed.

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Initial water × temperature interaction studies suggest that roots may be a major sink competing with the developing panicle for assimilates essential for setting a high seed number potential. Genotype differences for root assimilate requirements exist.

Our knowledge of how developmental processes limit yield is by no means complete but is coming into reasonable focus. However, knowledge of how essential physiological processes control or relate to developmental processes affecting yield components is very slim, indeed.

Discussion on the potential productivity of sorghum is difficult because the range of environments in which sorghum is grown is immense. In some low production areas, sorghum-growing environments are not well defined in terms of temperature, water availability, radiation, winds, etc. At the same time, only meager information on productivity in those environments is available. Therefore, remarks on productivity as it relates to environment will be limited to reasonably well-defined conditions. One may then speculate on the production potential in other areas. More complete environmental descriptions of remote sorghum production areas are being developed within both the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) and FAO.

The approach in this discussion is to relate environmental variables, especially water and temperature, to plant development processes which influence the components of yield.

BOTANICAL CHARACTERISTICS AND ECOLOGICAL CONSIDERATIONS

At least three recent publications review botanical characteristics and ecological factors concerning sorghum. Doggett (1970) reviewed the literature on the botanical description of sorghum and Martin (1970), the historical development of sorghum in North America. Harlan (1972a,b) detailed the genetic resources and outlined a new classification system in the "Sorghum in the Seventies" symposium. Murty (1972) dealt with the biometrical classification. A more complete agroecological description of sorghum-growing areas has been completed for Africa (Higgins 1978) and Southwest Asia (Higgins 1978). Reports on Southeast Asia and Central and South America are in preparation.

Cultivated sorghum appears to have originated in Northeast Africa (perhaps 3000 to 7000 B.C.) since the greatest diversity of types exists there. The most likely area is that now occupied by Ethiopia and perhaps part of Sudan from where sorghum soon spread to West Africa (Vavilov 1935, Clark 1959, Doggett 1970, Martin 1970). There was evidence of sorghum in Assyria by 700 B.C. and in India and Europe by 1 A.D. (Clark 1959). Sorghum spread to Botswana by the 10th century A.D. and to southern Africa by the 16th century. It may not have reached China before the 13th century and was carried from Africa to the Western Hemisphere in the 17th and 18th centuries.

Freeman (1970) and Doggett (1970) give detailed botanical descriptions of sorghum. Sorghum is a C-4 tropical grass. It can be made to exhibit a perennial growth habit but generally is handled as an annual in cropping systems except when

a ratoon crop is taken. In many Western Hemisphere cropping systems, it has a main stem with few or no tillers (because of population levels). Thinner stands in many developing countries give rise to various levels of tillering.

Hultquist (1973) reviewed the literature on vascularization in sorghum stems and conducted a series of experiments to partially define anatomical and functional characteristics of the system. As detailed in maize by Kumazawa (1961), both peripheral and central vascular structures exist and apparently function independently of each other most of the time. The peripheral system bypasses the nodal vascular plexus and may permit more direct assimilate movement from the flag leaf to the panicle. However, peripheral system bundles have a smaller diameter and less translocation capacity than central system bundles.

The inflorescence is a panicle of varying degrees of compactness, depending on length of the central rachis and attached primary panicle branches (Doggett 1970, Martin 1970). Spikelets usually occur in pairs except at the panicle tips where larger groups occur. One spikelet sets sessile and is fertile, but the pedicellate spikelet usually has no fertile florets. Ordinarily only one floret (upper) of the sessile spikelet is fertile. Seed twinning usually is the result of a fertile second floret. The crop is basically self-pollinated.

Native sorghums in developing tropical countries are frequently 2-3 m tall. Dwarf types about a meter high were developed in the United States to facilitate machine harvesting of grain. The tall, native sorghums usually mature later than their earlier dwarfed counterparts because the height and maturity genes are linked (Quinby and Karper 1945. Quinby 1963).

Physiological maturity of sorghumgrain is readily determined. Eastin et al (1973) demonstrated that visual darkening of the closing layer tissue in the placental area near the point of kernel attachment coincides with cutoff of $^{14}CO_2$ photosynthetically labeled assimilate translocation into the kernel. Dark layer determination signals physiological maturity (maximum kernel dry weight) and permits evaluating grain yield in terms of time and metabolic efficiency. After determining the functional significance of the dark layer, Giles et al (1975) detailed the ontogeny and structure of the dark layer. At maturity, phloem parenchyma cells become blocked with mucilages and pectic compounds forming the dark layer. This cuts off assimilate and water transport to the seed (xylem does not enter the seed), permitting seed desiccation to begin. This blockage is contrasted to that in maize where embryo growth supposedly crushes cells in the placental area and disrupts water and assimilate transport (Kiesselbachand Walker 1952). Premature dark layer closing in sorghum limits yield because seed size potential in most sorghum seeds is normally 25 to 35% greater than is realized. Sorghum leaves remain green long after the dark layer forms, but their production potential remains untapped because of phloem blockage.

Ecological considerations typically associated with sorghum production are summarized in the FAO Agroecological Zones Project Reports (Higgins 1978) for Africa and Southwest Asia. The Africa report illustrates climatic area characteristics, growing seasons, and yields generally associated with sorghum production in rainfed warm tropical lowlands, cool tropical highlands, warm subtropics, and cool subtropics. Table 1 summarizes yield levels projected in each category at two

Table 1. Projected rainfed sorghum yields in Africa on very suitable, suitable, and marginally suitable soils at high and low production input levels.[a]

Climate	Yield (t/ha)								
	Very suitable soil			Suitable soil			Marginally suitable soil		
	High input	Low input	Growing Season range (d)	High input	Low input	Growing season range (d)	High input	LOW input	Growing season range (d)
Warm tropical lowlands	4.1-5.1	1.0-1.3	150-209	4.1-2.0	1.0-0.5	15-269	1.0-2.0	0.0-0.4	75-269
Cool tropical highlands	6.2-1.8	1.6-2.0	210-269	3.1-6.2	0.8-1.6	75-299	1.6-2.0	0.4-0.8	150-329
Warm subtropics	4.1-5.1	1.0-1.3	150-209	2.04.0	0.5-1.0	150-239	1.0-1.3	0.3-0.5	120-269
Cool subtropics	6.2-7.8	1.6-2.0	210-269	3.1-6.2	0.8-1.6	120-299	1.6-2.0	0.4-0.8	120-299

[a]Extracted from Higgins (1978).

production input levels. The projected yield level ranges are not surprising. If the best lands were irrigated, yields in cooler areas should approach those in temperate North America where the growing period is a little shorter, seldom exceeding 120-130 days. Data on the precise nature of limitations to yield in the suitable and marginally suitable situations are not clear. However, water and temperature are the chief problems everywhere. They will be discussed in relation to development and physiological characteristics of the crop.

MAJOR CROP PHYSIOLOGICAL PARAMETERS

Leaf photosynthetic rate

Sorghum is a C-4 plant with typically high rates of photosynthesis. El-Sharkawy and Hesketh (1964a, b) were among the earliest to measure CO_2 fixation by gas exchange measurements. At light intensity values of 2.3 1x/minute, CO_2 uptakes of 50 to 70 mg/dm^2 per hour were obtained; the highest rates were near 40° C in greenhouse plants. We have measured rates as high as 80 mg CO_2 uptake/dm$_2$ per hour in field plants at 38° C. Several citations on photosynthetic rates could be given but the 60-80 mg uptake range will catch most maxima. Minimum rates tend to zero if stress is severe and long enough, or if a temperature of 10°-15° C persists.

Light intensities equal to or greater than full sun (El-Sharkawy and Hesketh 1964a) are required to saturate the photosynthetic apparatus. In lowlands and most temperate areas, field temperatures optimal for photosynthesis vary but generally range from 35° to 42° or 43° C (Norcio 1976). In different genotypes appreciable variability in temperature optima for photosynthesis exists (Gerik 1979). The photosynthetic apparatus appears to suffer from temperatures past 42° or 43° C in some temperate and tropical sorghums. Reduced photosynthesis may occur at lower temperatures in cool-tolerant genotypes adapted to high elevations.

Authors of the FAO Agroecological African Zones (Higgins 1978) give a generalized statement of photosynthesis characteristics for Group IV plants, which include *Echinochloa frumentacea, Setaria italica, Panicum milaceum, Sorghum bicolor,* and *Zea mays.*

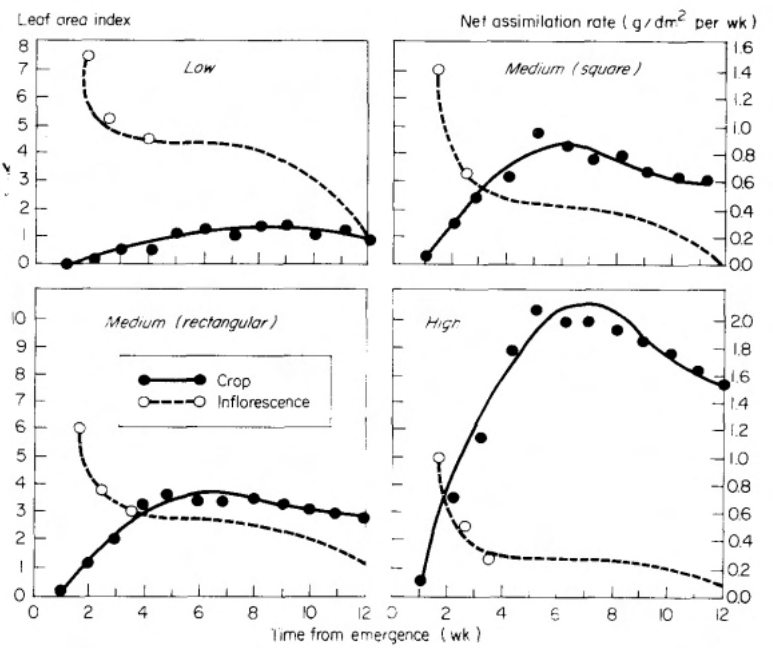
	Temperate and tropical highland cultivars	*Tropical cultivars*
Temperature response (° C)		
Optimum	20-30	30-35°C
Operative range		15-45°C
Radiation intensity at		
maximum photosynthesis (cal/cm^2 per minute)	1.0-1.4	
maximum net CO_2 uptake (mg/dm^2 per hour)	70-100	
maximum crop growth rate (g/m^2 per day)	40-60	30-60
Water use efficiency (g/g)	150-300	

Crop growth rate

Fischer and Wilson (1975) investigated factors controlling dry matter accumulation because assimilate supply during grain fill had been presumed limiting (Goldsworthy and Tayler 1970, Fischer and Wilson 1975). They checked leaf growth rates, leaf area indices (LAI), inflorescence growth rates, net assimilation rates (NAR) and crop growth rates (CGR) in low, medium, and high populations (14,352, 143,520, and 645,836 plants/ha). Plants were arranged in square (S) and rectangular (R) positions in medium density. CGR were 15.0, 27.5, 26.0, and 45.8g/m^2 per day for the low, medium (S), medium (R), and high populations, respectively. CGR were reported for plants in the FAO sorghum class (Higgins 1978). Maximum growth rates at all population levels and stand configurations occurred essentially a few days before anthesis, which is also the approximate time of highest LAI.

Leaf area index

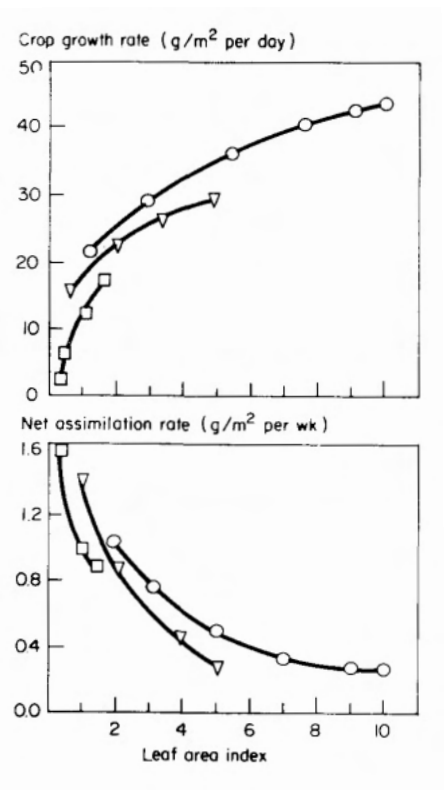
The development of leaf area in the low, medium (S), and high population stands is illustrated in Figure 1. Maximum leaf area for each density was achieved just before anthesis. LAIs for low, medium, and high populations are in the order of 1, 5, and 10. A LAI off 5 occurs in many productive commercial fields in North America where the HI on *combine sorghums* normally runs 0.44.5. Fields in drier areas can have LAI of 3 ± 1.



1. Crop and inflorescence growth rates of plants grown at low medium (square). medium (rectangular), and high population densities.

Note in Figure 2 the positive relationship between CGR and LAI, which is quite straightforward. The negative relationship between NAR and increasing LAI is clear. That both CGR and NAR are highest at the highest densities presumably relates to a canopy structure in high density which gives more uniform light distribution over a greater portion of the leaf area than in medium and low densities. Judging from CO_2 uptake vs light curves in C-4 plants, sorghum leaves are probably more efficient per unit of radiation at low levels than at higher. Energy conversion at high density was 2.5 X 10^{-6} gcal.

The work above was done with a typical temperate sorghum hybrid, which is a three-dwarf, relatively photoperiod-insensitive genotype. Most sorghums in the tropics and subtropics are tall and photoperiod-sensitive. Goldsworthy (1970) found comparative phenological characters for a native Nigerian sorghum (Farafara) and a U.S. short-season hybrid (NK300) (Table 2). The season length was about 1.8 times as long for Farafara, particularly the long vegetative period before panicle initiation. The time to heading for Farafara was double. Total dry matter production of NK300 was only one-half to one-third the 15 t of Farafara. However, NK300 grain production (1,349 g/m^2) was more than 70% greater than that of Farafara (203 g/m^2) in a little more than half the time. The apparent detriment to grain yield in Farafara is the low seed number associated with very heavy stover production. Stover production, however, is critical to some farmers.



2. Changes in leaf area index and net assimilation rate over time for plants grown at low, medium (square), medium (rectangular), and high population densities. The curve showing net assimilation rate was derived from equations describing total dry weight and leaf area index. Data points were calculated according to Watson (1952). Standard errors of the treatment means for net assimilation rate are 0.05, 0.04, and 0.09 at 3, 7, and 11 weeks respectively.
Values for R^2—low: 0.87, medium (S): 0.90, medium (R): 0.95, and high: 0.94.

Table 2. Comparative phenological and agronomic data on Farafara and NK300 sorghums grown in Samaru, Nigeria (Goldsworthy 1970).

Stage	Days from sowing	
	Farafara	NK300
	1966 sowing	
Panicle initiation	85	23
Heading	134	59
Harvest	174	100
	1967 sowing	
Panicle initiation	84	73
Heading	132	59
Harvest	181	I00

Total dry matter production, harvest index and daily grain production

The highest grain yield reported is 16,500 kg/ha (Pickett and Fredericks 1959), followed by 14,250 kg/ha (Fischer and Wilson 1975). Harvest index for the latter was 0.45 and total aboveground dry matter was about 3 1.667 kg/ ha. Production covered about 12 weeks from emergence (91 days from planting). Production rate for the 14,250 kg/ ha would be 348 kg/ ha per day for total dry matter production, or 157 kg/ ha per dag.

The above yields came from experiments where production was pushed. Table 3 contains unpublished data showing modest grain production levels common to commercial fields in the Great Plains. The seasonal production rate range is about 54-78 kg/ ha per day or 150 to 192 kg/ ha per day during grain fill. Dalton (1967) reported 227 kg/ ha per day for the period to half bloom on irrigated sorghum in the High Plains of Texas. Assuming half bloom represents 60% of the full life cycle, the seasonal production weight would be 136 kg/ha per day. HI of these sorghums ranges from 0.4 to 0.5.

RESPONSE TO ENVIRONMENTAL VARIABLES

The effect of environmental variables on yield can best be approached through their influence on yield components, which in turn relate closely to developmental sequences. Some of the most critical points deal with the influence of water and temperature on developmental processes.

The relative importance of seed size and seed number as yield components bears comment. In sorghum and in many other cereals, seed number per unit area has generally been the most important component of yield (Kambal and Webster 1966; Stickler et a1 1961; Blum 1967, 1970; Quinby 1963: Doggett and Jowett 1967; Beil and Atkins 1967; Fischer and Wilson 1975). However, the importance of seed size has also been demonstrated. Malm (1968) reported excellent yield improvement in hybrids by using R lines developed from large-seeded exotic germplasm, but his data did not show the influence of seed number. Neither component should be neglected in improvement work. Good diversity for both traits exists (Miller 1968).

Table 3. Sorghum grain and stover yield data for hybrids and respective parents grown with irrigation at Mead, Nebraska, 1970 (Eastin 1972).

Genotype [a]	Germination to maturity (days)	Grain stover [b]	Grain yield (kg/ha)	Seasonal production rate		Grain-filling period production rate			
				kg/ha per day	% of hybrid over parent	Days	% of hybrid over parent	kg/ha per day	% of hybrid over parent
RS 671	108	0.81	7461 [c]	69.1		39.8		187.5	
Redlan	112	0.77	6747 [e]	60.1	14.7	39.8	2.5	173.9	7.8
Rx 415	108	0.67	5817	53.9	28.2	38.8	2.5	149.9	25.0
RS 625	105	0.01	7816 [c]	74.4		42.6		183.5	
CK 60	106	0.83	6277	59.2	15.6	39.8	7.0	157.7	16.3
Tx 414	103	0.84	6184	60.0	24.0	37.8	12.6	163.3	12.3
RS 625	105	1.21	8053 [c]	76.7		42.7		188.6	
Martin	103	0.98	7288 [d]	70.8	8.3	38.2	11.7	191.8	-1.6
Tx 414	103	0.97	5925	57.5	33.3	37.8	12.9	156.7	20.3
RS 610	106	1.15	8250 [c]	77.8		44.0		187.5	
CK 60	106	0.90	6464	61.0	27.5	39.8	11.0	162.4	15.4
7078	104	0.93	6521	62.7	24.0	39.8	11.0	163.8	14.4
TR	108	0.81	6982	64.6		40.9		170.7	
Redlan	112	0.68	6891	61.5	5.0	38.8	5.4	177.6	–4.0
Tx 414	103	0.83	6280	61.0	5.9	37.8	8.2	166.1	2.8

[a] The first genotype of a set is the hybrid followed by the female and then pollinator parent. [b] Genotypes had equivalent stover productions. [c] Significant difference between hybrid and parent mean (P<.0l). [d] Significant difference between parents (P<.0l). [e] Significant difference between parents (P<.05).

In the discussion of developmental processes, the system used by Eastin (1972, 1974) is used:

Growth stage 1 (GS_1) — vegetative
Growth stage 2 (GS_2) — inflorescence development
Growth stage 3 (GS_3) — grain filling

Panicle development

Chen (1938) reported research on time from germination to floral transition. Paulson (1962) described the formation of the first panicle branch primordia as the onset of panicle initiation. Goldsworthy (1970) used a method that relied on the rapid growth in apex size just before primary panicle branch primordia appeared. Lee et al (1970) did a more complete description of panicle development, and showed the following approximate developmental sequence for sorghum in the upper Great Plains of the U.S.:

GS_2 stage	*Days*
Panicle initiation	0
Panicle branch primordia formation complete	7-10
Spikelet primordia	10-14

GS_2 stage	Days
Spikelet component differentiation	14-21
Bloom	30-36

A series of experiments shows the nature of development during this period. First, a set of tall (2 X 3 dwarf), normal, (3 X 3 dwarf), and short (4 X 3 dwarf) isogenic height RS626 hybrids were grown with irrigation at Mead, Nebraska, in 1970. Grain yield levels did not differ significantly, but seed weights differed as did total dry matter production (Table 4). Because seed size (weight) was about 30% larger in the 2 X 3 dwarf hybrid, and because yields did not differ, seed number in the 4- and 3-dwarf hybrids had to be higher. The differential reaction of the hybrids probably is due to the differential quantities of vegetative dry matter produced and the time they were produced.

As with many cereals, the sorghum panicle is initiated about the same time as the internodes begin to elongate or when the plant "joints." Consequently, at the time of panicle initiation (PI) there is no perceptible visual difference in height among the three isohybrids. Essentially all of the 16 to 19% greater dry matter in the 2 X 3 dwarf is produced between PI and bloom. Table 5 gives the regression of dry matter accumulation on days for two hybrids. Results suggested vegetative dry matter accumulation rate was 20% faster in the tall hybrid. This is a conservative value inasmuch as the difference in dry matter production occurred over a 35-day period instead of the entire growing time.

Presumably there is competition for available assimilates between simultaneously expanding floral and vegetative parts. Panicles in the 2 X 3 dwarf hybrid are noticeably shorter, and the seeds are visibly larger, reflecting the lower seed number associated with their increased size. In addition to existence of floral-vegetative competition, two points are clear. First, seed size capacity is at least 30% greater than

Table 4. Comparative production data for tall (2 x 3 dwarf), normal (3 x 3 dwarf), and short (4 x 3 dwarf) RS626 grown with irrigation at Mead, Nebraska, 1970. [a]

Height	Grain-stover ratio [b]	Dry weight (kg/ha)			Dry matter (kg/day)			G/M seeds	% of tall over others
		Grain	Total	% of tall	Grain	Total	% of tall		
Tall	0.76	7741	17,940	100	73.3	169	100	29.3	
Normal	1.14	7988	15,080	84	75.4	142	84	22.7	29
Short	1.08	7528	14.501	81	71.0	137	81	22.5	30

[a] Source: Eastin (unpubl.). Germination to maturity (G/M) was 106 days. Dry matter is adjusted to 14% moisture.
[b] Ratio is higher than normal because of leaf loss in a heavy unseasonal snow before final harvest.

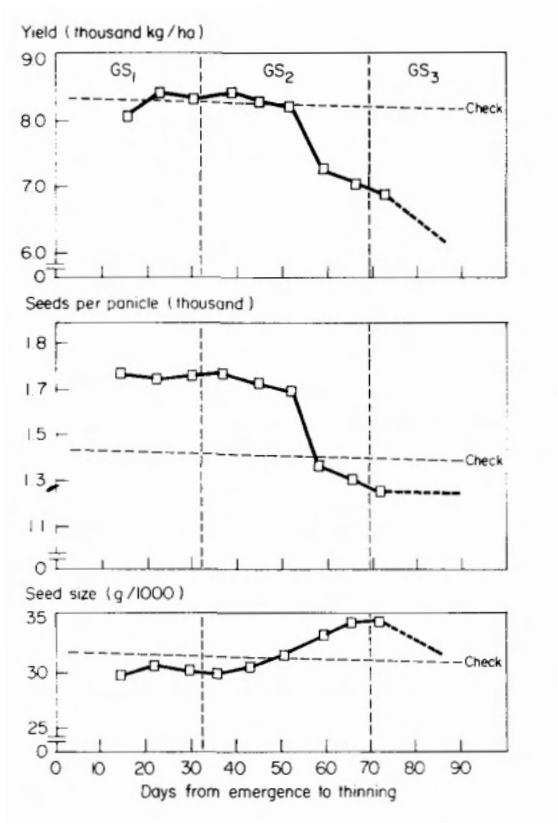
Table 5. Correlation coefficients and regression of dry matter accumulation on days from planting (1970) for RS626 grown with irrigation at Mead, Nebraska. Plots were sampled every 4 days beginning 36 days after planting (Eastin, unpubl.).

Hybrid	Samples	r	b ± $CL_{.05}$ in g/plant per day
2 x 3 dwarf	18	0.9 80	1.523 ± 0.0124
3 x 3 dwarf	18	0.945	1.267 ± 0.0123

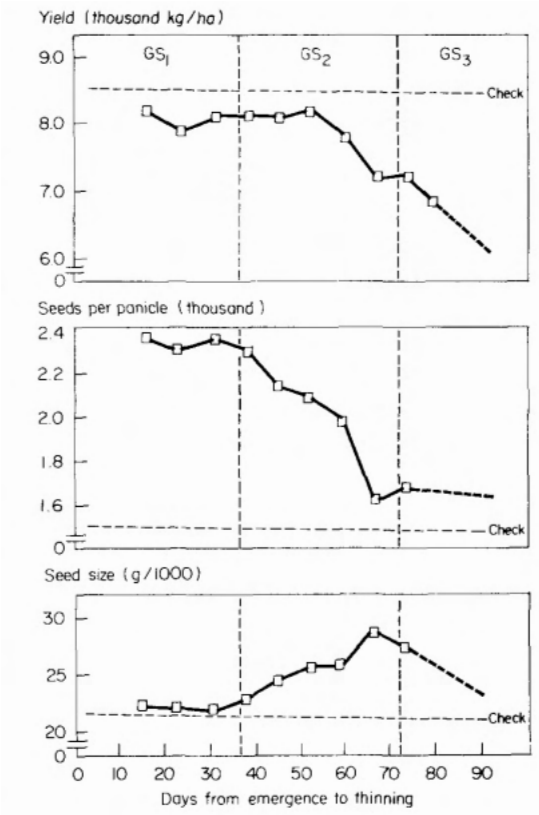
in normal crop production, hence, the need for a longer grain-filling period. Second, seed size as yield component is a yield-stabilizing factor and likely becomes more critical as production limitations become more severe and yield levels decline.

Knowledge of the floral-vegetative competitive effect raises the question as to when in GS_2 the crop is most sensitive to environmental variables. Castleberry (1973) thinned three hybrids from 300,000 to 180,000 plants/ ha at 13, 22, 30, 37, 44, 51, 58, 65, and 72 days after emergence. Thinning left a plant stand adequate for nearly complete interception of available photosynthetically active radiation (PAR) by mid-to late GS_2. Yield and plant data for the hybrid EH 101 are given in Figure 3. Yields were not reduced below the check level until past the mid-GS_2 thinning. Thinning gave about the same total canopy PAR interception but increased PAR per plant. The plant responded by increasing the seed number per plant enough to maintain production near the check level. Seed number compensation occurred up to about mid-GS_2, when the stamen and pistil primordia (floret differentiation – FD) were appearing. Thinning after that point left the plant with no means of yield compensation except through seed size, which was inadequate to maintain the check yield level.

A second hybrid, RS671 (Fig. 4), remained near the check yield level with thinnings up to mid-GS_2 but did so partially through increase in seed number and partially through seed size increase. Seed number increase up to PI was much greater



3. Effect, of thinning on EH 101 yield, seed number, and seed size. Dashed line at the end of each curve is an extrapolation of the data from experiments 1 and 3. GS = vegetative stage, GS_2 = inflorescence development, GS_3 = grain filling.



4. Effects of thinning on RS 671 yield, seed number, and seed size in Experiment 2. Dashed line at the end of each curve is an extrapolation of the data from experiments 1 and 3. GS_1, = vegetative stage, GS_2 = inflorescence development, GS_3 = grain filling.

in RS671. A third genotype, RS610, reacted differently. Yield started dropping soon after PI and was closely paralleled by a seed number drop. When seed number per plant dropped to the check level at thinning 1 week beyond FD, about an 8% seed size increase was noted which still left about 12% yield loss. As expected, light seriously hampered the plant's ability to adjust its yield when treatment occurred near FD. Later testing for temperature effects yielded similar results.

Temperature

Downes (1972) found that high temperatures (day night 33° /28° C) from germination to PI reduced grain yields as did high temperatures during the last part of panicle development. Temperature effect was slight during the first part of panicle development. Eastin et al (1976) further tested temperature effects during GS_2 and GS_3. Five genotypes ranging from temperate to cool tolerant were exposed to day/night temperatures of 29° /17° C, 29° /22° C, 29° 27° C, and 34° 22° C (Table 6) from PI to bloom. The first three temperature sets compare night temperatures with day held constant. The second and fourth treatments compare variable day-temperatures.

Three points are clear. First, the temperature response of the three hybrids differs, with the temperate hybrid doing best at 29° /22° C. Crossing the temperate hybrid female with a cool-tolerant male appears to move the temperature optimum down

Table 6. Temperature influence on sorghum grain yield in growth room plants under 4 day/night temperature regimes imposed from panicle initiation to physiological maturity.

Genotype	Grain yield[a] (g/head)			
	29°/17°C	29°/22°C	29°/27°C	34°22°C
RS 610[b] (CK6017078)	36.8 (14)	42.6 –	31.8 (25)	27.6 (35)
CK60/606[c]	32.8 (4)	34.0 –	21.7 (36)	30.0 (12)
33[d]/606	62.3	42.1 (32)	28.1 (55)	31.9 (49)
606	18.8 –	18.0 (4)	8.9 (53)	12.3 (35)
SJ7°/156°	50 7 –	38.3 (25)	26.8 (47)	30.9 (39)

[a]figures in parentheses shows % reduction from maximum yield. [b]Temperarc hybrid [c]Cool-tolerant genotype. [d] Intermediate-temperature genotype.

slightly - the 4% yield difference at 29°/17° C is not significant. The 33/606 and SJ7/156 hybrids clearly do better at 29°/17° C. Second, a night temperature of about 5° C above near optimum reduces yield by one-fourth to one-third, but 10° C above near optimum reduces yields about half. Third, daytime temperature elevations can be costly and variable, depending on genotype. The temperate genotype yield was reduced 35% by elevating day temperatures 5°C, and the yield of the cool-tolerant SJ7/156 was reduced 14%. These yield reductions occurred even though elevating temperature 4°C likely increased the photosynthetic rate about 25%. Eastin's (1976) additional agronomic data on temperate- and cool-tolerant hybrids relate to yield losses (Table 7).

Because of chamber limitations that require the temperature treatments to proceed from PI to maturity. GS_3 effects are confounded with those of GS_2. Statements about GS_3 may not always hold 100% true. In RS610 yield losses closely parallel seed number losses. Therefore, a major effect is a GS_2 effect. At a 5° C elevation the cool hybrid showed very little yield reduction through seed number loss, but 10° C above optimum cut both yield and seed number about 35%. A 32% reduction in seed number in RS 610 was associated with a 4% reduction in GS_2. SJ7/156 showed very little reduction in seed number even though GS_2 was reduced 9%. However, a 35% seed number reduction was associated with an additional 3.5% reduction in GS_2 when temperature was elevated 5°-10°C above near optimum.

Grain-filling period was reduced 65% in RS610 at a temperature elevation of 5° C above near optimum. GS_3 for SJ7/156 was reduced 20% by a 5° C elevation above near optimum and 26% by a 10°C elevation. Chowdhurry and Wardlaw (1978) noted a GS_3 reduction from 42 to 18 days going from 21°/16° C to 33°/28° C. Temperatures elevated above optimum reduce metabolic efficiency in terms of grams grain/GS_3 per day. These growth data are quite striking; therefore, the effects of night temperature in the field were evaluated.

A set point heater was designed to heat small, clear plastic tents (about 2 m x

Table 7. Temperature influence on agronomic characteristics of sorghum hybrids RS 610 [a] and SJ7 [b] /156.

Genotype	Day/night temperature [c]			
	29°/17°C	29°/22°C	29°/27°C	34°/22°C
		Seed number		
RS 610	2305 ± 172 (7.4)	2488 ± 133 (00)	1681 ± 210 (32.5)	1596 ± 105 (36)
SJ7/156	2518 ± 170 (00)	2440 ± 287 (3.3)	1648 ± 302 (34.6)	1960 ± 238 (32.2)
		Days in panicle expansion		
RS 610	39.3 ± .5 (00)	35.7 ± .5 (9.1)	34.1 ± .4 (13.2)	32.2 ± .3 (18.1)
SJ7/156	37.4 ± .4 (00)	34.0 ± .6 (9.1)	32.1 ± .5 (12.6)	31.3 ± .7 (16.3)
		Grain-filling days (GS_3)		
RS 610	44.3 ± .4 (00)	36.1 ± .6 (18.5)	33.2 ± .4 (25.0)	27.3 ± .4 (38.4)
SJ7/156	38.9 ± .5 (00)	31.2 ± .6 (19.9)	28.9 ± .4 (25.7)	25.3 ± .4 (35.0)
		Grain (g/GS_3 day		
RS 610	0.83 (29.6)	1.18 (00)	0.96 (28.6)	1.01 (15.4)
SJ7/156	1.30 (00)	1.23 (5.4)	0.93 (28.5)	1.22 (6.2)

[a] CK60/1018. [b] SJ7 is an A line developed by Mr. Paul Menge (Northup, King & Co.) and 156 is a cool-tolerant polinator. [c] Figures in parentheses are %reduction.

0.8 m × 1 m) placed over a field crop at 2000 hours and removed at 0700 hours. The units were operated 1 year and new units subsequently were designed to control temperature relative to the ambient. Ogunlela (1979) applied ambient + 5° C and + 10° C treatments to RS671 in the field for 2 years. The second year's data in Table 8 give yield components and metabolic efficiency of grain formation during four 1-week portions of GS_2 and the first week after anthesis. The most sensitive period is floret differentiation, when ambient +5° C reduced yields 28% (Castleberry 1973). The treatment immediately before floret differentiation and during floret development reduced yield 20%.

Note that percentage yield reductions are closely paralleled by percentage reductions in seed number and grams grain/GS_3 per day per plant in every case. The influence of sink size (seed number during grain fill) on metabolic efficiency (grams grain/ plant per day) needs further investigation. The work of Eastin et al (1976) suggests that seed number does not always decline with yield loss. Because yield losses can be nighttime effects, dark reactions (respiration and coupled synthetic processes) should be investigated. We chose a simple dark reaction system for a preliminary probe in 1974 shortly after data in Table 6 were collected. Seeds of seven hybrids and seven lines were weighed and germinated at 20° C. Lots were split to grow them at 25°, 30°, 35°, and 40° C for 4 days in the dark. New growth was separated from the seed to weigh both new growth and the remaining seed. Growth rates of hybrids and lines were the same at 30° C. Hybrids grew slightly faster at 25° C and appreciably faster at 35° and 40°C. Percentage of seed weight lost at all

Table 8. Influence of night temperature (ambient + 5°C) on yield and other characteristics of RS 671 grain sorghum at Lincoln, Nebraska, 1979. Night temperatures (field) were regulated at 5°C.[a]

	Grain (g/Plant)	Seed (no.)	1000-seed wt (g)	Grain (g/GS pay per plant)
Control	66.9	2659	26.6	2.09
PI_1 to PI_7[b]	59.3 a	2333	27.2	1.85
	(11)	(12)	(2)	(11)
PI_8 to FD_1[c]	53.4	21 74	21.8	1.71
	(20)	(18)	(5)	(18)
FD_1 to P_7	48.0	1855	29.7	1.49
	(28)	(30)	(12)	(29)
FD_8 to BL_1[d]	52.7	2176	27.8	1.66
	(21)	(18)	(5)	(21)
BL_1 to BL_7	55.9	2223	25.5	1.80
	(16)	(16)	(–4)	(14)

[a]Values in parentheses are percent reduction from the control, except for 1000-seed weight which is change from control. [b]PI is panicle initiation; subscripts are days. [c]FD is floret differentiation (stamen and pistil primordia). [d]BL is bloom.

temperatures was lower in the hybrids. The ratio of grams new growth/gram seed weight lost was calculated to get an estimate of growth efficiency or metabolic efficiency of the growth process. Grams new growth gram seed weight lost was the same at 30°C (suggesting near optimal conditions), but the hybrids were more efficient in converting seed reserves to new growth at temperature extremes on both ends of the scale. Metabolic pace as affected by temperature may influence metabolic efficiency which is associated with growth processes. Metabolic efficiency appeared to decline between 25° and 40° C. This observation and data in Tables 6 and 7 indicate that more study is needed on the influence of temperature on metabolic pace as it relates to metabolic efficiency. Chowdhurry and Wardlaw (1978) did work on developing kernel respiration rates in rice, wheat, and sorghum which bears on this.

A reasonably quick and rough indicator of metabolic pace as influenced by temperature is change in respiration rate with temperature change. Respiration, within reasonable limits, is linked to many synthetic activities. Gerik (1979) tested the influence of temperature on photosynthesis and respiration in 50 Ethiopian lines (mostly of high-elevation origin) in the greenhouse (10-leaf stage) under relatively cool conditions. Variability in whole-plant photosynthetic rate was considerable — 10-30 mg CO_2 dm^2 per hour at 30° C. Whole-plant dark respiration also varied — 4-10 mg CO_2 g per hour at 30° C. CO_2 exchange measurements were taken at several temperatures ranging from 13° to 40°C. Gerik (1979) checked dark respiration in vegetative sorghum plants from three hybrids and correlated them with panicle dark respiration. The temperature test range was 13° to 40° C. Respective R^2 values for respiration vs temperature in vegetative parts and the panicle were .85 and .80. The linear response equation was $y = 1.21 + 0.24X$ for the vegetative plant and $y = 0.85 + 0.12X$ for the panicles indicating lower slope of the panicle curve (much less

influenced by temperature). Mahalakshmi (1978) found a similar modest panicle respiration response to temperature in sorghum.

Gerik (1979) evaluated variability in panicle respiration response to temperature by selecting 100 field plants from each of 2 random mating populations. Within each set of 100 plants, 3 maturity groupings were selected. Values for respiration at different temperatures were achieved through tests at different times of the day. Mean, maximum, and minimum values for panicle dark respiration and other plant characteristics of the two populations follow:

Variable	*Units*	*Range of variability*		
		X	*Min*	*Max*
	TP_4 – RO^- sub –4 population			
Panicle respiration	mg CO_2/g per h	1.78	.31	5.22
Grain fill	days	31.4	30	41
Yield	g grain/panicle	74.5	19.5	167.9
Seed number	per panicle	2948	961	6356
	TP 11 population			
Panicle respiration	mg CO_2/g per h	2.10	.14	12.4
Grain fill	days	29.8	20	39
Yield	g grain/ panicle	73.8	23.5	171.4
Seed number	per panicle	3170	737	7366

Respiration values averaged over three temperatures show a great deal of variability in response to temperature. Selection for temperature response should be possible. Unpublished work from our laboratory shows that respiration in plants at PI increases 12 to 14% for each degree over the range from 12 to 27° C (measured at 5° C intervals). If metabolic pace relates to metabolic efficiency and is heavily influenced by temperature, more care in selecting the right metabolic pace (temperature response) for a given environment would be useful.

One last point in temperature effect on panicle development processes is of interest. Mahalakshmi (1978) and Gerik (1979) found that panicle respiration response to temperature was lower than that of whole plants. Mahalakshmi also tested the influence of temperature on starch synthetase activity in RS671 and RS626 at 10, 15, 20, 25, and 30 days after anthesis. Seasonal mean starch synthetase activities (µmole glucose incorporated per fresh weight per .10 min) at 3 temperatures are:

Hybrid	*32° C*	*37° C*	*42° C*
RS671	8.14	8.32	9.22
RS626	7.97	8.08	8.68

Enzyme response to temperature is modest as is respiration response. This may relate to the fairly stable grain fill rate within a genotype across a range of environments as observed by several workers (Eastin 1972).

Our knowledge of events during grain filling is limited. Dickinson (1976) applied high temperature to sorghum panicles in the field and found 7-9 days after panicle initiation the most sensitive period. Apparently this was close to the time endosperm cell expansion was ceasing and starch production beginning. If it was severe enough. heat treatment influenced seed number and modest treatments reduced seed size. Much research is needed in this area.

Considerable time was devoted to the study of temperature effects on development, at the expense of photosynthesis and heat tolerance. Sullivan et al (1977) tried methods Sullivan et a1 (1975) developed to test for heat tolerance and demonstrated a considerable range of tolerance among sorghums, which generally are less heat-tolerant than some *Pennisetum americanum* cultivars. The conductivity test reflects loss of cell solutes presumably due to membrane damage. Sorghums which Sulhan selected for their superior heat tolerance seldom gave higher field yields. However, selections within a fairly narrow genetic base (Ogunlela 1974) showed a positive correlation (r = .69) between heat tolerance and yield in 1975, in an exceptionally hot summer at the plot site (Mead Field Lab in Nebraska). Maximum air temperatures equaled or exceeded 35° C in 28 days and were 38° C or higher in 15 days. The highest temperature during the period was 41.1° C. If more or less equal yield parameters exist within the germplasm pool being tested, the heat tolerance test could be useful as a selection tool.

Norcio (1976) demonstrated differences in photosynthetic stability in sorghums as temperature increased. Photosynthesis in RS626 declined at about 40°C; in 4104. one of Ogunlela's heat-tolerant lines, it remained active at 43° C. Norcio (1976) also demonstrated high photosynthetic heat stability in a sorghum pollinator and low stability in a female. Their hybrid possessed high heat stability as did the male. suggesting that the trait is readily manipulated.

Considerable attention has been given to temperature because temperature treatments are easier to impose than are water treatments in defining limiting developmental factors. In nature, temperature effects are often associated with water effects. More attention needs to be given temperature × water interactions. Such investigations, however, are difficult to set up, especially in the field.

Water

Literature on water is far more extensive than can be covered in the scope of this paper. Whiteman and Wilson (1965) subjected sorghum plants to drought at various lengths of time during GS_1 and watered at PI. Flower emergence was delayed approximately in proportion to length of the drought treatment. The effect of drought at different times before PI was also tested. PI was altered by only 3 or 4 days. Earlier drought treatments on the small plants did not permit floral differentiation after drought was relieved until some added vegetative growth had been achieved.

Hultquist (1973) evaluated effects of drought on developmental and physiological characteristics of sorghum in greenhouse pots. He used RS626 and C-42Y, a DeKalb hybrid reputedly better yielding under drought conditions in the middle U.S. Great Plains. Droughting generally was defined as permitting photosynthesis to decline near the compensation point and hold it there 2 weeks. Severe stress at PI damaged

plants and delayed panicle development, as Whiteman and Wilson (1965) noted. Similar stress applied at peduncle elongation, which occurs about the same time that florets differentiate and expand, was very damaging. Portions of RS626 panicles were damaged from the tip down. Upon watering, 90% of the RS626 plants resumed leaf elongation and eventually exserted partial panicles. At the same time, tillering had begun. Reaction of C-42Y to stress was different. Dissected plants showed that if the panicle was damaged, the plant was essentially dead. Rewatered plants which lived exserted apparently undamaged panicles.

Water withheld at 50% bloom induced drought stress more quickly than during vegetative stage. Compensation points were reached in 6-10 days during panicle development, but by about 2 days at 50% bloom. Leaves desiccated rapidly but did not curl. Stomata were unresponsive after bloom. No grain harvest was made because treatments were severe.

Subsequent less severe stress treatments revealed similar apparently modest damage from PI stress and the same contrasting genotype reaction at peduncle elongation. When leaf margins became desiccated at the bloom stage, a small amount of nutrient was added daily to keep the plants alive and take plant and yield data. The photosynthetic compensation point at floret differentiation was reached at —15 bars water potential; that after bloom, at -20 bars.

Primary panicle branch numbers were not affected appreciably, but seed number was drastically reduced by the PI stress treatment and slightly by bloom treatment. Vegetative damage at PI appeared modest but seed number damage was severe. Seed size increased over 40% in the PI treatment because of low seed number, attesting again to the importance of the seed size component of yield under stress. Seed size from the bloom treatment was reduced 60%.

Additional stress treatments involved feeding $^{14}CO_2$ photosynthetically and observing distribution to the panicle and upper plant parts, and to the lower plant parts and roots. Generally under control conditions or when stress was relieved, C-42Y polarized assimilate transport to the developing panicle much more strongly than did RS626. The same assimilate transport characteristics must hold earlier, judging from the peduncle elongation treatments which either left C-42Y panicles relatively undamaged or else killed the plant. Treatments that severe at peduncle elongation seldom occur in nature. Therefore, the tendency to polarize assimilate transport heavily toward floral structures may usually be a positive drought resistance characteristic when grain yield is the primary consideration. While the C-42Y genotype transported a smaller portion of its available assimilate to the roots, the root hairs had a higher specific activity. This suggests that the working part of the root is more active than in RS626 during severe stress. Transport of less assimilate to the lower stalk and root may relate to relatively poor stalk strength under stres. Certainly, assimilate distribution patterns differed in the two genotypes when stress was imposed.

Bennett (1979) subjected sorghum grown in nutrient solutions to a −6.5 bar osmotic stress for 12 days during panicle development. A leaf water potential decline of 2 bars related to a 20% reduction in photosynthesis and a 42% yield loss primarily because of fewer seeds per plant.

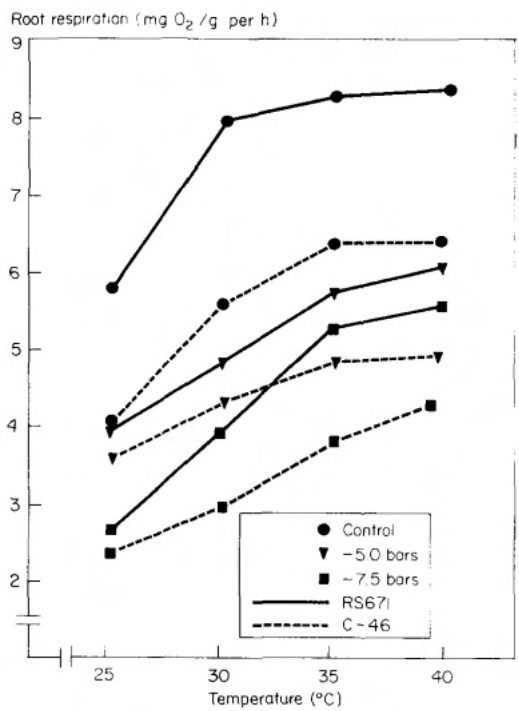
A −7.5 bar stress at tip bloom reduced leaf water potential −5.7 bars and yield

30%. The same stress applied at late bloom reduced photosynthesis little and grain yield none.

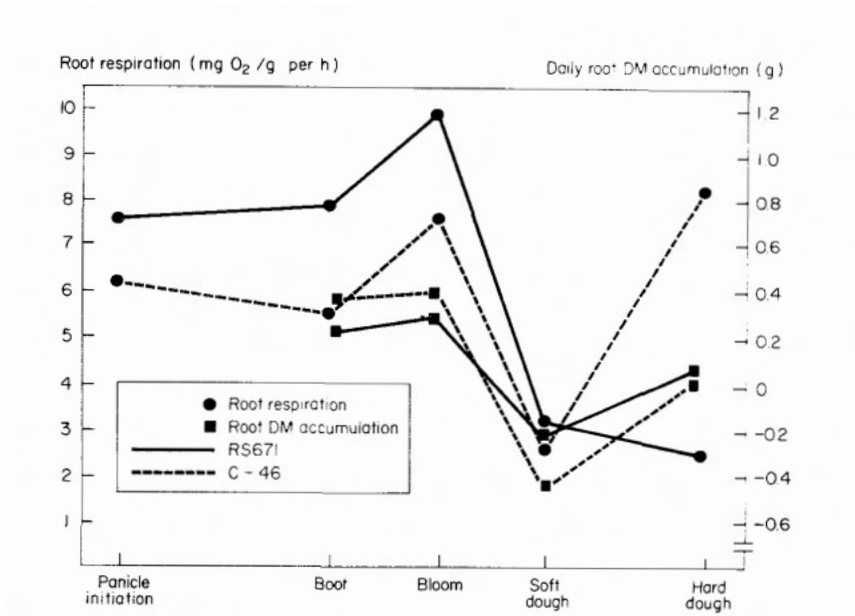
Leaf turgor potentials were reduced by stresses applied during panicle development. Stresses applied at late bloom caused equal reduction in leaf water and osmotic potentials resulting in turgor potentials equal to control plants.

Rice (1979) loaded up two sorghum genotypes with photosynthetically ^{14}C-labeled assimilates and then subjected them to water stress to check redistribution of stored assimilates. The more stress-tolerant hybrid retained a greater portion of assimilates in the stem and leaves during grain fill. Its yield potential did not equal that of the other hybrid. Stress significantly reduced the yield ofthe other hybrid but did not influence that ofthe stress-tolerant hybrid. Comparative respiration rates of the root systems in nutrient solution suggest that the stress-tolerant genotype has a 30% average lower root assimilate demand during panicle development, which may mean less competition for the simultaneously developing panicle (Fig. 5). Finally, in the dough stage, roots in the stress-tolerant hybrid have higher respiratory activity. which may relate to the superior standability of the stress-tolerant genotype (Fig. 6). Perhaps these characteristics relate to the greater persistence and yield stability of the stress-tolerant hybrid.

Garrity (1980) investigated the influence of limited irrigation (line gradient system) on yield. He concluded that applying a constant proportion of the maximum water used weekly was optimal. It permits the stress to intensify gradually. The relationship between evapotranspiration (ET) and yield (dry matter or grain) was



5. Effect of temperature (25°, 30°, 35°, and 40° C) on root respiration in RS671 and Dekalb C-46 grain sorghum, under control and water stress conditions during the boot stage.



6. Root respiration and daily root dry matter (DM) accumulation in RS671 and Dekalb C-46 grain sorghum, under control conditions, from panicle initiation through the hard dough stage.

linear. Reducing ET reduced yields. Likewise water use efficiency declined as ET declined.

Garrity (1980) like Hultquist (1973), found stomatal resistance sensitive to change in leaf water potential before anthesis and relatively insensitive after bloom. Control of transpiration apparently shifted after bloom, with leaf area reduction playing an important role.

The gradual application of a constant proportion of water throughout the season served as a prestress conditioning treatment which effected greater soil moisture depletion particularly during grain filling (Garrity 1980). That treatment resulted in the smallest yield reduction ratio (Stewart et al 1975):

Yield reduction ratio = % yield reduction % seasonal ET deficit.

A mobile chamber was designed to measure canopy photosynthesis in an 80-cm section of row in a 2- to 3-minute time span (Garrity 1980). Water stress did not reduce photosynthesis per unit leaf area after bloom. Canopy photosynthesis was reduced because of leaf loss. Significant loss of stomatal control may relate to the heavy water use during grain fill and to the general absence of water stress influence on photosynthesis. Such loss of stomatal control after bloom may make selection for water loss control during that period very difficult.

Many investigations related to temperature and water were omitted to concentrate on some processes relating to yield components. Many topics pertinent to sorghum are covered in Garrity's (1980) substantial review.

NEEDED INVESTIGATIONS

Significant positive correlation between seed number and grain yield in cereals is common, particularly at modest to high yield levels. The most sensitive period during panicle development (setting seed number potential) is floret differentiation. Specific activity of photosynthetically labeled ^{14}C assimilate in the panicle at PI is higher than that in juvenile vegetative tissue (Eastin. unpubl.). Relative specific activity of the developing panicle declines about 50% by the time floret parts begin differentiating (about 2 weeks after PI), which suggests a weaker polarization of assimilate transport to the developing panicle than at PI. 'This may relate to the lower seed number potential being set in response to subtle temperature and water stresses at that time. Plant factors that render the plant susceptible to stress damage at this stage need to be investigated. Range of plant response to stress needs to be documented to see whether or not selection against floret differentiation damage is feasible.

Since the panicle is very small compared to the remainder of the plant, sink strength or inability to adequately polarize assimilate transport to the developing panicle at floret differentiation is probably more limiting than is photosynthesis.

Photosynthesis is not always the first limiting process, but merits much study especially under water and temperature stress conditions prevalent in many sorghum-growing environments. Variations in CO_2 uptake rates under temperature and water stress are known to exist, but a much wider screening of genotypes and basic studies on mechanistic differences is in order.

Increasing length of grain fill is a prime consideration for increasing yield because sorghum seeds normally are capable of achieving seed weights (size) 30 to 50% greater than is normally realized. Leaves remain green long after seed dark layers. 4 key to progress may be in averting senescence of the phloem parenchyma cells interfacing with the placento-chalazal tissue.

Genotypes should be screened for seed site capacity attainment because this is the only mechanism remaining to adjust yield once the seed number has been set. Seed size may be particularly important in traditionally high stress-low yield areas.

Metabolic or grain production efficiency during grain fill is rather heavily a function of seed number per unit land area. However limited, results of metabolic pace may relate to metabolic efficiency. This area needs to be investigated.

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SOYBEAN

D. K. Whigham

The soybean has been used in Asia for thousands of years but is a relatively new crop in the Western Hemisphere. In recent years, it has been evaluated in many tropical locations and found to have potential. Soybean is an important food source because of its high protein content and reasonably high oil content. Considering the world's demand for proteins and carbohydrates for human diets, the soybean is an extremely important crop.

The soybean is a member of the Leguminosae family; the cultivated species is *Glycine max* (L.) Merrill. Its exact origin and history are unknown. Some historians believe that it was domesticated during the 11 th century B. C. in the eastern half of North China.

Soybean was, and still is, primarily eaten fresh, fermented, or dried. In the Orient, it was also used for religious and medicinal purposes. Later, oil was extracted from it for food and industrial purposes. The value of its oil catapulted soybean into prominence as the major world crop that it is today (Probst and Judd 1973).

The soybean was introduced as a novelty crop into Europe in the early 1700s and into North America in the early 1800s. It was not mass-produced until the early 1900s in the United States, where it was grown primarily as a forage crop. After its acceptance as a forage crop in North America, the first commercial oil extraction occurred. By 1929, a significant portion of the soybean crop was being crushed for oil. After oil extraction, the soybean meal has high (40-50%) protein content and is a valuable component of livestock and poultry feed (Probst and Judd 1973).

Today about 90% of the soybean oil produced is used for human food, the remaining 10% for various industrial purposes. The edible forms of soybean oil range from cooking oils and margarines to pharmaceuticals and medicines. The oil is also manufactured into disinfectants, printing inks, and soaps. About 98% of the world soybean meal production is used for livestock and poultry feed, the remaining 2% for human food. A variety of soy food products made in different parts of the world include fermented food, soy beverage, soy flour, whole bean confectionery products and textured vegetable protein (TVP) used as simulated meat, fruit, and nut products.

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The world soybean production for 1979-80 is forecast at 94.5 million tons. The leading producers, in decreasing order of production, are the US, Brazil, mainland China, Argentina, and Paraguay. The world's area under soybean cultivation during 1979-80 is estimated at 50.8 million hectares. Countries are ranked for area under cultivation in the same order as for total production except that mainland China ranks ahead of Brazil in this category. The world average soybean yield is 1.9 t/ha. The US has the highest average yield of 2.2 t/ha, followed by Argentina and Brazil (USDA 1980).

Many farmers report yields of 4-5 t/ha with top management and favorable environment. Yields greater than 6 t/ha have been recorded for several cultivars in international variety trials at several sites. Experimental plot yields reported from Chile in 1977 and 1978 exceeded 6 t/ha. In 1977 Italy reported a yield of 6.2 t/ha and in 1975 Sri Lanka reported a yield of 6.1 t/ha (Judy and Hill 1979, Whigham and Judy 1978). The world record soybean yield is 7.4 t/ha (Gabel 1979). Improved soybean management practices and higher yielding cultivars will lead to higher soybean yields.

CROP CHARACTERISTICS

The cultivated soybean is an annual plant that grows erect and may or may not branch profusely depending on plant competition and environment. Considerable diversity exists among cultivar types and environments. Mature plants vary in height from 0.3 to 2.0 m. The first leaves that appear are simple and opposite; all other leaves are trifoliolate and alternate. Flowers are borne on racemes at nodes; each raceme may contain numerous flowers. Mature pods produce from 1 to 4 seeds.

Seed

The soybean seed is usually oval but may vary from spherical to elongated. Each seed weighs usually from 120 to 200 mg for popular cultivars, but its size may vary considerably under extreme conditions. Cultivars with hard seed coats take longer to germinate, but may withstand more mechanical damage during harvesting and storage than other seed-coat types.

Most cultivated soybeans have seed coats that do not require scarification for rapid germination. With favorable moisture, temperature, and planting depth, soybean seedlings will emerge in 4 or 5 days. After sufficient moisture has been imbibed, the radicle extends downward through a break in the seed coat, establishing the primary root. The hypocotyl elongates toward the soil surface. During elongation of the hypocotyl, the cotyledons are pulled above the surface of the soil when light strikes the arch, causing the hypocotyl to straighten. During emergence, the seed coat is usually separated from the cotyledons and remains in the soil. Once above the soil surface, the cotyledons separate and become green. They are called cotyledonary leaves and carry on some photosynthesis, but serve primarily as food storage organs until the seedling is established and produces its first true leaves. Cotyledons turn yellow and drop when their food reserves have been exhausted (Hinson and Hartwig 1977).

Roots

Optimum plant growth and grain yield are dependent on a root system adequate to absorb nutrients arid moisture. The soybean radicle that emerges from the seed during germination develops into a modified taproot that normally consists of lateral roots arising from the upper portion of the primary root. The lateral roots penetrate horizontally for some distance before growing downward and may reach depths of about 2 m if the soil environment tolerates penetration. Soil type and soil preparation affect the penetration of soybean roots.

Root growth. Root growth continues throughout the life cycle of the plant; however, its rate varies among cultivars. The rate of root penetration is most rapid during early flowering (Kaspar et a1 1978). The major concentration of soybean roots occurs in the top 10 cm of the soil profile. The top-root ratio is about 4:1 during early vegetative growth and 9:1 at full flowering (Sivakumar et a1 1977). Various factors, including soil temperature and permeability, water level, and the toxicity levels of minerals, affect root penetration. The absorbing surface of the root is greatly increased by the development of root hairs which first appear ai the tip of the primary root soon after germination. Root hairs continue to develop on the young roots as the root system penetrates the soil (Hicks 1978).

Nodulation. As a legume, the soybean has the potential for symbiotic nitrogen fixation when in association with the nodule-bacterium *Rhizobium japonicum.* This potential is one of the main reasons soybeans have become an important international crop in recent years. The bacteria enter the soybean root through the root hair. The infection of the root hair causes a swelling known as the nodule. Not all infections induce nodule formation, however, The nodule is the site of nitrogen fixation. Nodules begin to develop early in the root system life cycle and remain active for 6-7 weeks. New nodules develop continuously through most of the plant's growth cycle.

Many different strains of *Rhizobium japonicum* have been identified. Some are more efficient than others. The bacterial population is usually maintained in field situations if a soybean crop is grown on the field periodically. Artificial inoculation (placing a carrier that contains the bacteria either on the seed coat or in the soil) is commonly practiced by soybean farmers. It is relatively inexpensive and is one way of ensuring the availability of bacteria in the soil environment (Shibles et a1 1975).

Vegetative development

Top growth. The vegetative development of a soybean plant begins with the emergence of the young seedling from the soil surface. Stem and leaf tissue develop from the small plumule that grows from between the two cotyledons. The first node of the soybean plant is the point of attachment of the cotyledons. The second node is characterized by the development of opposite unifoliolate leaves. Starting with the third node, trifoliolate leaves develop on alternating sides of the plant until the plant completes vegetative development.

The initiation of floral primordia occurs within 7 days of emergence. Axillary buds in the leaf axils develop into branches or flowering structures.

Temperature strongly influences vegetative development. Warm temperatures

(30° C) favor rapid leaf development and stem elongation but reduce the number of branches. Photoperiod positively correlates with plant height and node number (Shibles et a1 1975).

Growth habit. Three growth habits have been described for soybean. In the determinate habit, vegetative development is nearly complete before flowers become visible. Flowering occurs at nearly all nodes at about the same time. Racemes containing multiple flowers are common on determinate soybean and leaflets at the terminal apex of the plant are nearly the same size as other leaflets. Determinate soybean usually has fewer nodes per plant and is shorter at maturity than other growth types.

In contrast, the indeterminate growth type begins to flower before vegetative development is complete, and throughout its life cycle develops vegetatively and reproductively. At the terminal apex of the indeterminate types, the flowering structures are smaller, the pods fewer, and the leaflets smaller than those of the determinate types. Indeterminate types are generally taller, have more nodes per plant, and tend to lodge more under environments that favor rapid vegetative development.

The third growth type is referred to as semideterminate. It includes many characteristics that fall between the indeterminate and determinate growth types. Plants are shorter than the indeterminates but generally taller than the determinates. Racemes at the upper nodes are longer than those in the indeterminate types but usually shorter than in the determinate types. Genes that control different growth types are being manipulated to develop new varieties with high yield potential and more resistance to lodging.

Reproduction

Genotype and environment affect flower initiation. Flowering may become visible as early as 25 days or may be delayed until 50 days when certain genotypes and environments interact. Flower color vanes from white to purple. A flowering cluster may contain from 2 to 35 flowers, but extensive floral abortion can occur during any stage of development. The number of pods per node may vary from 0 to 20 at maturity.

Self-fertilization is almost complete in soybean flowers and cross-pollination is usually less than 1%. Flowering may occur over 4-6 weeks, depending on the environment. The duration of flowering in the indeterminate growth types is determined by the rate of flowering development from the lower nodes to the terminal nodes. In the determinate growth type, the length of flowering depends primarily on the duration of flowering at any given node (Shibles et al 1975).

After fertilization of the flower, the pods develop slowly for the first few days, then the rate of development increases until the pod reaches maximum length after 15 or 20 days. After pod development, seed enlargement is the primary reproductive function. Both genotype and environment affect the final seed size produced by a plant. Seed size and seed number usually compensate for each other to produce similar yields for a given environment and genotype.

The physiological maturity of soybean cultivars varies considerably from one environment to another. Under short day lengths, certain cultivars may mature in

approximately 50 days. Other cultivars in cool, long day-length environments may require more than 200 days to mature. Therefore, variety selection and cultivar development are extremely important for maximum production in a given environment. Physiological maturity is characterized by maximum dry matter accumulation in the seed and is best identified by the development of the mature pod color. The seed moisture content at physiological maturity is approximately 50%; for safe storage, it is 13%. Therefore, the drydown period from physiological maturity to harvest maturity may range from a few days, under extremely warm temperatures and low relative humidity, to several weeks under humid, cool environments.

Seed composition

The major components of the soybean seed at maturity are protein and oil. Amounts of the two are negatively correlated. Commonly grown soybean cultivars may range in oil content from 15 to 25% and in protein content from 35 to 45%. Environmental factors may influence chemical composition of the seed. Plant breeders are developing soybean cultivars with improved quality and quantity of both oil and protein.

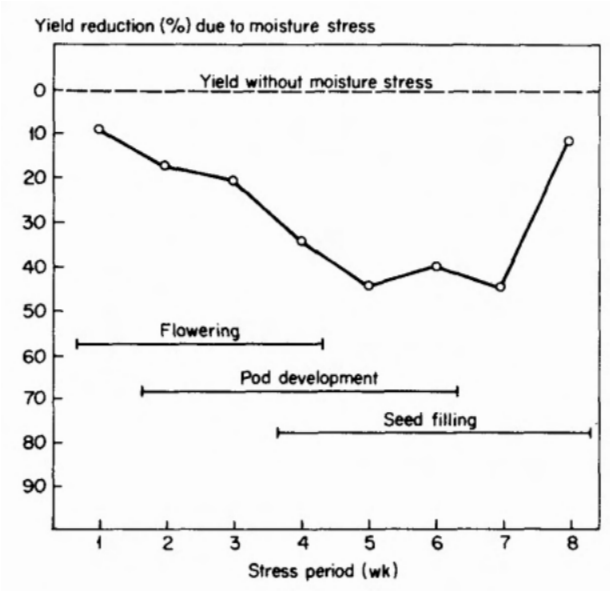
ADAPTATION

The environmental adaptation of soybean is similar to that of maize. The crop is grown from latitudes of 0 to 55°. However, management practices, cultivar selection, and the concentration of commercial production vary considerably across those latitudes. In tropical latitudes, soybean is grown from below sea level to 2,000 m altitude. The variation in environmental conditions for this latitude and altitude range illustrates the adaptability of soybean to different environmental conditions. The major commercial production of soybean is between 25 and 45° latitude at altitudes of less than 1,000 m.

Soybean is temperature sensitive and usually is grown in environments with temperatures between 10 and 40° C during the growing season.

Soybean is considered a short-day plant. Cultivars differ in critical day length. Therefore, the day length consideration is extremely important in determining the appropriate cultivar for a given environment. A few photoperiod-insensitive cultivars have been identified. They require approximately the same number of days from emergence to flowering regardless of day length. However, most cultivars have a specific day length requirement, and they require fewer days to flower under short-day conditions. Temperature may also affect the time to flowering but is usually less important than day length.

Soybean is normally considered an upland crop. Most production occurs in areas where normal rainfall provides the entire moisture supply for the crop. However, in recent years soybean has been raised in areas where irrigation is available and education and research on the specific requirements of irrigation have been expanded. The most critical period for moisture availability occurs during the reproductive phase (Fig. 1). However, moisture must be available in different quantities throughout the growing season to maintain adequate growth and development. Cultivar selection must be based partly on rainfall patterns. If a cultivar matures before the end of the rainy season, it may be impossible to harvest until the



1. Soybean yield reduction at 1–week intervals of moisture stress (adapted from Shaw and Laing1966).

rains stop. If the harvesting is delayed, the grain quality and yield may be reduced. On the other hand, the number of days to maturity must closely parallel the length of the rain period because moisture stress during crop development also reduces yield. In many tropical locations, the selection of soybean cultivars to match cropping rotations may favor selection of a shorter season cultivar to fit rainfall periods and allow the growth of more than one or two crops per calendar year. However, the soybean crop can withstand brief periods of drought with less reduction in grain yield than other crops grown in similar environments. The same is true for brief periods of flooding.

Soybean is grown on nearly all well-drained soil types. In general the crop is sensitive to saline soils but there are cultivar differences. Cultivar selection may be extremely important for successful production in salty soils. The water-holding capacity and the nutrient content of various soils will usually determine the degree of success. Nitrogen fertilization is less important with this crop than with nonlegume crops that can be grown in similar environments because the crop can symbiotically fix nitrogen when in association with *Rhizobium japonicum.* Producing a soybean crop may cost less than producing other crops that require nitrogen fertilization. Phosphorus and potassium nutrients must also be available and several micronutrients may be needed depending on the soil analysis. Micronutrient toxicity has also reduced the productivity of soybeans in certain soils. The optimum soil pH for soybean is near or slightly below neutral. Extremely acid or alkaline soils may reduce the availability of certain nutrients and cause stress.

RESPONSE TO CLIMATIC FACTORS

Light duration

Soybean cultivars have been selected for different production areas because of their responsiveness to light duration during the growing season. A change in the day length will affect the length of time of flowering as well as the length of time to

maturity for a given cultivar. As previously mentioned, soybean is a short-day plant, which means it has a critical night length at which time the flowering mechanism is triggered.

If a cultivar adapted to a tropical environment were moved to a temperate environment, the longer day length would delay its flowering. The cultivar might grow taller, have more nodes, and produce more flowers than normal. However, such a morphological response might result in severe lodging and delayed plant maturity. If the temperate environment were subject to freezing temperatures or arid conditions, the tropical cultivar probably would not produce satisfactory yields and the seed quality might be poor.

On the other hand, if a temperate-adapted cultivar were moved to a tropical zone. the cultivar would probably flower in fewer days than normal because of its adaptation to longer day-length environments. The tropical conditions would also provide the critical night length in a shorter period. Plant height would likely be inadequate, the number of nodes fewer, and the number of flowers reduced from the normal. Because of the smaller plant factory, the cultivar's yield response in such an environment would likely be low. Pods would be close to the soil surface and mechanical harvesting would be inefficient.

Soybean cultivars from other environments must be introduced with caution. They should first be evaluated to see how they would respond to the new environment. A high-yielding cultivar in one environment may not be high yielding in another. International variety trials conducted by the International Soybean (INTSOY) Network should be a valuable tool for selecting cultivars adapted to given environments. Day length is not the only environmental factor that affects the adaptation of soybean cultivars, but it is probably the most important one.

All stages of soybean development are photoperiod responsive to some degree (Shibles 1980). Seasonal variation and day length become more important for the adaptation and eventual production of soybean cultivars at increasingly higher latitudes. Therefore, in temperate zones the planting date becomes critical in the selection of cultivars for high grain yields. The maximum seasonal variation in day length at 10° latitude is only 1 hour 45 minutes. However, at 45° latitude, the change in day length from June to December is almost 7 hours. The growing season, of course, does not continue into December at 45° N. Day length variation during the growing season is close to 3 hours, enough to alter the growth and development of soybean cultivars. The planting date at a given location may affect the number of days to flowering and maturity of a cultivar as much as latitude. Therefore, cultivars must be selected on the basis of latitude and length of the growing season.

Shibles (1980) suggests four soybean mechanisms that are primarily responsible for the wide range in adaptability of soybean to different seasonal durations. They are:

1. inverse response of leaf and branch development to temperature;
2. different genetically controlled growth types that allow determinate, semideterminate, and indeterminate growth to better use environmental resources;
3. genetic variability for photoperiod response that may delay flowering until adequate vegetative development has occurred; and
4. response to photoperiod that affects the length of the vegetative and reproductive periods at any time during the development of the plant.

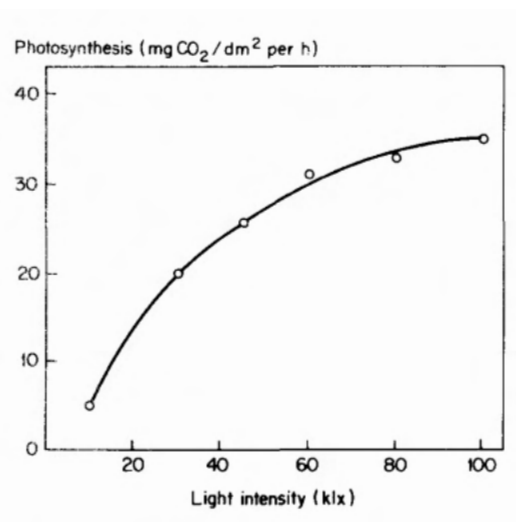
Light intensity

Light influences many soybean characteristics including nitrogen fixation, total dry matter production, and grain yield. The light intensity of a given environment is affected by many physical and environmental conditions such as cloud cover, twilight, altitude, angle of incidence, and competitive shading. The level of light saturation for photosynthesis in the soybean canopy depends upon row spacing, plant population, and plant height (Fig. 2). At normal population densities and row spacing for a given environment in the central US, light saturation of the canopy occurs at approximately 108 klx, whereas with larger spacing the plants are not light saturated even at 161 klx (Beurlein and Pendleton 1971). Differences in light saturation exist among cultivars. The top leaves of the soybean canopy are considered to have a higher level of light saturation than lower leaves of the same canopy.

Low light intensities have been associated with a high rate of pod abscission, lower seed weight, and lower yield. As light intensity changes from 2 to 100 lux in an artificial 24-hour day length environment, days to flowering, internode number, and plant height increase (Major and Johnson 1974). However, seed yield, days from flowering to maturity, and length of flowering period were unchanged in the same experiment.

Light quality may also be changed as light penetrates the soybean canopy. However, under normal production conditions, the agronomic characteristics of the soybean are not changed by differences in quality.

Temperature may modify the response of soybean to light. Huxley and Summerfield (1974) have shown that day length and night temperature and their interactions affect plant characteristics. Cultivars adapted to short day-length environments are less responsive to the effect of temperature than those cultivars adapted to temperate environments (Whigham and Minor 1978). Long day length and cool temperature are additive and delay flowering, but short days are more important than cool temperatures in their effect on the number of days to maturity. High temperatures and long day lengths increase the amount of flowering and pod abortion, and



2. Soybean leaf photosynthesis at different light intensities. The light intensity on clear days was about 100 klx (adapted from Singh et al 1974).

growth rate and plant height are greater. Delayed flowering caused by long photoperiods may also be offset by high night temperatures because early maturity is usually associated with high night temperatures.

Temperature

Air and soil temperatures affect soybean growth and development, physiological processes, nitrogen fixation, seed quality, protein and oil content, and pest damage. The optimum air temperature for seed germination and hypocotyl elongation is about 30° C. Optimum temperature for photosynthesis is between 25 and 30° C. For nodule formation and the development of nitrogen fixation, 27°C appears to be optimum. Nutrient uptake is also favored by temperatures between 25 and 30° C. The minimum for germination is 5° C while the maximum temperature is 40° C. Growth and activity increase as temperatures increase from about 10°C to the optimum and then tend to decline as temperatures exceed the optimum. Extremely high soil temperatures may be lethal to *Rhizobium.*

Air temperature and relative humidity affect seed quality after soybean harvest. Viable seed may be stored for a considerable time if low temperature and low relative humidity are maintained in the storage environment. Seed deterioration occurs rapidly at temperatures above 40° C.

High temperatures during the growing season may lead to the development of pathogens that reduce leaf area, seed quality, and grain yield. On the other hand, certain organisms thrive in cool environments. Development stages of insect life cycles are also controlled by temperature. Each stage of insect development may have a different optimum temperature, but optimum temperatures for plant growth will likely favor buildup of insect pests. Extremely high and extremely low temperatures usually reduce insect activity.

Temperature plays an important role in interrupting the buildup of diseases and insects in temperate zones. Cold temperatures stop the activity of one generation, and an organism must have overwintering characteristics to survive until the next growing season. Tropical environments may lead to a buildup of disease and insect pests that may ultimately reduce soybean yields.

Soybeans developed in the US were evaluated at tropical cultivars sites and analyzed for variation in protein and oil content (Whigham and Minor 1978). The oil contents of 14 cultivars averaged 1.9% more when they were grown at tropical locations than when grown at the temperate locations. The average protein contents did not differ. Warm temperatures during the growing period 20-40 days before maturity appear extremely important for increasing oil content. Low temperatures from flowering to maturity were correlated with a high iodine number in the oil. A negative correlation exists between linolenic and linoleic acids of soybean oil and temperature (Collins and Howell 1957). Late-planted soybean in which seed matured during cool temperatures had lower oil content than early-planted soybean which matured earlier in the growing season.

Although temperature has little effect on the protein content, protein and oil content are inversely related. Methionine is positively correlated with air temperature (Krober 1956). These results suggest that soybean grown in tropical environments may have a better balance of amino acids than that grown in temperate zones.

Water

Wind and high temperatures increase the water demand of the soybean crop. Normally, less than half of the water absorbed by the soybean roots is lost into the atmosphere through evaporation. The remainder of the moisture is used primarily in transpiration. Soybean demands the most water, 0.5-0.8 cm day, during seed filling (Hinson and Hartwig 1977). The transpiration ratio is the ratio of the weight of water absorbed by the plant during its growth to the weight of dry matter produced by that plant. The transpiration ratio for soybean is 580 g of water to produce 1 g of dry matter (Kato 1967) — higher than that for other crops in similar environments. However, this does not mean that soybean is extremely sensitive to moisture stress, because the total dry matter produced per unit area of land is less than that in most major cereal crops. Soybean requires less total water to produce a crop than maize or rice.

Wilted leaves are an indication of severe moisture stress. Moderate stress occurs in the plant before the visible symptom. Drought stress during the vegetative stage may reduce leaf enlargement, photosynthesis, and grain yield. Other consequences are reduced nitrogen fixation, smaller stem size, and shorter plants. If drought stress occurs during flowering, abortion of flowers and pods will likely increase. However, soybean may compensate for flower and pod abortion by producing larger seeds in the remaining pods. Moisture stress during seed filling may reduce seed size. Premature yellowing of the leaves may result from moisture stress during maturation. In addition to the direct effects of a moisture deficiency on the plants, those subjected to severe moisture stress may be weakened and therefore be more susceptible to disease and insect damage.

Excess water may also cause problems. Waterlogged soils may reduce growth and development of the root system. Without oxygen, seeds will not germinate and roots will not function normally. Waterlogged soils will probably have fewer viable nitrogen-fixing bacteria, and the crop would suffer from nitrogen stress. The ponding of water on certain soils may result in soil crusting, which can hinder stand establishment.

Flooding of soybean fields results in shorter plants and reduced yield at nearly all stages of development except during maturation. Flooding during flowering appears to reduce yields the most. As a consequence of reduced grain yield, oil percentage may be increased but protein is usually decreased. Seed quality is usually reduced and germination may be about 50% of normal after severe flooding stress.

Atmospheric humidity may also affect the growth and development of soybean plants if other environmental factors are normal. Low relative humidity may reduce yields more than high relative humidity. Yield reduction can be attributed to increased flower abortion and fewer pods. Low relative humidity stress may also reduce total dry weight and node number. It may increase evaporative demand, causing internal plant moisture stress even though soil moisture may be adequate. During maturation and after, low relative humidity markedly increases shattering. However, a considerable amount of cultivar variability exists for resistance to shattering (Whigham and Minor 1978).

Wind

Wind may severely deter maximum soybean yields in many environments. Wind decreases relative humidity and increases heat loss from within the canopy. However, wind may also replenish the canopy carbon dioxide supply that has been used by the crop. If the wind orients the soybean leaves in a manner that reduces light absorption for photosynthesis, mild stresses may occur.

Wind may cause mechanical or abrasive damage to soybean plants depending upon its velocity, duration, and direction. When accompanied by severe rain or hail, wind may cause severe plant defoliation and reduce yield potential. Wind-blown sand may also cause defoliation that would severely reduce the photosynthetic surface of the plant. Lodging is a factor that may be attributed to wind. Plants that are weakened by pests are more vulnerable to lodging by wind. High plant populations may also result in weak-stemmed plants that are susceptible to wind lodging. Wind may also move small plant pests from one field to another and increase the loss due to pest damage.

MAJOR PHYSIOLOGICAL PARAMETERS

Photosynthesis

Photosynthesis is the carbon assimilation process. Soybeans are C-3 plants, in which light stimulates respiratory activity. Photorespiration, or light-stimulated increase in respiration, is considered an inefficient process in carbon metabolism. When the chemical composition of soybean seed is considered. the cost of photosynthate for soybean seed is 2.3 g/g seed (Brun 1978). Cereal crops normally average about 1.3-1.4 g and other legumes about 1.5 g/g seed. However, the soybean photosynthetic cost for seed production is similar to that of other oil crops such as sunflower, cotton, peanut, and sesame.

Leaves are the primary site of photosynthesis in the soybean plant. However, the first photosynthetic activity appears in the cotyledon 4-6 days after emergence. Green pods contribute very little in the form of photosynthate. As leaves unfold, their carbon dioxide assimilating capacity increases and reaches a maximum shortly after they are fully exposed to sunlight. Young leaves are more active than older leaves in the canopy. The photosynthetic rate varies with light intensity, genotype, and leaf area index (LAI). With high light intensity, maximum carbon dioxide assimilation occurs at 5-6 LAI, but with low light intensity, the assimilation rate reaches a maximum when the LAI is 3-4 (Shibles et al 1975). Leaf photosynthetic rates at the top of a canopy under normal field conditions are about 20 mg CO_2/dm^2 per hour. However, photosynthetic rates of leaves in the lower and middle portions of the canopy are reduced considerably (Johnston et a1 1969). With high light intensity, photosynthetic rates of 65 mg CO_2/dm^2 per hour have been reported (Beuerlein and Pendleton 1971).

Much of the variation in photosynthesis among soybean genotypes has been attributed to differences in the chlorophyll content of the leaves. The chlorophyll content is at a maximum in the fully expanded leaf and gradually decreases until

senescence. Buttery and Buzzell (1977) found that in field-grown soybean, 44% of the variability in photosynthetic rate during flowering was attributed to chlorophyll content of leaves.

Atmospheric carbon dioxide concentration will also affect the rate of carbon assimilation. When atmospheric carbon dioxide rates were increased from 300 ppm (normal air) to 1,670 ppm (enriched air), the photosynthetic rates increased from 20 to 60 mg CO_2/dm^2 per hour (Brun and Cooper 1967). This raises the question of whether it is practical for a farmer to increase the carbon dioxide concentrations within a soybean canopy environment.

Atmospheric oxygen concentrations inhibit soybean photosynthetic rates. However, there appears to be little variation in the normal atmospheric oxygen concentration (21% by volume). Therefore, the soybean producer may not be able to alter the oxygen concentration in the soybean field environment.

The leaf photosynthetic rate may also be affected by moisture stress. Mild moisture stress may reduce leaf size, and if the LAI is reduced significantly, photosynthesis could be inhibited. Moisture stress may also increase the stomatal resistance, reduce carbon dioxide diffusion into the leaf, and affect photosynthesis (Brun 1978).

Seasonal development patterns of the soybean canopy also affect photosynthetic rates. The maximum rate of photosynthesis occurs at beginning of flowering, then drops slightly, and remains stable through the early seed-filling stage. After early seed filling, photosynthetic rate drops sharply as the plant approaches maturity (Sakamoto and Shaw 1967). Sakamoto and Shaw ascribed the sharp decline to reduced LAI because of leaf senescence.

Assimilate distribution

Following the assimilation of elements through photosynthesis. the photosynthate is distributed from the site of fixation to a sink (location of demand). Sucrose is the major form of sugar that is translocated. The sinks may be new vegetative material, flowers, seeds, or roots. Developing leaves sene as sinks until they are about 50% expanded, at which time they become exporters of photosynthate (Brun 1978). The sink closest to the source, or the sink with the greatest demand. usually receives the available photosynthate. Therefore, the pods at the axil of each leaf serve as the first sink for photosynthate produced by adjacent leaves. When rapid seed development begins, the roots and nodules attract very little photosynthate. During the seed-filling period, nodule activity declines sharply, probably the result of competition for available photosynthate (Hume and Criswell 1973. Lawn and Brun 1974).

Respiration

Dark respiration is the photoperiod-insensitive respiratory activity found in all living cells. It occurs during the day although it may be inhibited slightly by light. The rate of dark respiration is controlled primarily by temperature, but is also affected by the availability of water and nutrients. Young leaf tissue and developing pods respire at rates much higher than do older leaves. During the active growth period of the soybean plant, respiration may reduce the photosynthate accumulation by 1/3 each day (Shibles et a1 1975).

Nitrogen assimilation

The high protein and oil content in soybean seed means that nitrogen must be assimilated in large quantities for maximum yield production. Nitrogen assimilarion is carried out by two systems.

Nitrogen fixation. A characteristic of legumes is their ability to assimilate nitrogen in root nodules through a symbiotic relation between the root cells of the soybean plant and *Rhizobium japonicum.* Molecular nitrogen absorbed from the soil atmosphere is reduced in the nodule using energy provided by photosynthates that have been transported from the leaves. The reduced nitrogen is then translocated to nitrogen sinks throughout the plant. Nitrogen fixation does not contribute much nitrogen until the plants are 34 weeks old. Maximum nitrogen fixation occur? during pod or early seed development (Brun 1978). The contribution of the nitrogen fixation system to total soybean nitrogen needs is estimated to range from 25 to 75% Yields remain relatively constant regardless of the nitrogen source (Deibert et al 1979).

Nitrate reductase. Nitrogen assimilation through the nitrate reductase system occurs in a manner similar to that of other plants. Nitrogen is absorbed into the root and transported to the leaves where it is reduced to amino nitrogen. The amino nitrogen combines to form various amino acids. They, in turn, combine to form proteins, either in the leaves or in other sinks (Brun 1978). Nitrogen assimilation by the nitrate reductase system reaches a maximum at full flowering and declines steadily until maturation.

The nitrogen assimilation systems complement each other because they peak at different times during plant development. Early in the soybean life cycle, the nitrate reductase system is necessary to provide nitrogen for newly established seedlings, but too much nitrogen from the nitrate system or N fertilizer inhibits nitrogen fixation (Table 1). Soybean yields achieved by using only one nitrogen assimilation system have not exceeded yields produced when both nitrogen assimilation systems were active (Deibert et al 1979).

Crop growth rate

Soybean leaf area production begins rather slowly but increases at a linear rate until flowering. Maximum leaf area production for the determinate cultivars may occur near the beginning of flowering, but indeterminate cultivars reach a maximum leaf area near the end of flowering. Maximal LAI values may range from 5 to 8. After the

Table 1. Percentage of total nitrogen from different sources in soybean seed at harvest.[a]

Rate of N fertilizer applied at planting (kg/ha)	Nitrogen (%)		
	From fertilizer	From soil	Fixed
0	0	34	66
45	6	32	62
89	19	49	32
134	29	40	31

[a]Adapted from Diebert et al (1979).

maximum LAI is reached, it declines slightly as maturity approaches, at which time the values may be 4-6 (Shibles et al 1975).

The net assimilation rate (NAR) is the increase in plant dry weight per unit leaf area per unit of time. As LAI increases, the efficiency per unit leaf area is reduced slightly as a result of competition for light, and the NAR decreases (Fig. 3).

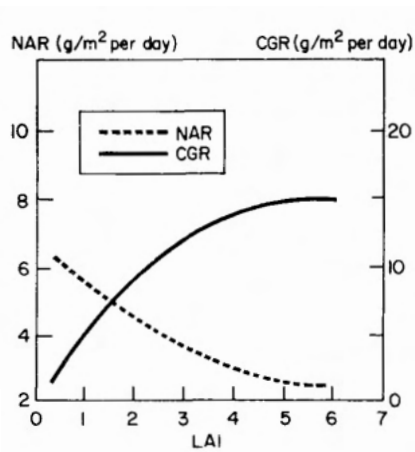
Crop growth rate (CGR) is a function of NAR and LAI. Total plant production is determined by the CGR, a function of light interception by the leaf area of the crop. Soybean LAI values of 3.1-4.5 are required for 95% light interception (Shibles and Weber 1965). The amount of leaf area necessary for 95% light interception depends upon plant density and row spacing. Most researchers who have evaluated the optimum LAI values for maximum CGR have found no evidence for an optimum LAI in soybean.

The rates of dry matter accumulation in the seed of different cultivars appear similar (about 9.9 g/m^2 per day). However, the CGR in the linear phase of development varies considerably among cultivars (Hanway and Weber 197la). The length of the seed-filling period appears more important for seed-yield differences among cultivars than the rate of daily growth (Shibles et al 1975).

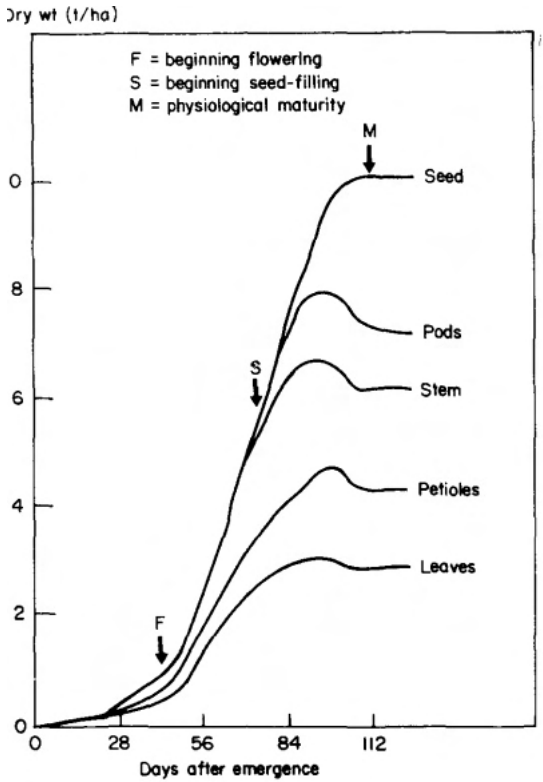
Changes in dry matter accumulation during the growing season show rapid accumulation from flowering until late in the seed-filling period (Fig. 4). Vegetative dry matter accumulation peaks during seed filling, but total plant dry matter accumulation, including the seeds, continues until physiological maturity. The loss of dry matter in the vegetative portion of the plant is caused by respiration and the translocation of photosynthates from vegetative materials to seeds.

Total dry matter production

The total accumulation of dry weight by the plant during the growing season is referred to as total dry matter (TDM) production. However, it normally includes only the aboveground dry matter accumulation and is sometimes referred to as biological yield. Maximum TDM yields of 10.2 t/ha have been reported in the temperate zones (Hanway and Weber 1971b). Of this total, 29% was accumulated in the seeds at physiological maturity. The TDM accumulation in soybean is a function



3. Relation between leaf area index (LAI), net assimilation rate (NAR), and crop growth rate (CGR) (adapted from Buttery 1970).



4. Dry weight accumulation of the aboveground soybean plant parts (adapted from Hanway and Weber 1971b).

of the cultivar, number of days to physiological maturity, and environmental inputs available to the crop.

Harvest index

Harvest index is the portion of the biological yield represented by the economic yield, which is the weight of the plant organs that constitute the product of economic or agricultural value. The economic product of the soybean plant is its seed. Therefore, the harvest index (HI) is the percentage of the plant's total TDM contributed by the seed. In an Iowa study, the aboveground portion of the mature soybean plant consisted of 28% leaves, 15% petioles, 17% stems, 11% pods, and 29% seeds (Hanway and Weber 1971b).

When the maximum dry matter production was 10.2 t/ ha, the associated seed yield was 2.8 t/ha. Therefore, the HI was 27%. The total plant weight increased steadily from the time of full flowering until seed development was complete. The daily rate of accumulation was nearly constant during this time and averaged about 186 kg/ ha per day, including leaf fall due to senescence (Hanway and Weber 1971 b). Leaf and petiole weights continued to increase until the full-seed stage when the total leaf production was calculated. Leaf senescence started before flowering and became very rapid during the seed-filling period. As the plants approached maturity, leaf drop increased markedly until harvest maturity, when no leaves remained on the

plants. Pod weights started increasing after full flowering and continued through full seed development. Stem weight also continued to increase during the same period. After full seed development, weight loss in the stems, leaves, and pods was significant. Seed weight began increasing rapidly after full seed development and continued until physiological maturity.

YIELD COMPONENTS

The yield components affecting soybean grain yield most vary with the stresses that occur in the environment. Many of the components interact and compensate for one another. This leads to the wide adaptability of soybean and relatively stable yields from properly managed fields. The most important yield components are plants per hectare, nodes per plant, pods per node, seeds per pod, and weight per seed.

Plant population

Maximum grain yields have been reported from populations ranging from 200,000 plants/ ha to more than 600,000 plants/ ha. There are mixed reports about soybean yield responses from these plant populations. However, with optimum management, grain yield usually increases slightly as harvest plant population increases within this range. Low populations usually result in increased branching and an increased number of fruiting nodes per plant, At lower population levels, yield declined because of insufficient number of plants. whereas at high population levels yield decreased because of extreme competition among plants. An increase in plant population or density will usually result in an increase in plant height and in the height of the lowest pod. However, increased density has little, if any, effect on the number of nodes per plant, the number of seeds per plant, or seed size. A detrimental effect of increasing plant population could be plant elongation, which may result in weaker stems and increased lodging. Lodging may result in lower photosynthate production, lower quality seed, and more difficult harvest (Shroyer 1980).

Nodes

The number of nodes per plant may be increased if the populations permit branching. However, most of the plant height change resulting from changes in population results from internode elongation rather than from the development of additional nodes. The number of nodes per plant may be controlled by genetics; several genes that affect this yield component have been identified. The indeterminate growth type produces the greatest number of nodes, followed by the semideterminate types, and then the determinate growth types (Shroyer 1980). Where temperature or moisture is a limiting environmental factor, delayed planting will reduce the number of nodes developed per plant.

Pods

The total number of pods per unit area of land is a function of plant population, number of nodes, and number of pods per node. The number of pods per node varies depending upon the amount of stress during development. The number of pods per

node will usually decrease as plant population increases and row spacing decreases (Shroyer 1980). The number of pods and seed yields of the three different growth types of soybean were compared. The plants were divided into three sections with an equal number of nodes in each section for each growth type. The middle section of the determinate and indeterminate growth types produced the largest number of pods. The semideterminate produced the largest number of pods in the upper section. Of the three growth types, the indeterminate produced the lowest number of pods in the upper plant section. The lower sections in all three growth types produced the fewest pods. The number of pods per plant decreases with delayed planting, reduced row spacing, and increased plant density.

Seed number

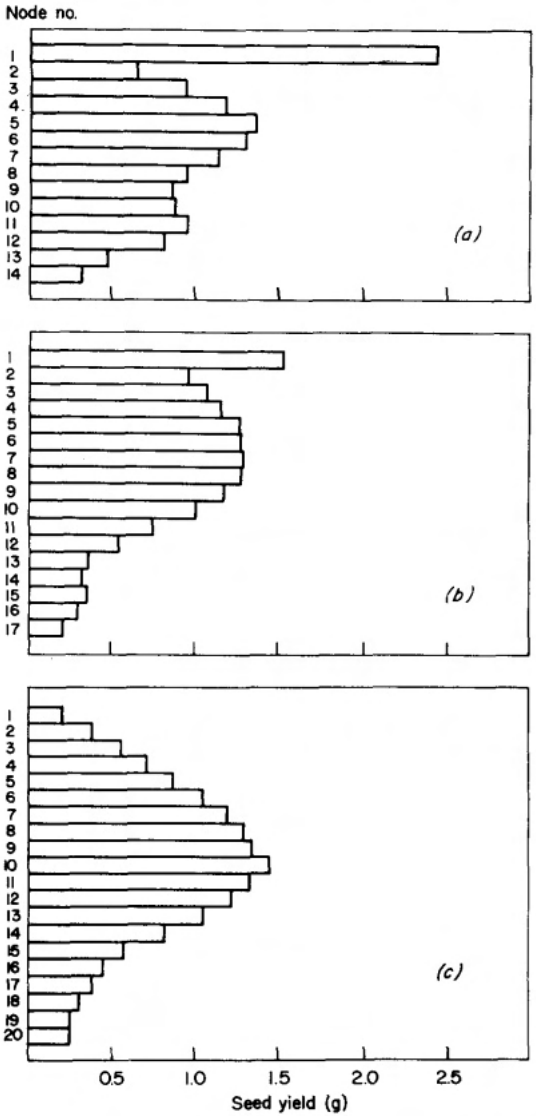
The number of seeds per pod ranges from 1 to 5 and averages between 2 and 3 per pod. It decreases as the date of planting is delayed or the population density increases. Seeds within a pod develop at different rates. First the apical seed tends to develop most rapidly, then the basal seed (Shibles et al 1975). Flower and pod abortion may range from 40 to 80% and ovule or seed abortion after pod development may occur at a rate of 9-22%. Most of the abortion that occurs during the early stages of embryo development is stress induced. The most frequent abortion site within a pod is at the basal position. Stresses that promote abortion include long photoperiods, high temperatures, light stress. and cool temperatures before flowering.

Seed size

Unless stress or poor management occurs, yield is not well related to seed size. Seed size is influenced by the genotype and the environmental conditions that exist during the growth period. Based on 13% moisture content, the seed size may vary from less than 100 to more than 300 mg/seed. Seed size is often a compensating factor for reduction in other yield parameters such as pod number and seeds per pod. A reduction in seed size is usually a response to delayed planting. reduced row spacing. or increased plant population. Small seeds retain their viability and may be stored for longer periods than larger seeds. Large seeds are more susceptible to mechanical and physical damage during harvesting and storage.

Seed yield distribution

Seed yield distribution differs with growth type (Fig. 5). When soybean plants were equally divided into three sections, the percentage of yield contribution differed among growth types (Table 2). A choice of high-yielding cultivars from Each of the growth types for different environments would be ideal. However, certain growth types dominate particular areas of production. In the US, at latitudes of 40° or higher, nearly all cultivars are the indeterminate growth type. In the southern US at latitudes lower than 40°, most cultivars are the determinate growth type. Cultivars of semideterminate growth habit are now being developed for commercial production. The preference for a particular growth type is determined by the length of growing season and temperatures of that environment.



5. Seed yield contribution by node of a) determinate, b) semideterminate, and c) indeterminate soybean growth types grown at a density of 33 plants/m^2 (adapted from Shroyer 1980).

Table 2. Seed yield distribution of the upper, middle, and lower plant sections of 3 soybean growth types. [a]

Growth type	Contribution to seed yield (%)		
	Upper	Middle	Lower
Indeterminate	28	52	20
Semideterminate	45	42	13
Determinate	43	38	19

[a] Adapted from data of Shroyer (1980).

CROP MANAGEMENT

After adapted, high-yielding soybean cultivars are selected for planting, good crop management is the key to satisfactory yields. A comparison of 10 cultivars grown at 25 sites in 10 countries indicated that management was more important than environment for acceptable soybean yield (Whigham et al 1978). The altitudes of the sites averaged 246 m and latitudes, 10°. The mean yield was 2.0 t/ha with a range of 0.5-4.5 t/ha. The days to flowering averaged 32 and the days from flowering to maturity, 63. Plant height averaged 44 cm. Management variables accounted for 56% of the yield variability among sites. Environmental variables accounted for 27% of the yield variation. Therefore, it is extremely important to train farmers to use the proper management techniques for high yields.

Experimental soybean yields of more than 4 t/ha have been produced in many environments and by many different cultivars (Whigham 1975, 1976; Whigham and Judy 1978; Judy and Whigham 1978; Judy and Hill 1979, 1980). More than 20 countries have reported soybean yields exceeding 4 t/ha. Most of the sites were in tropical or subtropical environments where soybean is not commonly grown. The highest reported yield from the INTSOY trials was 6.9 t/ha in 1977 at Santiago, Chile. The length of the growing season was about 118 days and the economic yield was 58 kg/ha per day.

In a 4-year study of INTSOY results, Davis was the most consistent high-yielding cultivar at altitudes less than 500 m and latitudes less than 20° (Judy and Hill 1979). Within the same altitude range but between lat. 20 and 30° the cultivar Bossier yielded slightly more than Davis. Davis flowered in about 30 days and matured in less than 100 days in environments at less than 20° lat. An undesirable characteristic of Davis in tropical locations is its extremely short plant height (35-40 cm).

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FIELD BEAN

D. R. Laing, P. J. Kretchmer, S. Zuluaga,
and P. G. Jones

Common bean (*Phaseolus vulgaris* L.) is an important world crop with relatively low productivity in most cropping systems. Physiological factors influencing yield and adaptation are discussed with respect to field research in the tropics. The comparative earliness of the majority of the germplasm is closely associated with sub-optimal canopy development leading to lower yield potentials. Leaf area development is dependent on the basic nodal structure as is the potential sink. Increases in nodal structure led to increases in both source and sink and consequently yield. The species is comparable to soybean in terms of various efficiency parameters (yield per unit leaf area duration, harvest index, and yield per day of growth cycle) and differences in crop growth rate are proportional to differences in leaf area. Water stress tolerance and specific adaptation to temperature extremes have been identified in the species. The results of photoperiod response evaluations appear to have future application in predicting phenological responses.

The common bean *Phaseolus vulgaris* L. is the most widely grown of the four cultivated species of *Phaseolus* from the American tropics. It is the most important grain legume for human consumption in the world. Of the mean annual world production of 8.3 million t (1976-78), 47% was produced in Latin America and the Caribbean, 16% in Africa, 15% in China, 11% in North America, and 8% in Europe (J. H. Sanders, CIAT, unpubl. 1980).

The dry edible bean is an important protein and calorie source in human diets in developing countries, particularly eastern Africa, and throughout most of the Americas. The green pod is one of the most widely eaten vegetables in the world. Weighted mean per capita dry bean consumption (1975-77) was 15 kg/ year for the main producing countries in Latin America and 12 kg/ year for those in Africa.

The common bean is not a high-yielding species - its national average yield is less than 1 t/ ha in most developing countries and below 1.4 t/ ha in most developed

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countries. This paper discusses some aspects of the physiology of yield and adaptation in tropical fields with particular reference to work at the Centro Intemacional de Agricultura Tropical (CIAT).

GERMPLASM

Phaseolus vulgaris is a highly polymorphic legume species that varies considerably in growth habit, vegetative characters; flower color, and in size, shape, and color of seeds and pods. The world germplasm bank at CIAT consists of 26×10^3 individual collections, of which 9.5 X 107 have been evaluated (CIAT 1980). The collection is classified into four main types of growth habit: determinate bush (I), indeterminate erect bush (II), indeterminate prostrate and semiclimbing (III), and indeterminate climbing (IV) types. Data in Table 1 demonstrate their wide variability in key parameters when evaluated at CIAT-Palmira. The relative degree of determinacy for the growth habits can be compared by noting the change in mean number of main stem nodes between flowering and maturity. Mean seed weight is higher in type I and IV materials.

The most common growth habit is represented by the prostrate, heavily branched type III materials. This probably reflects human selection pressure for land races that are appropriate for low density seeding in rustic production systems usually involving maize-bean intercropping. Most type I collections are derived materials from temperate latitudes. Most type IV land races occur in cropping systems at altitudes> 1800 m in the tropics, while types II and III are common at lower altitudes (500-1800 m). Most of the climbing type IV materials are grown in association with maize at higher altitudes, while the bush types are grown in monoculture and in relay and direct associations, chiefly with maize.

ECOLOGY

Agroecological surveys (CIAT 1979) of the production areas in Latin America have defined a preliminary set of 110 microregions to which mean monthly temperature, rainfall, and estimated evaporation parameters have been assigned. Bean production statistics show a remarkable concentration of production (76%) occurs in

Table 1. Mean data[a] for selected morphological and phenological characters for the 4 growth habits of *P. vulgaris.*

Parameter	I Determinate bush	II Indeterminate bush	III Indeterminate semiclimbing	IV Indeterminate climbing
% of total evaluated	23.1	23.2	33.3	19.8
Plant height (cm)	44 (18)	92 (44)	103 (28)	160 (50)
Nodes[b] at flowering	8.3 (1.5)	13.3 (1.9)	14.3 (2.1)	14.8 (4.0)
Nodes[b] at maturity	8.6 (1.4)	17.0 (2.0)	18.9 (2.6)	22.7 (4.0)
Seed weight (mg/seed)	336 (100)	236 (80)	257 (89)	294 (1 07)
Days to flowering	34 (3)	39 (4)	38 (5)	40 (6)
Duration of flowering	22 (6)	25 (5)	28 (6)	29 (7)

[a]Data derived from evaluation of 9.5 x 10^3 germplasm collections at CIAT-Palmua (3°N, 1000-m altitude, mean temperature 23.8°C) at density of 20-25 plants/m^2. Mean and standard deviations in brackets. [b]Number of main stem nodes.

microregions with mean flowering period temperatures of 19-23°C (Table 2). Although these microregions are located over an extremely wide range of latitudes and altitudes, annual cropping systems that have evolved reflect the general temperature adaptation characteristics of the species.

A high proportion of production is affected by mean growing season water deficits of more than 0.1 mm/day in areas without irrigation. In most of these microregions, increasing late season stress toward the end of the tropical and subtropical wet season appears to be the main type of deficit experienced. It probably reflects the common practice of relay cropping maize and beans, with beans in the latter phase of lower mean temperatures (in the subtropics) and declining mean rainfall.

The production distribution of the species reflects the moderate temperature conditions in the centers of diversity in the highlands of Meso-America and northern South America. Areas of diversity and of domestication (Evans 1976) occur at an altitude of 500- 1800 m with a high frequency of wild types recorded at about 1200 m in Meso-America (Miranda 1974). Smartt (1969) and Evans (1973) discuss the evolution and domestication of the species from wild climbing ancestral materials, of which *P. aborigineus* is probably a modern survivor.

PHOTOSYNTHESIS

Photosynthesis of single leaves

Phaseolus vulgaris is a C-3 plant. Maximum net photosynthetic rate (Po) during the ontogeny of individual leaves is 25-40 mg CO_2/dm^2 per hour (Tanaka and Fujita 1979, Izhar and Wallace 1967, Louwerse and Zweerde 1977), which is comparable with that for rice, a C-3 cereal crop (Tanaka et al 1966). In an extensive experiment on beans in Hokkaido, Tanaka and Fujita (1979) have shown a normal increase in Po during leaf expansion and a decline with leaf age with large differences in the shape of the Po curves versus time, depending on leaf position, nitrogen content of the media, and other factors. A very high correlation of Po with leaf N content was recorded with the highest Po values at ~16 mg N/dm^2 of leaf. Saturating light intensities for individual leaves also vary considerably with leaf age and irradiance conditions during leaf growth (Louwerse and Zweerde 1977). Light saturation values of 150-250 J/m^2 per second are reported by most workers. Tanaka and Fujita

Table 2. Distribution of production of common bean (*P. vulgaris*) in Latin America according to cluster analysis of crop climate for 110 microregions of production.

Mean cropping season water balance regime (mm/day)	Percent of Latin American production[a]				Total
	>23°C	19°-23°C	14°-19°C	< 14°C	
Excess water (>0.1)	1	3[b]	n	n	4
Adequate water (0.1 to -0.1)	n	17	n	1	18
Water stress (–0.1 to –3)	6	42	11	n	59
Severe drought (<–3)	n	14	n	n	14
Total					95[c]

[a]Production in mean climates within each two-way cluster group. n = negligible production indicated in preliminary data survey. [b]Highest rainfed municipio yields in Latin America occur in this grouping e.g. western El Salvador. [c]5% of total annual production not allocated.

(1979) found no significant differences in Po of bean cultivars under comparable conditions of leaf age. On the other hand, Izhar and Wallace (1967) report cultivar differences of 9-35%. Po rates in the Hokkaido studies were initially reduced by adjacent sink removal (pods) but recovered because of more available nitrogen. Stem carbohydrate accumulation was very sensitive to source-sink manipulation (leaf and pod removal).

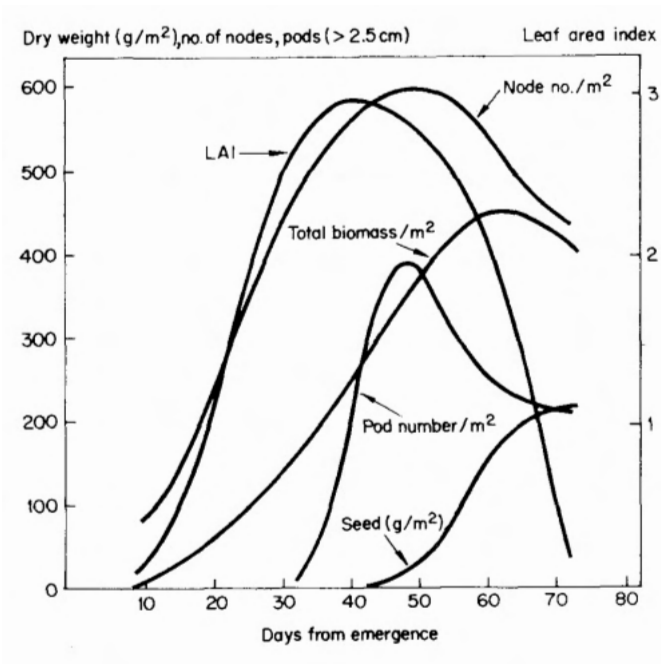
Photosynthesis of the crop canopy

Sale (1975) reports one of the few studies available on field canopy photosynthesis. In a high radiation environment (20 MJ/m^2 per day) in southern Australia, bean canopies had maximum canopy net photosynthesis (Pn) of 354 mg/dm^2 per hour at saturating irradiance of 600-650 W/m^2 and LAI of >4.5. No change in Pn was recorded over 4.5-7.3 LAI. Similar findings had been observed in soybean (Jeffers and Shibles 1969) and wheat (Puckridge and Ratkowsky 1971, Walcott and Laing 1976). Soybean, however, showed some Pn response to increasing LA above 4.5. As in many other species 95% of incoming radiation is intercepted by bean canopies at a LAI of ~4 (Aguilar et al 1977).

CROP GROWTH AND YIELD

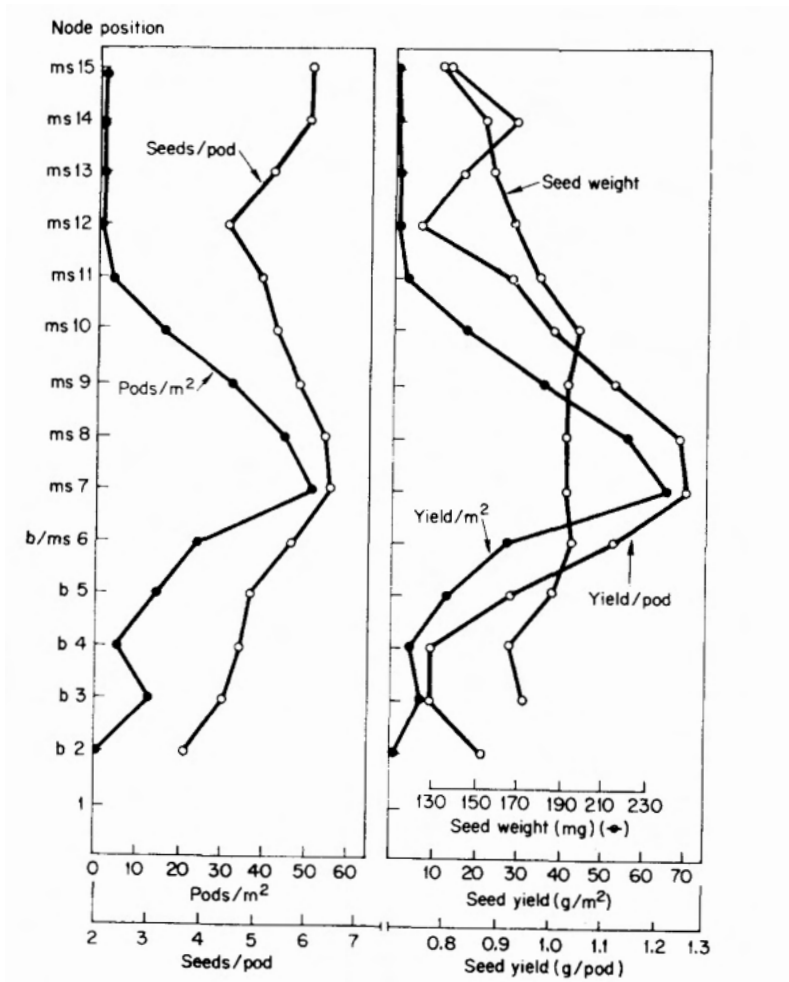
Studies on a single cultivar

Key growth parameters are presented in Figure 1 for a typical indeterminate bush cultivar (Porrillo Sintetico, growth habit II) grown at CIAT-Palmira. The crop yielded 2.4 t/ ha (14% basis) in 76 days from emergence to physiological maturity (DE). The maximum leaf area index (LAI) value at 40 DE was less than 3 with a



1. Key growth parameters for cultivar Porrillo Sintetico at given days from emergence in irrigated and protected experiments. Established plant density is 25/m^2 CIAT-Palmira.

maximum biomass accumulation of 4.5 t/ha at 62 DE. Pods (counted when>2.5 cm long) were maximum at 46 DE and declined with small pod abscission. The flowers that ultimately abscissed were those that opened later particularly on the upper nodes and on the branches (CIAT 1977). The rapid decline in LAI and pod number coincided with the rapid grain growth phase (50-65 DE). Rapid senescence was closely associated with grain growth as photosynthate and other metabolites were translocated to the developing grain. Leaf senescence occurred first at the lower nodes and proceeded sequentially up the main stem and the branches. The profile structure of yield in a similar experiment with the same cultivar (Fig. 2) shows peak yield/node per m^2 at node 7 and a close association of yield per node with pod number per node. Seeds per pod and particularly seed biomass were more conserva-

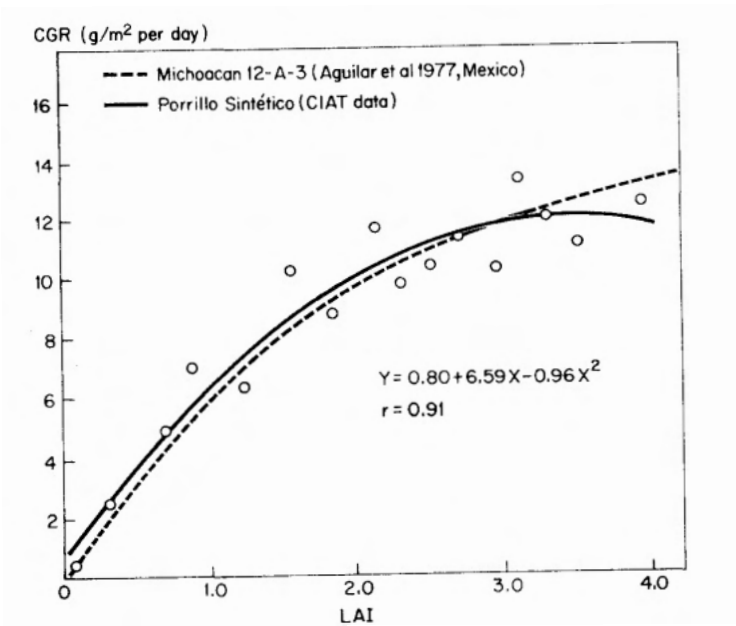


2. Yield and yield components profile by main stem (ms) node number for Porrillo Sintético in a typical experiment; b refers to nodes at which branches were subtended. CIAT-Palmira.

tive, but the highest seed yield per pod was recorded also at node 7. The first flowers to open in this cultivar normally were on racemes borne at node 7. In most Porrillo Sintetico crops ~10% of the yield was normally borne on branches subtended at nodes 3-5. Branch yield as a proportion of the total normally increases with the degree of lodging on normally erect bush materials.

The crop had a short duration compared to most field crops, and thus did not have sufficient time for increase in LAI before the onset of grain growth. Earlier formed reproductive tissue had the advantage in terms of partitioning of current photosynthate. Maximum main stem carbohydrate content (sugar plus starch) of 12-15% of stem dry weight occurred before the onset of grain growth and rapidly declined to 2% with grain growth. The actual maximum level of stored carbohydrate in the stem varied considerably from crop to crop and appeared related to crop vigor and leaf area availability. In many CIAT experiments no increase in stem carbohydrate storage has been observed during the grain growth phase. Tanaka and Fujita (1979) found increasing carbohydrate storage during grain filling. They suggest that is evidence of a sink limitation to yield during the filling phase. No such conclusion can be drawn from available CIAT data.

Mean crop growth rate (CGR) of Porrillo Sintetico over a number of experiments shows a curvilinear response to increased LAI (Fig. 3). An approximate curve for a similar type II cultivar under similar solar radiation conditions (16-18 MJ/m^2 per day) in Mexico (Aguilar et al 1977) closely agrees with the CIAT findings at least up to a LAI of ~4. The Mexican crop was grown at a higher plant density (28/m^2) and



3. Mean crop growth rate (CGR) in Porrillo Sintetico over a series of experiments for the same time periods versus the main leaf area index (LAI). Data for a hand-drawn curve from Aguilar et al 1977 are for comparison.

had a longer growth cycle (~95 DE). The crop developed a higher maximum LAI of 5.3 and a CGR of 16.5 g/m^2 per day with a final seed yield of 4,210 kg/ha. In normal Ponillo Sintetico crops at CIAT maximum LAI was normally <3.5.

Crops with LAI >3.2 (Fig. 3) were generated artificially by extending the growth cycle. The moderately photoperiod-sensitive Porrillo Sintetico was grown in normal yield plots 0-25 m from a linear light source (300W incandescent lamps) giving an effective day length of 16 hours 30 minutes near the source compared to the natural 12 hours 20 minutes prevailing at a distance > 12 m. The long-day-sensitive cultivar near the lights flowered 15 days later. Physiological maturity occurred 26 days later than in the control plot. Yield increased by 48% to 4,123 kg/ha at a maximum LAI of 4.0 (Table 3). Vegetative node no./m^2 increased by 45% due to the longer preflowering period. The increased proportion of yield on branches was a product of the extra nodes formed on them. The only yield component significantly affected by the treatment was pods/m^2. Fitted LAI curves (Fig. 4) show the effects of the increased growth cycle length on development. The basic form of the curves was not altered by the treatment.

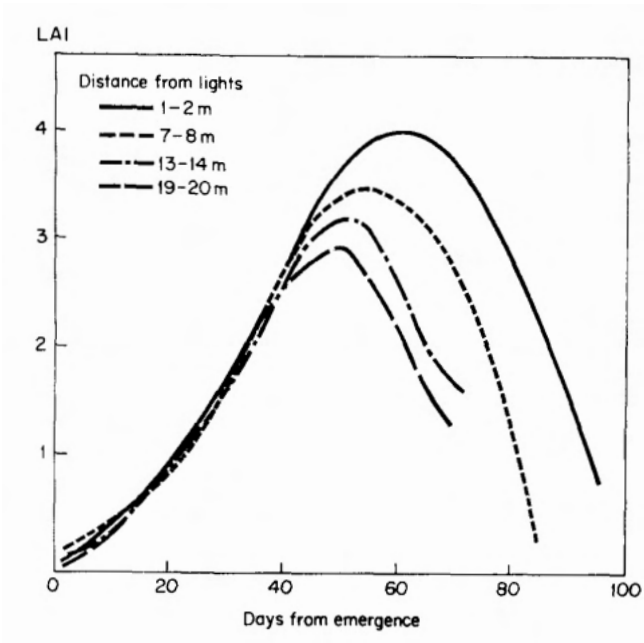
Physiological and phenological constraints on yield of normal crops are clearly demonstrated in the data for a single cultivar. By increasing the length of the growth cycle, an increase in both the basic nodal structure and leaf area duration (LAD) allowed a concurrent increase in both source and potential sink (racemes subtended in the extra vegetative nodes). The percentage of flower abscission decreased significantly as yield increased, suggesting that the extra leaf area available produced a more favorable photosynthate status in the plant and allowed a higher proportion of flowers to set pods. The yield per unit LAD from emergence to physiological maturity and the harvest index declined as yield increased, suggesting lower canopy yielding efficiency at the high yield levels.

A series of experiments with Porrillo Sintetico grown in different semesters gave

Table 3. Effect of photoperiodically extending the growth cycle of *P. vulgaris* (Porrillo Sintetico) on selected growth and yield parameters in the field. CIAT-Palmira, Colombia, 1976.

Parameter	Plot distance from linear light source				
	1-2 m[a]	7-8 m	13-14 m	19-20 m[b]	
Seed yield[d] (kg/ha)	4123	3474	2983	2772	
Harvest index (%)	49	50	51	54	-0.87
Days to flowering	51	43	36	36	0.98
Days to physiological maturity	95	84	71	69	0.99
Seed yield (kg/ha per day)	43	41	42	40	0.77
Pods (no./m^2)	314	255	214	208	0.99
Seeds (no./pod)	5.7	5.8	5.6	5.5	0.69
Seed weight (mg/seed)	197	201	210	207	-0.92
Nodes main stem (no./m^2)	520	460	407	370	0.99
Nodes branches (no./m^2)	268	272	147	179	0.82
%yield on branches	82	39	18	14	0.99
Flower abscission[e] (%)	59	–	–	68	–
Maximum leaf rice index	4.0	3.8	3.0	2.7	0.95
Leaf area duration (LAD) (days)	187	150	110	99	0.99
Yield/LAD	2.2	2.3	2.7	2.8	–0.95

[a]Effective day length 16 hours 30. [b]Represents normal control crop — photoperiodic effect of 300 W incandescent lamps diminished to zero at ~12 m; effective day length 12 hours 20. [c]Correlation with yield, r = 0.91 required for significance at 1%. [d]14% moisture basis; plant density 25/m^2. [e]Percent of opened flowers that finally abscissed.

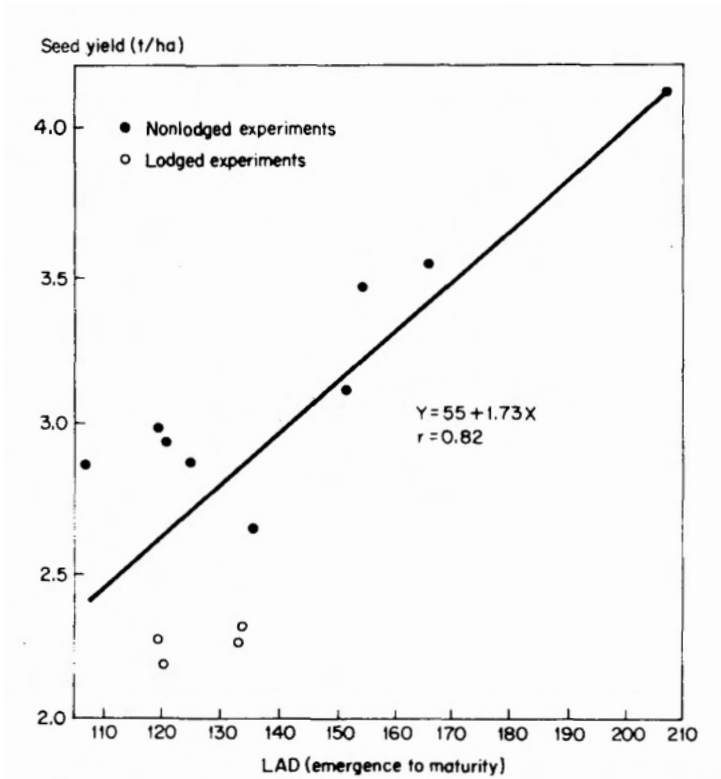


4. Leaf area index (LAI) for Porrillo Sintetico against days from emergence for 4 treatments at different distances from a linear light source (curves fitted by trigonometric functions).

control yields from 2.19 to 4.12 t/ha. The variation in yield was associated with such constraints as soil alkalinity, poor drainage, and uncontrolled diseases and insects (CIAT 1977). The combined data for these trials and those of the extension experiment show a high positive correlation of yield with LAD (Fig. 5), pods/m^2 (r = 0.94), and total dry matter (0.81), and a negative correlation with harvest index (–0.28). Yield variation in this cultivar was therefore associated with a concurrent increase in both source and potential sink. Data from the experiments of Aguilar et al (1977) also show a strong relationship between post-flowering LAD and yield for a single cultivar at varying densities. The latter authors suggest that these data do not necessarily indicate a cause and effect relationship since pod number was also highly correlated with yield.

Experiments using Porrillo Sintetico evaluated the effects of increasing (through canopy CO_2 fertilization) and decreasing (through shading) photosynthate supply at postflowering. CO_2 fertilization at 1,200 ppm increased yield by 40% when applied from –5 to 15 days from first flowering in open-topped field chambers (CIAT 1977). This increase was mainly through improved pod set at secondary positions on existing racemes. A small increase in seeds per pod and seed size was also recorded.

Shading treatments (66% interception) when applied for 8 consecutive weeks from –13 to 43 days from flowering reduced yields by a maximum of 18.5% immediately after first flowering with much lower reductions after 22 days. The yield components were affected sequentially; the highest yield reductions were associated with reduced pod set during the critical phase of determining final pod number per plant. Seeds per pod and seed weight were less affected but reduction in yield was associated with effects on these parameters when shading was applied during the critical period for each parameter.



5. Seed yield against leaf area duration (LAD) for 13 crops of Porrillo Sintetico grown in different semesters and fields, including 4 data points from the photoperiod extension experiment (Table 3).

Yield in Porrillo Sintetico was increased either by increasing source and sink concurrently through an extension of the growth phase or by increasing photosynthate supply by CO_2 fertilization for a given leaf area. Since lodging considerably lowered yields at a particular LAD (Fig. 5) an improvement in this character is one means of improving canopy efficiency particularly in potentially high-yielding crops where lodging is more serious. Other means of improving canopy efficiency through improved leaf display or leaf shape, or both, are yet to be explored. Considerable research on beans at Cornell University (Wallace et al 1972) has not shown a clear relationship between yield and genotypic differences in photosynthesis efficiency of individual leaves.

Comparative studies among growth habits

Key parameters (Table 4) for a typical CIAT experiment comparing selected cultivars from the four growth habits show conclusions similar to those obtained for a single genotype. Over a wide range of maximum LAI values (3.4-6.0) yield was positively correlated with node number and the amount of available leaf area. A decline in the canopy efficiency parameters (yield/LAD and harvest index) was associated with increased yield, particularly in the type IV cultivar. In the latter, the

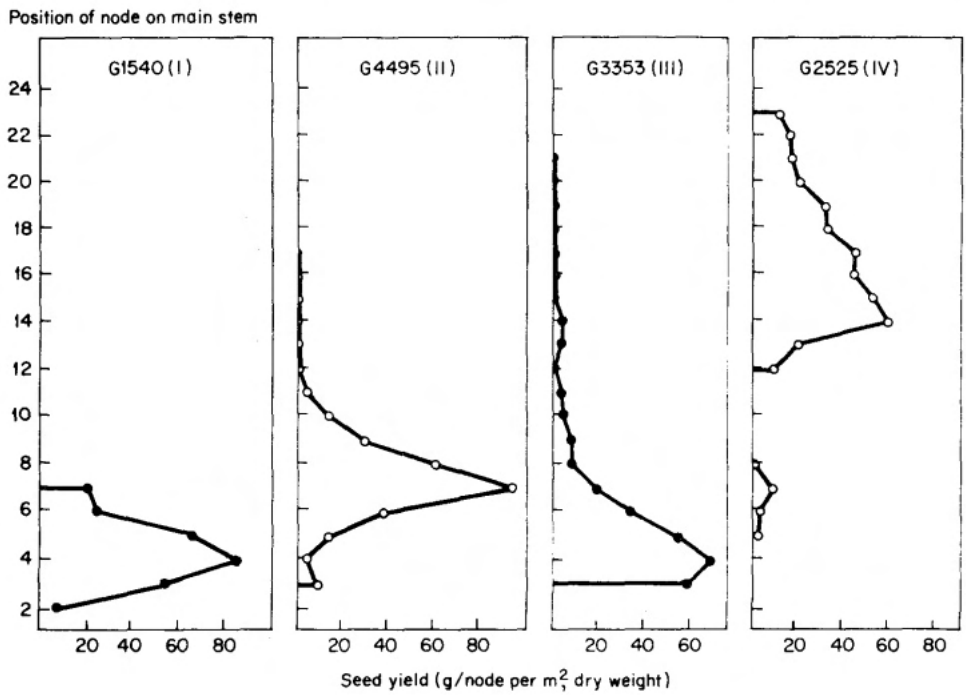
Table 4. Mean yield and other key growth parameters for selected and representative cultivars of *Phaseolus vulgaris* L. from 4 growth habits in growth analysis experiments. CIAT-Palmira, Colombia, 1977.

Parameter	Cultivar[a] and growth habit				
	G1540 I	G4495 II	G3353 III	G2525[b] IV	
Yield[d] (kg/ha)	2423	2130	3221	3653	
Yield/day (kg/ha)	34	35	37	39	0.83
No. nodes/m^2 at harvest	413	587	923	864	0.94
Maximum leaf area index	3.4	3.6	4.1	6.4	0.94
Leaf area duration[e] (LAD) (days)	114	130	164	261	0.93
Yield per unit LAD	2.1	2.1	2.0	1.4	–

[a]CIAT collection number. [b]Type IV cultivar supported on 2-m-high trellis. [c]Correlation with yield. [d]14% moisture basis. [e]Integrated from emergence to maturity.

artificial support necessary for these climbing cultivars and the longer growth cycle allowed more leaf development. The profile structure of yield by node number in the four cultivars (Fig. 6) indicates that the lower nodes of type IV cultivar suffered almost complete flower abscission probably because of excessive leaf area development and self shading, which decreased the levels of photosynthate availability to lower nodes during the pod number determination phase. In other type IV cultivars, where leaf area is not excessive, pod set on lower nodes is more normal.

Under optimum conditions at CIAT yield differences among high-yielding culti-



6. Yield profile by main stem node number for representative cultivars from 4 growth habits (see Table 4).

vars for each growth habit are more or less in proportion to the yield differences in Table 4. In each growth habit higher yields than those shown in Table 4 have been obtained in both germplasm bank and improved materials. Across experiments and seasons consistent yields of 2.5-3.0, 3.0-3.5, 3.0-3.8, and 4.04.5 t/ha for each growth habit have been measured in well-bordered and irrigated monoculture plots. In general, later cultivars are higher yielding.

Comparative studies among grain legume species

Grain legume species are morphologically similar in that the basic building block of the plant is a nodal unit with leaf and pod attached. A comparative experiment at CIAT evaluated the importance of the factors already outlined for *P. vulgaris* across a wide range of species. The best adapted genotypes for most of the species were selected from trials that included the best improved materials from international and national programs. The climatic conditions at CIAT-Palmira are sufficiently moderate (mean temperature 23.8°C) and no particular species was disadvantaged. *P. coccineus* could not be included in the trial because it is relatively unadapted to prevailing temperatures. Mean species seed yield ranged from 2.2 to 4.5 t/ha. Harvest index was negatively related to yield, while biomass, LAD, and days to maturity were all highly and positively correlated (Table 5).

Common beans were intermediate in yield and, unlike *Vigna* spp., they were highly synchronized with respect to pod maturity. Harvest index, yield/ LAD, and yield per day were comparable with soybean and higher than for other species. The difference in CGR between soybean and common bean was consistent with the difference in maximum LAI. Detailed comparison of trends in growth parameters with time for one common bean cultivar (Porrillo Sintetico) and soybean (Fig. 7) indicate that the growth patterns in the two species are similar except that common bean matures earlier and has lower LAI and CGR. Peak grain growth rate in beans is much higher and the grain growth phase is proportionally much more rapid.

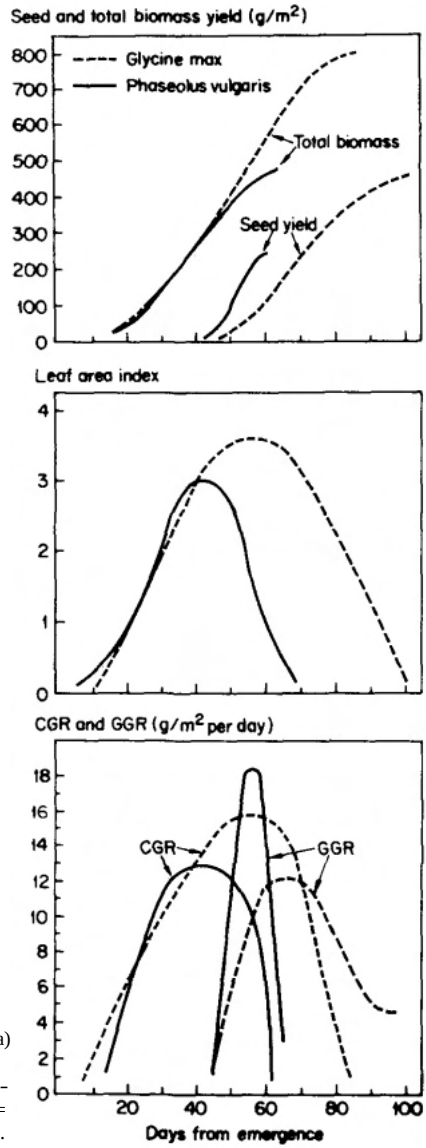
Although soybean commenced flowering at the same time as beans, the post-flowering phase was proportionally much longer. The indeterminate soybean cultivar had a longer flowering period because of the extra nodes on the main stem, which must go through the flowering process. The grain-filling process in soybean proceeds at a lower maximum rate and is spread over a longer period. The rate of decline in LAI during senescence is slower. In general, pod number per plant is the dominant yield component in beans, while seeds per pod and particularly seed weight show only comparatively small changes across environments and treatments. These data suggest that the common bean is more conservative in an evolutionary sense. Bean plants apparently adjust potential sink size (pod number) to the available source and then proceed to fill that sink as rapidly as possible. This in turn influences the rapid rate of senescence of the leaf canopy.

Seed yield in relation to LAD for each of the 16 genotypes in the 9 species is plotted in Figure 8. *Arachis hypogaea* (peanuts), the only species with a drastically different morphology, is also the obvious outlier in this relationship. The quadratic curve fitted to the data does not include *A. hypogaea.* For the rest of the species the single variable LAD can be used to explain a large proportion of the yield variation. Since all the species are made of similar building blocks it seems logical to conclude

Table 5. Key parameters of growth and yield for 9 grain legume species. CIAT-Palmira,[a] Colombia, 1979.

Species	Genotypes (no./species)	Yield[b]		Yield (kg/ha per day)	Days		Maximum LAI	CGR at max LAI	LAD[c] (days)	Yield/ LAD	Total biomass (kg/ha)	Harvest index[d] (%)
		kg/ha	% at first harvest		Flower	Mature						
Chianus cajan	1	4479	68	26	67	174	5.2	10.1	298	1.5	9400	41
Glycine max	2	3899	100	38	34	102	4.2	14.9	195	2.0	5440	62
Phaseolus lunatus	2	3682	68	26	35	139	3.6	8.5	179	2.1	5990	53
Vigna unguiculata	2	3292	82	30	43	109	4.0	8.7	147	2.2	6145	46
Arachis hypogaea	1	3080	100	27	28	114	6.0	13.8	323	1.0	5570	48
Phaseolus vulgaris	3	2637	100	34	35	78	2.8	10.0	108	2.4	3733	61
Vigna radiata	2	2533	83	26	38	99	3.0	10.8	99	2.6	4295	51
Vigna angularis	1	2748	100	31	35	88	4.0	14.3	158	1.7	3930	60
Phaseolus acutifolius	2	2110	100	29	39	76	3.6	12.4	105	2.1	3125	60
LSD (0.05)		271		3	4 9	23.1	2.9	6.9	25	1.0	1428	3.8
OJ (%I		9.4	9.4	9.9	1.4	3.1	14.3	11.9	16.0	2.4	16.7	5.8
r (versus yield)[f]		–	–	0.04	0.56	0.86	0.50	-0.16	0.92[e]	– 0.59[e]	0.9 1	–0.50

[a]Latitude 3°N, altitude 1000 m, mean temperature 23.8°C. LAI =leaf area index, LAD = leaf area duration, CGR = crop growth rate. [b]14% moisture basis. [c]Integrated area under LAI curve emergence to final physiological maturity. [d]Dry seed yield/total biomass minus leaves and petioles, at maturity. [e]Correlation does not include data for *A. hypogaea fr* = 0.73 for significance at 1%.

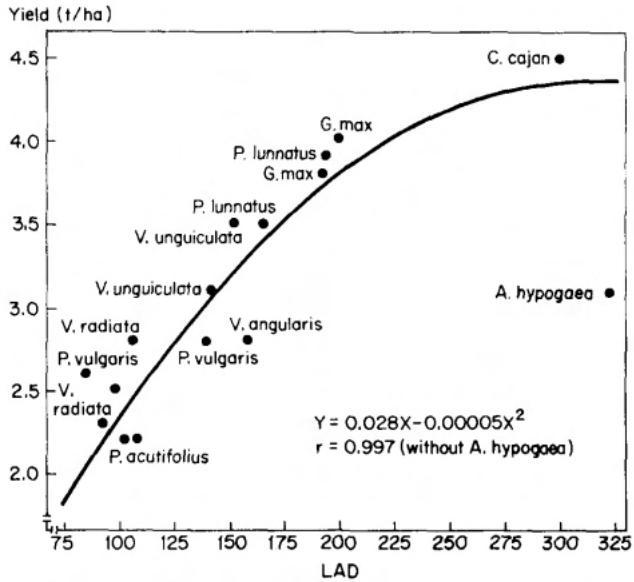


7. Growth parameters for *P. vulgaris* (Porrillo Sintetico) and *Glycine max* (ICA-Tunia) in growth analysis experiments at CIAT-Palmira, Colombia. Curves derived from trigonometric curve fitting procedures. CGR = crop growth rate, GGR = grain growth rate.

that yield among grain legumes is simply related to the number of building blocks present, which is in turn chiefly a function of time.

COMPONENTS OF ADAPTATION

Regression of analysis of the 1976 IBYAN (International Bean Yield and Adaptation Nursery) (CIAT 1977) data showed for the first time that some photoperiodically insensitive type II black-seeded cultivars, e.g. Jamapa (Mexico) and ICA Pijao (Colombia), are widely adapted to both tropical and temperate latitudes in growing



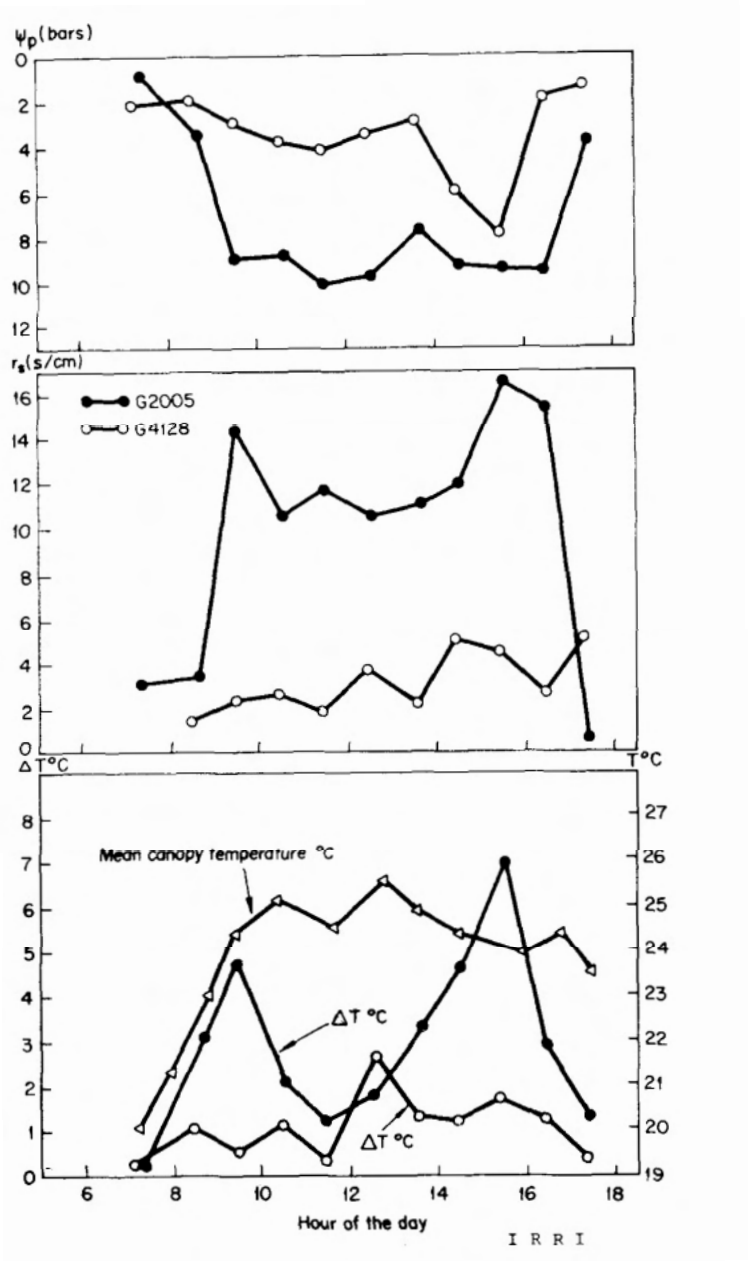
8. Seed yield (14% moisture basis) in relation to leaf area duration (LAD) integrated from emergence to final physiological maturity for 16 genotypes from 8 legume species. CIAT-Palmira, Colombia 1979.

seasons with mean temperatures of 17-25° C. In the IBYAN program the highest experimental yields were obtained in irrigated experiments in Chile and Israel with long days, low relative humidity, relatively high solar radiation, and lower fungal disease pressure. The lowest yields have consistently been produced in high rainfall humid tropical lowland situations (mean temperature >25° C) where fungal disease and insect pressure can be extremely limiting. Research on the physiological components of adaptation at CIAT has mainly concentrated on responses to water stress, temperature, and photoperiod.

Water stress tolerance

Water stress is a common feature of production conditions in Latin America (Table 2) and most probably in other tropical and subtropical regions with limited irrigation.

Common bean, with a very short growth cycle, is particularly susceptible to short stress periods during the flowering and early pod determination phase (Stoker 1974). Cultivar differences in yield response (% yield reduction from well watered controls) to stress periods up to 23 days after flowering have been demonstrated (CIAT 1979). Diurnal curves (Fig. 9) of pressure bomb measurements of plant water potential ('up determined on stem tissue), stomatal resistance (r_s sec/cm, upper exposed leaves), and canopy temperature (T° C infrared thermometry) were determined on a tolerant and a susceptible cultivar. The stress-tolerant cultivar (G4128) has a higher Ψp during the day than the susceptible cultivar (G200.5). Stomatal resistance was extremely high through the warmer period of the day in the susceptible cultivar. Mean canopy temperature in the irrigated plot rose to a maximum of 25.5° C which was ~2° C less than ambient air temperature. The temperature differential ($\Delta T°$ C)

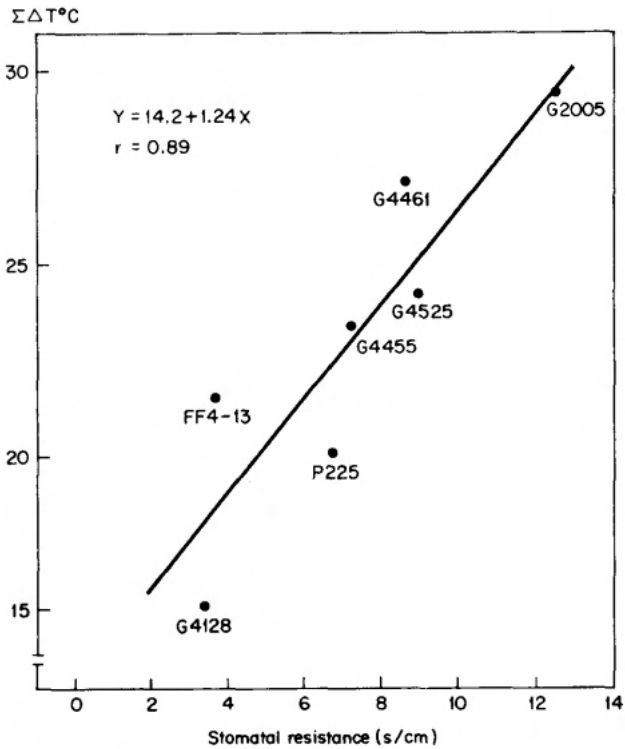


9. Diurnal curves of stem water potential (ψ_p), stomatal resistance (r_s), and canopy temperature differential (ATC) in 1 day in the stress cycle of a drought-tolerant (G4128) and drought-susceptible (G2005) *Phaseolus vulgaris.* Mean canopy temperature (TC) refers to nonstressed control plot. $\Delta T^{\circ}C$ is differential temperature between control and stress plot for each cultivar.

between the irrigated and stress plots rose to 6.5° C for the susceptible cultivar and 2.5° C for the tolerant.

Infrared thermometry is a rapid means of characterizing the stress in field plots of homogeneous genotypes. Blum et a1 (1978) discuss the use of infrared photography for this purpose. Measurements were made on each day of the stress cycle on adjacent stressed and nonstressed plots. The accumulated daily values of $\Delta T°C$ for the whole stress period provide an index of the stress experienced. A reasonable correlation across genotypes (Fig. 10) between CAT and the mean of repeated determinations of r_s from 1100 hours to 1300 hours on each cultivar, was obtained. A high correlation for individual cultivars was also evident between the yield reduction percentage of stress plots and that of adjacent nonstressed plots and $\Sigma\Delta T$. In this experiment paired plots of a range of cultivars were grown at random positions in a large field (150 m × 150 m) to evaluate the degree of field variability in severity of water stress. The data suggest that cultivars differ in the degree of internal stress over a stress cycle and also in the slope of yield response to stress. Water stress had its greatest impact on pod number in these experiments while seeds per pod and seed size are again more conservative.

Further research on the tolerance mechanisms involved is in progress. The data so far suggest that the tolerant materials were able to maintain a higher leaf water potential where soil water supply is limited or under high evaporative demand, or both. This suggests that tolerant materials probably have a stronger root system that



10. Relation of canopy temperature differential (AT C) accumulated over 6 days during the drying cycle and the mean of repeated measurements of stomatal resistance (r_s) from 1100 h to 1300 h on 1 day in the cycle.

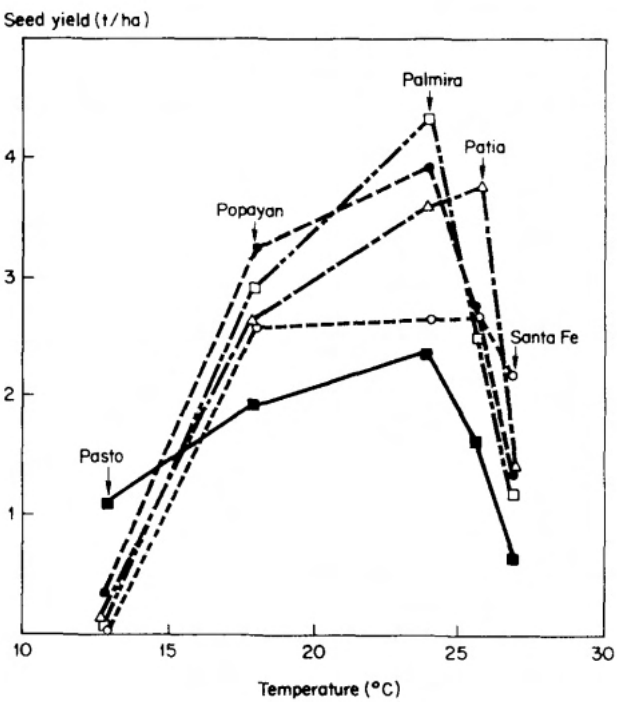
is better able to exploit available water reserves during stress. Other physiological factors could explain these differences, but it seems clear that the first priority for research should be on root systems.

Temperature response

The comparatively narrow range of mean temperatures under which most common beans are produced (Table 2) suggests that temperature may not be as critical as water stress in influencing adaptation in traditional areas of production. Increasingly, there is a need for materials adapted to more extreme conditions, particularly materials with high temperature tolerance for production in irrigated areas where high atmospheric humidity is not a factor.

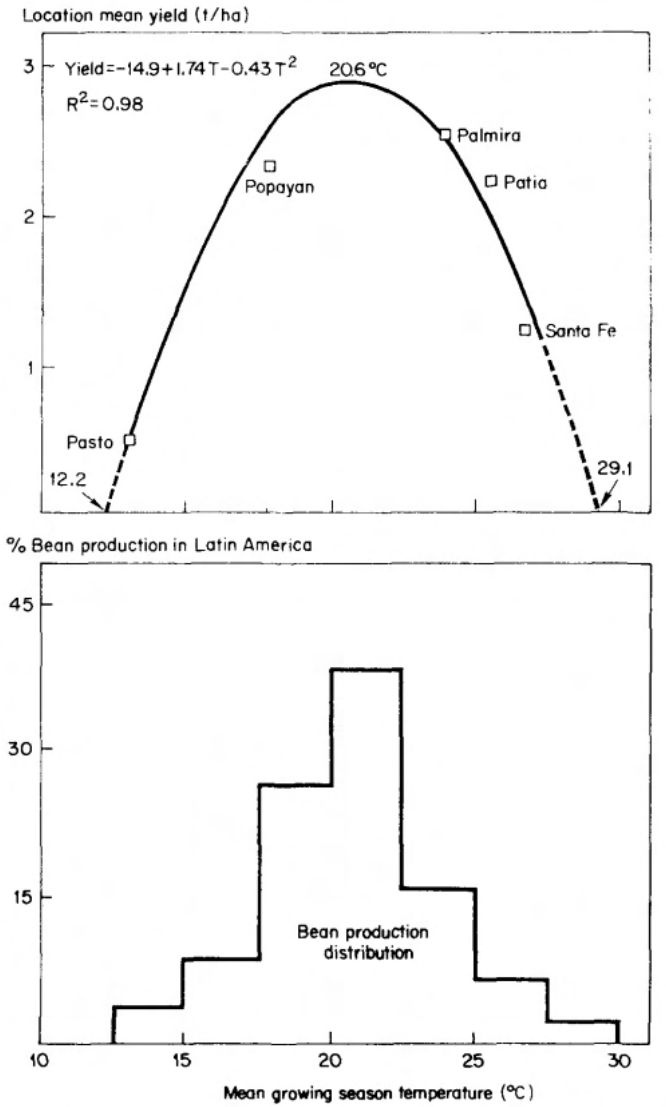
Replicated experiments were conducted with 250 promising parental materials and some advanced lines at 5 different altitudes in Colombia under irrigated and protected conditions. Yield results (Fig. 11) for the five highest yielding lines at each location, when plotted against the full range of temperatures, suggest that at the temperature extremes specific cultivar adaptation is involved. At the lowest temperature location the large seeded types I and IV materials were the best adapted, but these particular lines performed poorly at the other locations.

At the high-temperature location, small black-seeded materials from types II and III were best adapted in terms of yield, but performed poorly at the intermediate-temperature locations. Reproductive failure at various stages was the main symp tom of poor adaptation at the low-temperature sites where only 68 of the 250 entries actually set viable seed. At the highest temperature, flower abscission was high in



11. Mean yield of 5 highest yielding lines at each of 5 locations or altitudes in Colombia, plotted against the mean growing season temperature at each location or altitude. The place names refer to the curve for the mean for the 5 best lines at that location. Altitude ange was 350 m to 2700 m.

unadapted materials although vegetative growth was relatively unaffected. The vast majority of the entries did, however, produce viable seed. Material well adapted at each of the three intermediate temperature locations performed reasonably well at the two other locations. The latter evidence supports the observation that there are genotypes with wide adaptability to the temperature conditions prevailing in the



12. Quadratic function fitted to mean yield of 250 genotypes at each of 5 locations or altitudes in Colombia versus mean growing season temperature at each location. Yield mean includes only entries which actually set seed at each location, Data for the distribution of bean production in Latin America by growing season temperature are presented for comparison (see Table 2).

major production areas. Specific selection for the temperature extremes appears necessary.

A close correspondence (Fig. 12) exists between a quadratic function fitted to the mean experimental yield (including only material with more than zero yield) at each location and the estimated distribution of bean production in Latin America in relation to growing season mean temperature (from Table 2). The minimum, optimum, and maximum mean temperatures suggested by this curve are 12.2, 20.6, and 29.1° C, respectively. These rather rough extrapolations are intended only as a practical guide to the temperature limits on growth in the field. Jones (1971) measured the effects of temperature on photosynthesis of leaf discs in *P. vulgaris.* The optimum temperature for Po was 21° C.

Photoperiod response

Photoperiod response and photoperiod by temperature interaction responses have been extensively studied by various authors (Padda and Munger 1969, Come 1967, 1970, Hartmann 1969, Ojehomon et al 1968). Genotypes of *P. vulgaris* have been identified as either day length neutral or responding to long days by delayed flowering. Temperature interactions, particularly night temperature, modify the flowering response in individual genotypes. The degree of flowering delay in a particular long day environment depends on the genotype, and has been evaluated at CIAT-Palmira at an effective day length of 18 hours compared to the normal (control) 1220 hours.

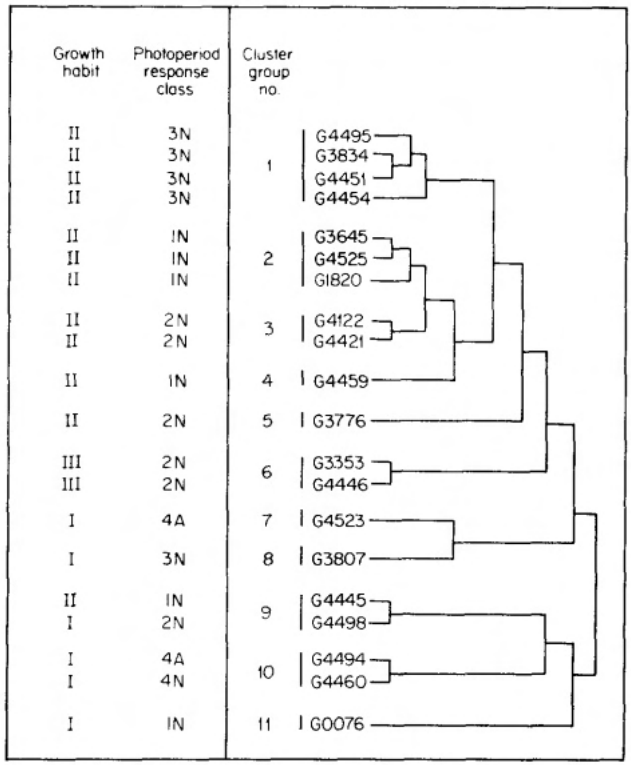
Flowering delay responses have been classified into five basic groups by increasing sensitivity (Table 6). The distribution of more than 800 germplasm collections according to growth habit over the five response groups indicates that the percentage of materials in the highly photoperiod-sensitive classification (<30 days delay) is higher with increasing indeterminacy while types I and II contain the highest proportion of photoperiod-insensitive materials. Speculation as to the evolutionary reasons for these trends is hampered without information as to the exact origin of many of the materials. The demonstrated wide adaptability of certain genotypes is undoubtedly due, at least in part, to photoperiod insensitivity.

As a first step in developing a generalized phenology model, the IBYAN data for 1976 were utilized to study the response of cultivars from the different photoperiod

Table 6. Summary of photoperiod response of field screened *Phaseolus vulgaris* L. germplasm bank materials. CUT-Palmira, Colombia.[a]

Growth habit	Entries (no.) in each photoperiod response group and days flowering delay[b]					Total
	1 <4 d	2 4-10 d	3 11-20 d	4 21-30 d	5 >30 d	
I	91	22	59	30	18	226
II	163	40	67	17	7	294
III	61	26	41	38	40	206
IV	15	7	18	10	32	82
Total	336	95	185	95	97	808

[a]Mean temperature 23.E°C, altitude 1000 m. [b]Days of flowering delay at 18 h days compared to natural day length of 12 h 20 min.



13. Results of cluster analysis of the similarity of the parameter days to flowering at 27 world locations for 20 entries common to all locations in the 1976 IBYAN. Data to the left of the vertical line is the photoperiod classification of the material determined at CIAT. See Table 6 for photoperiod classification definition. A = abnormal flowering in long days, N = normal.

response classifications. Cluster analysis on days to flowering data for entries common to all locations indicate that cultivars of the same growth habit and photoperiod classification had similar phenological response across locations in both tropical and temperate latitudes (Fig. 13). The few exceptions appear related to photoperiod by temperature interaction in these particular genotypes. The data suggest that a simple photoperiod classification could be used as a basic input into a phenology model (Jones and Laing 1977) to predict phenological responses of genotypes in particular locations. This model could help considerably in international germplasm programs.

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COWPEA

R. J. Summerfield, F. R. Minchin, E. H. Roberts,
and P. Hadley

Cowpeas *Vigna unguiculata* (L.) Walp., with five interfertile subspecies - two of them wild, and all reproductively isolated from other *Vigna* species - are cultivated as seed, vegetable, and fodder legumes in the semiarid and humid tropics. There has been a significant underestimation of world production. The major economic subspecies (*unguiculata*) contributes protein-rich seeds to diets which otherwise would consist primarily of carbohydrates.

Genotypes and environments interact to produce what seems to be a bewildering diversity of growth habits. Nevertheless, dry matter production and reproductive development of more or less determinate cultivars are surprisingly amenable to generalized and predictive interpretation. Differences in phenological potential (number of reproductive nodes) and associated changes in the total number of flowers which open at the lowermost racemes of inflorescences have large effects on economic yield. Many ecological characteristics of the crop (e.g. responses to edaphic factors, nutrients, and water) are often misunderstood, and few reliable generalizations can be made. A traditional components-of-yield analysis on mature crops may *describe* variations in seed yield; but to explain them, a more dynamic analysis is needed. Sole crop cowpeas grown with adequate protection from pests and diseases can produce excellent yields of protein-rich seeds per hectare per day, but ignorance of variations in the spatial and temporal interactions between carbon metabolism and dinitrogen fixation precludes reliable selection by breeders of symbiotic combinations which utilize both elements efficiently.

A discussion of botanical features and ecological characteristics is undoubtedly a reasonable basis for introducing many of the major crops included in this book; a similar approach for cowpeas would not only be inappropriate but would also be misleading. Rather, we describe briefly several additional features of the taxonomy, production statistics, and current status of the crop, hoping to dispel at least some of

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the confusion and contradictions which are not only prevalent in earlier publications but also perpetuated in the current literature.

TAXONOMIC STATUS

Many of the predominantly annual, herbaceous legumes of principal economic importance in world agriculture are classified within just five tribes of the Papilionoideae, the largest subfamily, and in 13 different genera, one of which is *Vigna.* There has been considerable confusion about the delimitation of some genera in the tribe Phaseoleae (notably with regard to *Phaseolus, Vigna, Dolichos* and their satellite genera), not only in ancient times but also during the past 25 years (e.g. see Faris 1965, Ebong 1970, Verdcourt 1970, Summerfield et al 1974, Smartt 1976). Hence, the reappraisals of Verdcourt and others (see Verdcourt 1980) and by Steele and Mehra (1980) are especially timely. The latter cogently describe Vigna as a pantropical genus which comprises about 160 species, most of them African. Only six species are cultivated and five of these are Asiatic forms (see Jain and Mehra 1980).

Vigna unguiculata (L.) Walp. (syn. *V. sinensis* (L.) Savi ex Hassk), has five interfertile subspecies: (a) ssp. *unguiculata,* the cowpea, the most widespread and economically important subspecies; (b) ssp. *cylindrica,* the catjang, a fodder and seed type from India; (c) ssp. *sesquipedalis,* the yard-long bean, a green pod vegetable crop of India, Southeast Asia, and China; and (d,e) ssp. *dekindtiana* and *mensensis,* wild and weed forms from Africa, the progenitors of the cultivars. The *cylindrica* types may not merit the status of a distinct subspecies, as they can be accommodated within the range of diversity in ssp. *unguiculata* (Steele and Mehra 1980). But the current status of the genus is sufficiently precise for both researchers and administrators to adopt appropriate taxonomic and nomenclatural terminology.

PRODUCTION, UTILIZATION, AND CROP STATUS

Cowpeas are grown in some very dry and agriculturally-difficult places; they are seldom irrigated or fertilized with inorganic nutrients. The crop is cultivated for many purposes (Table 1) but is especially important as a seed, vegetable, and fodder legume in the diverse agricultural systems of traditional farmers in the semiarid and humid tropics. The major economic subspecies (ssp. *unguiculuta*), a West African, Neolithic domesticate, contributes protein-rich seeds to diets which otherwise consist primarily of carbohydrates.

Pests and diseases are the major constraints to increased cowpea production in the tropics. In the savannahs of Africa, where most cowpea crops are grown, insect pests cause greater losses of yield than do diseases; in the humid forest belt, diseases are probably more important (Singh and Allen 1980).

The most commonly cited official statistics for cowpea production are between 1.1 and 1.4 million t annually, which would represent less than 2% of the estimated world total production of grain legumes (Siegel and Fawcett 1976). But cowpeas do not usually enter into international trade, so world production figures are inade-

Table 1. Diversity of products provided by cowpea crops grown in "traditional" and "advanced" agricultural systems. [a]

Crop component	Utilization
Immature foliage	Pot herb or spinach
Mature foliage	Green manure, fodder, silage
Foliage	Cover crop, hay
Roots	Human consumption (Ethiopia, Sudan)
Peduncles	Retted for fiber, fishing lines, and nets (N. Nigeria, Togo)
Leaves	Manufacture of green dye (India)
Immature seeds/whole immature fruits	Fresh, canned, or frozen vegetable (USA)
Mature seeds	Roasted as a coffee substitute or as a snack food (USA)
Mature seeds	Boiled, roasted, or ground into flour
Mature seeds	Damaged or surplus seeds fed to livestock (USA)
Mature seeds	Protein concentrate
Fruit walls (haulms)	Fed to livestock

[a] Compiled from numerous sources published within the last decade.

quate. Official statistics may underestimate production and should be increased by 10-15% (Kay 1979), by 50% or more (Rachie and Rawal 1976), or by a factor of 5 times for the lowland tropics alone if the estimated amounts of the various crop products (Table 1) are converted into dry seed weights on the basis of equivalent protein contents (Rachie 1977). Unreported farm and "kitchen garden" production in the lowland tropics, the multiplicity and diversity of crop products which are utilized, and misclassification of species have each contributed to unreliable official estimates.

Yields vary greatly; Table 2 summarizes yield and other information extracted from the literature.

BOTANICAL FEATURES

Morphological variability within cultivated forms of *Vigna unguiculata* is enormous, and genotypes and environments interact to produce a diversity of growth habits. Any classification of plant form in cowpea must therefore include precise information on location and date of planting. Nevertheless, extensive research in controlled environments substantiated later by detailed, quantitative records of growth and phenology in field crops has permitted certain generalizations.

Vegetative structure

Cultivated cowpeas are glabrous or glabrate annual legumes with strong primary (tap) roots and much-branched secondary and higher-order lateral roots. Within 12 days from germination the total root length of cowpea seedlings can exceed 6 m, and not all secondary roots have equivalent elongation potential (Summerfleld and Minchin 1976). This might have implications for infection by strains of nonspecific *Rhizobium.*

Table 2. Selected examples which indicate the variation in seed yield reported for cowpea crops grown in various agricultural systems and environments.[a]

Seed yield (kg/ha)	Comments	Crop duration (days between sowing and harvest)
380	Calculated world mean based on official statistics	–
0 (crop failure) - 3823	Maximum ranges	60-240
1825-3823	Highland Ethiopia (multilocation trials), IITA cultivars	120-139
1800-2500	Rainfed; improved cultivars; trials	85-88
365-1302	within India; IARI	70-120
1600-3000	No fertilizer or irrigation; all major	75
1500-2000	pests controlled; improved cultivars; sole crops; IITA	
1000-2800	Sole crops; seldom irrigated; USA	90-155
1200-2000	Sole crops; Brazil and Mexico	–
1500-1800	Philippines	90- 120
1000	Japan	–
949	Rainfed sole crops; Turkey	–
858	Irrigated sole crops; Iraq	–
495	Rainfed sole crops; Australia	–
100-300 (a)	Traditional mixed cropping systems	–
170 (b)	in (a) West Africa and (b) India	–
534-1525	Intercropping trials (with maize); IITA	–

[a]Compiled from numerous sources published within the last decade. IITA = International Institute of Tropical Agriculture, Nigeria; IARI = Indian Agricultural Research Institute.

Distinct populations of primary, secondary, and tertiary nodules supply the host with symbiotically fixed dinitrogen; their relative contributions depend on the strain of *Rhizobium,* the stage of reproductive development of the host, and the edaphic and aerial environments. Differences in the relative rates and durations of dinitrogen fixation by successive populations of nodules during crop ontogeny can have important consequences on yield (Minchin and Summerfield 1978, Summerfield 1980).

The spherical, determinate nodules have flattened surface lenticulations which, by restricting gaseous diffusion, probably contribute to the relative intolerance of cowpeas for short periods of anoxia (Minchin and Summerfield 1976). The morphology, vascular anatomy, principal export products, and water relations of cowpea nodules can each be considered as components of a convenient strategy for coping with warm, dry environments (Sprent 1980).

Although germination is epigeal, cowpea cotyledons do not persist; they can lose as much as 91% of their dry weight by emergence (Ndunguru and Summerfield 1975). Such effective mobilization of cotyledonary reserves probably contributes to rapid hypocotyl elongation and might improve emergence in adverse edaphic conditions (Wien 1973). However, the commitment of cotyledonary reserves so early in crop life might invoke a penalty later; there will be no additional photosynthetic area to aid seedling growth and, in particular, the establishment of a nodule population (characteristically after 14-20 days from sowing). Thus, plants rooted in soils deficient in inorganic nitrogen may suffer a period of nitrogen hunger which is likely to restrict vegetative growth and to limit yield (Minchin et al 1980).

The first pair of simple, opposite leaves are followed by alternate, trifoliolates which are initiated much more rapidly in warmer than in cooler average temperatures and which expand much faster when the crop experiences warm rather than cool nights (Summerfield et a1 1978a, Littleton et a1 1979a). Rapid, reversible movements of leaflets vary from diaheliotropism in the morning to paraheliotropism in the afternoon and are thought to substantially reduce heat load, water use, and water deficits in crops subjected to drought (Shackel and Hall 1979).

The growth habits of cowpea are erect, semi-erect, trailing, prostrate, and climbing; determinate types with terminal inflorescences are rare. Although variations in the angle of attachment of branches to the main stem contribute to this spectrum of diversity, differences in the number and length of branches are far more significant. Each leaf subtends three buds, of which usually only the central one expands to produce a potentially indeterminate, monopodial branch or a racemose inflorescence (Steele and Mehra 1980). Branching is also affected by crop density (Ojehomon and Bamiduro 1971), soil fertility (Sellschop 1962), and water stress (Summerfield et a1 1976) and seems especially dependent on the interactions of genotypes with differences in day length and night temperature (Summerfield 1976). The lengths achieved by branches are determined by their rates of elongation during the preflowering period and then by the proportion of all nodes that bear reproductive structures and the rate and synchrony of fruit development. The sooner and more profusely a cowpea plant produces flowers and bears fruit, the larger the demands of the reproductive loan on carbon metabolism and on dinitrogen fixation (Ojehomon 1970), the fewer and the shorter its branches, and the more erect its growth habit. Steele and Mehra (1980) have produced what appears to be an eminently suitable classification system based not only on growth habit but also on genotypic differences in flowering response to the aerial environment.

Reproductivestructure

Cowpea inflorescences are compound racemes of several modified simple racemes borne on peduncles usually 10-25 cm long. A typical investment of 10-15% of maximum total plant dry matter into peduncles might be considered inefficient, but these structures might equally be regarded as useful crop products (Table 1); in any event, they can be important organs from which nitrogen is remobilized to developing fruits (Eaglesham et a1 1977). Each simple raceme has 6-12 buds, but only the oldest pair develops; they open into typically papillonaceous flowers usually several hours after the anthers have dehisced (Krishnaswamy et a1 1945). Although most flowers are self-pollinated, there is probably always a small proportion of outcrosses, especially in humid climates (Purseglove 1968) and, since insect vectors can show a distinct preference for flower color, accessions with uniform corolla coloration may be needed to assess the prevalence of outcrossing reliably. Rachie et al (1975) have described a floral anomaly which confers mechanical male sterility; petals are constricted in such a way that the stigma and style emerge at a prereceptive stage but stamen development is restricted. Plants which experience a large diurnal variation in root temperature during the reproductive period also produce a large proportion of flowers which do not set fruits and which are remarkably similar to those

generated by the recessive, genetically-inherited mechanism (Stewart and Summerfield 1978).

The period of anthesis in cowpea is characterized by a profligate loss of flower buds and open flowers and, thereafter, of immature fruits (Ojehomon 1968). Numerous factors have been suggested for this loss in reproductive potential, e.g., abnormal pollen formation, poor pollen germination, a large proportion of assimilates sequestered in older pods to the detriment of younger ones, the production of hormones by older pods that promote the abortion of younger ones, warm and dry weather, and insect pest damage (Sinha 1977, Summerfield and Wien 1980); the problem is which factors are most important and in what particular circumstances? Some salient facts must be considered rather carefully. In general, the first two flowers to open in any cowpea inflorescence are likely to produce fruits; the third pair, if indeed they open, have little chance of doing so. We estimate from the detailed observations of Ojehomon (1968) that the respective contributions of racemes I, 2, and 3 (in acropetal order within any inflorescence) to the total number of open flowers per plant are in the ratio of 6:3:1. Furthermore, there is little variation in the likelihood of premature abscission of flowers from specific racemes: about 10, 34, and 52% fail to produce immature fruits at racemes 1,2, and 3 (Stewart et a1 1980). Variations in phenological potential (the number of nodes per plant which become and remain reproductive) are therefore likely to have large effects on seed yield whereas only in rather specific situations will the premature abscission of potentially fruitful flowers become of major significance. This suggestion implies that, providing there are not large changes in the proportion of nodes which become reproductive, economic yields might be expected to show a close positive relationship with total plant dry weight. A greater number of nodes means a larger number of leaves and, depending on the length of internodes, a longer main stem and/ or increased branching. Leaves, main stem, and branches together often represent at least 50% of total plant dry weight. Such positive relationships have been recorded both for spaced plants in controlled environments and for crops in the field (Wien 1973, Summerfield et a1 1978b, Littleton et a1 1976b).

In addition to evolutionary changes in morphology in cowpea, selection under domestication has effected considerable changes in reproductive strategy and structure. Plants have allocated a progressively larger proportion of dry matter into fruits than into vegetative components once flowers have been initiated (modern types are more “annual” than primitive ones) and fruit and seed size have increased (Hutchinson 1970, Rawal 1975, Smartt 1978). The larger seeds of domesticated cultivars give rise to seedlings which can emerge from deeper sowings sooner and more successfully than those from the smaller seeds of wild cowpeas; cultivated seedlings are also larger until at least 40 days after sowing despite the larger relative growth rates of the smaller, wild seedlings (Lush and Wien 1980).

Most cultivars of ssp. *unguiculata* produce fruits which are between 12 and 20 cm long; their carnage is typically pendent. The seeds usually contain 20-40% storage protein in cotyledonary cells. The average duration from anthesis to maturity of individual cowpea fruits is only about 19 days, with a genetic variation of 16-22 days (Wienand Ackah 1978). Cowpea fruits appear to be less dependent on the photosynthetic activity of leaves at the parent node than in many grain legumes with sessile

fruits, except perhaps for determinate types with limited leaf area duration (IITA 1976, Lush and Rawson 1979). Notwithstanding the limited time available for seed growth and their spatial location relative to other organs on the parent plant, cowpea fruits usually contain more mature seeds (621) than either soyabean, pea, or bean (2-9) and which, individually, are as heavy as those in soyabean or pea (90-300 mg compared with 60-250 mg) but smaller than in *Phaseolus* (200-1,000 mg).

Although a number of generalizations seem to apply, further studies on seed growth in cowpea are needed to assess whether variations in these attributes are likely to be worthwhile selection criteria. Some cowpea genotyes that have been selected produce fruits supported by peduncles above the leaf canopy; fruits held in this manner are easier to hand harvest and may suffer fewer pest depredations than those produced within the foliage. However, they can also attain temperatures some 4° C warmer than even ambient tropical values (IITA 1976) and so may be forced into maturity more rapidly, inducing an intense demand for carbon and nitrogen from the parent plant, especially if the reproductive load is large or many fruits are filling concurrently.

ECOLOGICAL CHARACTERISTICS

Although the vast majority of cowpea (98% of more than 6,000 accessions described by Porter et al 1974) are botanically indeterminate, many investigations have concentrated on types with a more or less determinate habit.

The modern centers of production of cowpea for seed are India, Brazil, and the semiarid, sub-Sahelian region of West Africa. Cultivars of ssp. *unguiculata* are said to be well adapted to hot, semiarid environments, are drought resistant, and grow well at temperatures even above 35° C. Certainly, cultivars with an appropriate crop duration can avoid substantial water stress by maturing relatively early (within 70 days from sowing) in sub-Sahelian environments (Elston and Bunting 1980). At the other extreme, crop growth and seed yield can be seriously affected by even ephemeral periods of root anoxia as a result of transient flooding (Wien et al 1979a). Days as warm as 33°C can drastically reduce yield, commonly by about 50% compared with yields at 27° C in the many cultivars screened to date (Summerfield et a1 1978a, b), and drought stress during the reproductive period can hasten maturity and reduce yields substantially (Hall et al 1979).

Edaphic factors and mineral nutrition

Cowpeas are grown on a wide variety of soils, from sands to heavy, expandable clays; they are deep rooted and grow best on well-drained, sandy substrates. Whether grown in rotation with maize or cotton in the southern USA, or variously interplanted with millet, sorghum, cassava, or maize in traditional farming systems of the tropics, the cowpea crop is often subjected to tillage practices developed primarily for the companion crop. Although zero tillage in conjunction with an appropriate herbicide can improve nodulation, vegetative growth, water use efficiency, and seed yield of cowpeas in the humid forest zone of Nigeria (Lal et al 1978), the effect apparently is by no means universal, even at nearby sites (Ezedinma 1964), and should be evaluated in semiarid environments.

Cowpea shares with most other green plants the ability to improve nutrient uptake by mycorrhizal associations between the roots and soil fungi (IITA 1977c). Along with other legumes, the potential for assimilation of dinitrogen through symbiosis with *Rhizobium* creates special demands for molybdenum, cobalt, boron, copper, phosphate, and zinc (Munns and Mosse 1980). However, neither mycorrhiza nor root nodules are essential for cowpea growth, and since both can be partially or completely replaced by appropriate fertilizers it seems absolutely essential to evaluate and to quantify the changes in microbial dependence which are likely to result from applications of inorganic fertilizers to crops. Unfortunately, this is seldom done and so it is hardly surprising that estimates of the nutrient requirements of cowpea crops differ widely (Table 3). Nevertheless, we can be confident that cultivars of ssp. *unguiculata* are potentially extremely productive grain legumes: they can fix quantities of dinitrogen sufficient for very large seed yields (Table 4).

The selection history of cowpea and the edaphic conditions with which most crops have been forced to contend have proved indirect pressures for "symbiotic potential." Little of this potential can be expressed against the fertile backcloth of crop rotations in the USA (Table 4), and cowpea breeders will need to select for nodulation and dinitrogen fixation (Gibson 1980); that is, they will need to restrict applications of inorganic fertilizers to their breeding plots. Otherwise, the symbiotic potential of cowpeas could well decline in proportion to the breeding effort put into the crop. If the amount of nitrogen removed when the crop is harvested is greater than the amount fixed during growth, then a legume crop will deplete soil reserves, negating its beneficial role in crop rotations (Agboola and Fayemi 1972).

Water relations

Most cowpea crops are rainfed, a small proportion are irrigated, and others utilize water residual in the soil after a crop of rice has been harvested. Cultivars with an appropriate crop duration have a wide range of adaptation in the tropics, from the semiarid regions to the humid, forest belt.

The weekly mean maximum evapotranspiration (ETm) from a well-watered crop of cultivar TVu 6207 grown in drainage lysimeters at Ibadan was closely related to the prevailing weather: small values of ETm were associated with small values of net radiation, mean saturation vapor pressure deficit, and wind speeds, but the seasonal trend was closely related to leaf area index (LAI; Lawson 1979). Some of these data can be compared with others for irrigated cowpea crops (assumed to have optimal water supply) in Senegal (Table 5). Data for the three short-duration crops agree reasonably well whereas the longer-duration crop in the hotter, drier, northernmost site transpired more than twice as much water despite a crop duration increase of only 64%. Dancette and Hall (1979) have stressed that maximum water requirements of annual crops in one region are strongly dependent on crop duration; the two variables may even be linearly correlated, but data for cowpea are not sufficiently extensive to prove this is so.

A series of experiments during the dry season at Ibadan, when there is little chance of rain for several weeks but where temperatures are similar to those which prevail during the main cropping season, involved irrigating crops in the field at weekly intervals except for 2 weeks either just before or just after the onset of flowering

Table 3. Estimates of nutrients removed in cowpea seeds for crops producing an economic yield of l000 kg/ha (data for soybean included for comparison).

Nutrient[a] (kg/1000 kg seeds)						Comments	Reference
N	P	K	Ca	Mg	S		
40	7.4	39.8	11.4	9	4	Unqualified statement	Rachie and Roberts 1974
56.7	4.4	16.6	NI	NI	NI	Unqualified statement	Kassam 1976
42.9	5	13	NI	NI	NI	Calculated from nutritional data	Isom and Worker 1979
71	6.1	20.3	3	3	1.7	Soybean (USA crops)	Scott and Aldrich 1970
66.8	6.3	17.8	NI	NI	NI	Soybean; calculated as above	Isom and Worker 1979

[a]All data converted to elemental equivalents to facilitate comparison. NI = no information given.

Table 4. Annual symbiotic fixation of soybean and cowpea (After Nutman 1976).

Attribute	Symbiotic N fixation (kg/ha per annum)	
	Soybean	Cowpea
Properly conducted field experiments		
Range	1–168	73–354
Average	103	198
4-yr av in 2 countries		
USA farms	88	25
Egyptian farms	NI[a]	192

[a]No information.

Table 5. Comparative attributes of the water requirements[a] for cowpea crops at different locations (calculated or extracted from Dancette and Hall 1979, Lawson 1979).

Cultivar	Crop duration (days)	Location	CWR (mm)	Ep (mm/day)	ETm (mm/day)	ETm/Ep
		Nigeria				
TVu 6207	77	Ibadan (7°N)	275	5.0	3.6	0.72
TVu 6207	77	Ibadan	311		4.1	0.82
		Senegal				
B 21	75	Bambey (14°N)	336	5.9	4.5	0.76
–	125	Guede (16.5°N)	715	8.8	5.7	0.65

[a]CWR = total crop water requirement, Ep = class A pan evaporation, ETm = mean weekly maximum evapotranspiration. Ep and ETm are av values for cropping season.

(Wien et a1 1979b). Stomatal conductance declined from a value of 0.6 cm/ s, typical for the nonstressed controls, to a minimum of 0.2 cm/s after 7 days of water stress; the stomata were closed and probably remained so for most of each subsequent day without water. Although leaf water potential was consistently smaller on the stressed than on the control plants, it remained more or less stable throughout the stress

period (between –1 and –0.8 MPa) whereas values for soybean decreased from –1.1 to –2.2 MPa during this time. Wien and his colleagues considered that the resistance to water movement through the plant might decline as the severity of water stress increased, although in well-watered plants grown in containers leaf water potential is linearly and negatively related to transpiration rate, which implies a constant resistance to water movement through the plant (Hailey et al 1973).

Withholding water during vegetative growth decreased the rate of initiation of main stem leaves, but Wien et al (1979b) were not able to show a significant relationship between rate of leaf appearance and leaf water potential and concluded that leaf water potential would not serve as a good indicator of plant water stress. On the other hand, Cutler (1979) described the seasonal changes in midday leaf water potentials for rainfed crops at Niomo, Mali, and concluded that midday values of about -0.82 MPa could be considered a critical leaf water potential, that cowpea is very sensitive to relatively mild (–1 MPa) midday deficits, and that differences in the rate of leaflet elongation provide a very sensitive indication of the onset of detrimental water deficits in vegetative plants.

One of the cultivars studied in Mali, TVu 662 (an indeterminate type classified as intermediate between semi-erect and semiprostrate in habit) was by far the best drought avoider, being able to maintain a more favorable water status in a droughty environment. On the other hand, TVu 37 (an erect, indeterminate, vigorous cultivar with a tendency to twine) was described as the most sensitive to drought of the five cultivars tested. We had previously screened these two cultivars in glasshouses (Summerfield et al 1978b) for their ability to produce seeds in warm days, a major feature which influences adaptability to the tropical aerial environment. On the average, yields of the 22 cultivars tested were 42.3% smaller in warm (33° C) then in cool (27°C) days and the responses of TVu 662 and TVu 37 were at opposite extremes (Table 6). TVu 662 was the only cultivar to produce dramatically larger yields in warm than in cool days; TVu 37 was the most sensitive, and yield declined by 65% in the warmer daytime regimes.

The fact that such large genotypic differences in response to adverse environments were detected among even such a small collection of germplasm offers encourage-

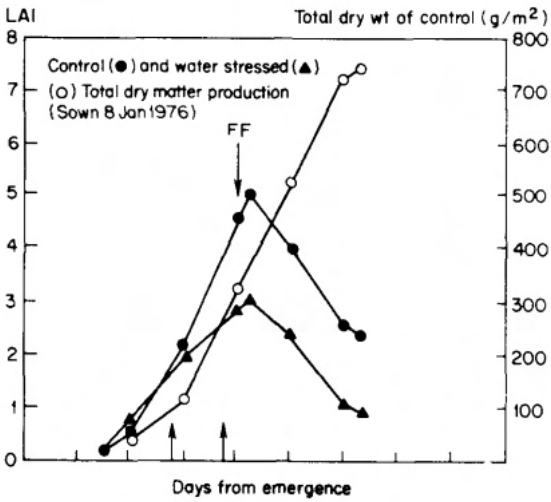
Table 6. Relative changes in seed yield of selected cowpea cultivars grown in factorial combinations of warm and cool days (33° and 27°C) with warm and cool nights (24° and 19°C) in a glasshouse (Summerfield et al 1978b).

Cultivar	Mean seed yield (g/plant) in				Relative effect (%) of warmer temperature[a]
	Warm days	Cool days	Warm nights	Cool nights	
Overall average of 22 cultivars tested	17.9	31.0	–	–	-42.3
	–	–	27.0	21.8	+23.9
TVu 662	42.3	27.9	–	–	+51.6
	–	–	33.9	36.3	- 6.6
TVu 37	19.2	55.2	–	–	-65.2
	–	–	50.3	24.0	+109.6

[a]Calculated relative to seed yield recorded in respective cooler temperature regime.

ment to the physiologist and plant breeder alike. There seems to be a potential for using precisely controlled glasshouses in which to screen nodule-dependent, well-watered, pot-grown plants not only for adaptability to temperature per se but also, indirectly, for genotypic differences in ability to withstand the consequences of drought. Table 6 also shows the beneficial consequences of warm nights on yield of cowpea; the main effect is mediated through changes in phenological potential, and a combination of warm days and cool nights has proved least conducive to seed production.

Probably the most extensive data on the consequences of water stress in cowpea have been generated for TVu 4552, an erect, acutely branched, nontwining, nonvigorous, more or less determinate cultivar with a typical crop duration of between 60 and 80 days. Withholding weekly irrigations to induce a 10-day period of progressively more severe water stress immediately before the onset of flowering increased leaf temperatures so that they were at least as warm as ambient air during the middle of the day, reduced net photosynthesis by at least 27% at full irradiance, and restricted leaf area development so that the maximum leaf area index (LAI) achieved was only about 3 compared with 5 in the nonstressed plots (Fig. 1). The stressed plants had shorter main stems which, together with peduncles, contributed a smaller proportion to total plant dry weight at maturity when fruits represented 55 and 45% of the total in the stressed and control plants. Drought stress significantly reduced nodule dry weight per plant and symbiotic activity during the stress period but, after drought was alleviated, dinitrogen fixation efficiency (specific activity) became significantly larger than in the control. Overall, the stressed plants accumulated about 25% less total reduced nitrogen during a crop duration of 63 days. but remobilized a larger proportion from vegetative components into fruits. A reduction of 15.3% in the number of pods per m^2 was completely offset by a 14.8% increase in mean seed weight so that the stressed plants produced seed yields as good as those of the controls; however, their fruits contained almost 20% less nitrogen. Presumably,



1. Temporal changes in leaf area index (LAI) and total dry matter production for TVu 4552 grown in different seasons at IITA and experiencing hot conditions after a cool period of about 2 weeks duration from emergence and subjected to a period of 10 days water stress immediately before flowering. Redrawn from Wien et al 1979b.

the seeds contained a smaller concentration of protein.

Wien et a1 (1979b) discussed the problems involved in screening for drought resistance. They urged that it is important to use field conditions whenever possible and that several traits will need to be measured. Plants grown in pots may develop atypically large leaf water potentials; they probably develop water deficits at rates which are abnormally rapid and which preclude the acclimatization responses which seem to be typical of field-grown plants (Hall et a1 1979). Indeed, the only generalization which might be made to date is that cowpea seems better able than soybean to withstand drought in tropical temperature conditions. Although water stress is undoubtedly an important selective force, there is little evidence for any species that it has a direct regulatory action on flower initiation (Murfet 1977). Whether or not severe drought stress has a greater adverse effect on phenological potential or on the subsequent realization of this potential will probably depend on previous and subsequent environmental conditions, on whether or not the rate of a particular process (e.g. leaf initiation or leaf expansion) is changed permanently or only temporarily, and whether the cultivars concerned are effectively nodulated or largely dependent on inorganic nitrogen.

ACCUMULATION AND PARTITION OF DRY WEIGHT

The rate at which a crop increases in dry weight depends at any instant on the product of the area of the photosynthetic system and the rate of assimilation per unit of that area (LAI and net assimilation rate [NAR], respectively). Changes in LAI depend on the relative rates of two processes, growth in leaf area and senescence; NAR reflects the balance between the photosynthetic gain and respiratory loss of carbon. Our knowledge of these four processes and how they are affected by various environmental factors is incomplete (Elston et a1 1975); they are all under either direct or indirect genetic control, but it seems unlikely that all are equally amenable to exploitation by breeding (Evans 1974).

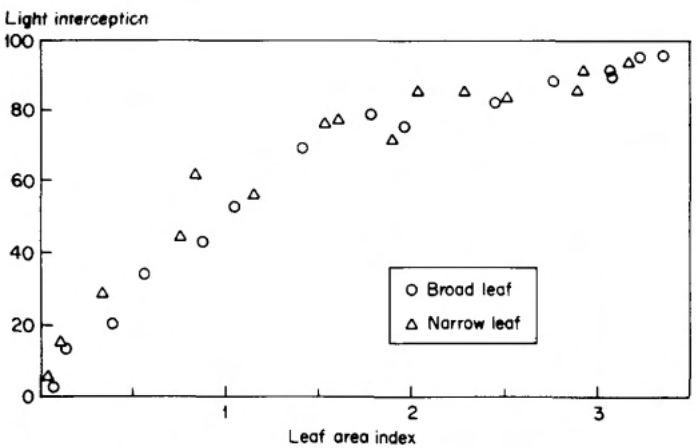
Growth of leaf area

Leaf area development of cowpea seedlings varies significantly between cultivars and planting dates (Ezedinma 1967, Sinha 1977) and with differences in the intensity of incoming solar radiation. Changes in insolation by cloud cover were said to be primarily responsible for variations in the time course of LAI and dry matter production in southern Nigeria, and far more important than availability of water or seasonal variations in temperature during the usual cropping season (Ezedinma 1973, Njoku 1959,1960). However, Monteith (1975) has questioned the usefulness of experimental and analytical techniques such as those used in some of these early investigations; to assume a base temperature as cold as 6.7° C for leaf development and dry matter production by cowpea is unlikely to be realistic, and there is little point in describing the effects on crop growth of any environmental factor unless both ratesanddurations of responses are quantified (Monteith 1979). Considerable research within the last decade leaves little doubt that the growth of leaf area in cowpea crops is markedly dependent on seasonal variations in temperature and water supply, whether in the humid or in the semiarid tropics.

The analysis of growth and development of several cowpea crops at Ibadan (Littleton et a1 1979a, b) in conjunction with the quantitative information now available for numerous cultivars in a diverse range of experiments in the same location (Wien 1973, 1975), compared and contrasted where possible with data for cowpea crops grown in other tropical localities, e.g., in Tanzania (Enyi 1973) and in India (Chaturvedi et a1 1980) and in controlled environments (Summerfield et a1 1978a), seems an appropriate basis for discussion. In general, both determinate and indeterminate cultivars achieve a larger LAI at closer (25 X 25 cm) than at wider (25 X 125 cm) spacings and so intercept more light earlier in the season. Maximum light interception is achieved with a LAI of 3 both in traditional cultivars with broadly ovate, planophile leaflets and in breeders' lines with narrow hastate leaflets (IITA 1979; Fig. 2). Thus, although notable that many lines with hastate leaflets produce large yields in off-site trials (IITA 1977a, b, 1978), this character *per se* seems to confer no inherent physiological advantage, at least for crops grown in the edaphic conditions of an experiment station where an application of just 30 kg N/ ha can provide most of the plants' nitrogen during early vegetative growth (IITA 1977a, b). If combined with nonvining, erect genotypes that can be planted at large population densities without lodging, the hastate leaf character might allow better light penetration into the canopy and so improve yields (IITA 1976).

Many more or less determinate cultivars have a maximum LAI of 3, but vary considerably in the time taken to achieve that: from about 30 days in Delhi (24 plants/m^2) to 34 days in southern Nigeria for well-watered crops experiencing average air temperatures of 28.1°C, to 42 days at a mean temperature of 27.2° C but with 10 days water stress immediately before the onset of flowering, to 48 days for crops at 25.8° C, and to 60 days for crops at 24.8°C (Chaturvedi et a1 1980, Littleton et a1 1979a, Wien et a1 1979b).

Maximum LAI values, whether close to 3 or much larger and typical of values for indeterminate cultivars (>5), coincide with the appearance of first flowers in many



2. Relationship between leaf area index and light interception for 2 cowpea cultivars differing in leaf shape, 1978 second rains (IITA 1979).

more or less determinate types, but if cool average temperatures are prolonged, then crops may not achieve maximum light interception until well into the reproductive period.

Leaves are initiated about twice as rapidly at an average temperature of 300 C than at 200 C (irrespective of genotypic differences in the rate of leaf production at a given temperature), whereas dense plant population (Grancher and Bonhomme 1972) and water stress (Wien et al 1979b) retard initiation. Neither the duration of expansion of individual leaves nor the weighted mean growth rate during this period correlated significantly with insolation in Littleton's crops. Since cowpea leaves increase in area mostly at night (Schoch and Candelario 1973), minimum temperatures can limit expansion; base temperatures for leaf appearance and expansion are estimated to be close to 16° and 21° C, respectively (Littleton et a1 1979a). The onset of leaf death is hastened by warm average temperatures but then proceeds at a rate which probably depends more on fruit load and the rate and synchrony of seed-fill. Since the onset of reproductive growth is also affected by temperature (Huxley and Summerfield 1974, Littleton et a1 1979b), as is the rate of seed filling (Wien and Ackah 1978), whether or not leaves begin to die early or later in the reproductive period will depend on temperature effects both before and after the onset of flowering. Atypically warm or cool periods during vegetative growth can have important consequences: delaying or hastening, prolonging or curtailing growth of leaf area and reproductive development (Littleton et a1 1979a). The plasticity of response shown by TVu 4552 leaves no doubt that seasonal variations in the thermal environment and in water supply can have dramatic effects on the development and persistence of the canopy and on attendant differences in dry matter accumulation and partition.

Dry matter production and partition

At LAI values smaller than those required for full light interception, the rate of accumulation of dry matter (crop growth rate) increases linearly with LAI (IITA 1972, Enyi 1973). The limited data available (Grancher and Bonhomme 1974, Littleton et a1 1979b) indicate that vegetative cowpea crops intercept about 50% of total incoming solar radiation during this linear period and assimilate dry matter with a conversion efficiency of 1.7-1.9% (an overall efficiency of about 0.9%). These values compare favorably with those achieved by several temperate crops supplied with adequate fertilizers and water (Monteith 1977). In general, interseasonal variations in incoming radiation, in the proportion intercepted, and in the efficiency of conversion were about equally responsible for differences in dry matter production between crops of TVu 4552. Large amounts of dry matter are produced when crops of more or less determinate cultivars maintain relatively large and healthy leaf areas for prolonged periods; in the crop which produced the most dry matter in Littleton's trials an early cool period delayed the onset of leaf death, and warm conditions after 20 days produced a large leaf area at flowering, so that relatively young leaves were present when plants became reproductive (and see Stewart et a1 1978). For large yields, leaf area indices between 1 and 2 are required for as long as possible after flowering but need to be coupled with efficient partitioning of dry matter into fruits (IITA 1975). In more or less determinate types (e.g. Prima and TVu 4552), which bear a large proportion of fruits on the main stem, reproductive structures soon

become the major sink for carbon and nitrogen (IITA 1977a, c), with individual fruits filling their seeds during a linear period of growth as short as 6–13 days compared with 23-36 days in soybean (Wien and Ackah 1978, Roberts et al 1978). Cowpea seeds accumulate protein far more rapidly than soybean or mungbean and at a rate which changes little throughout seed growth and maturation (Chaturvedi et a1 1980, IITA 1975). Thus, a longer seed development period might increase seed protein concentration and/or seed yield if the overall reproductive period were also prolonged and coupled with appropriate partitioning of carbon and nitrogen into fruits (IITA 1973,1975). Of course, events during the reproductive period cannot be divorced from vegetative growth and crop development (Summerfield and Wien 1980, Summerfield 1980). It seems that many cultivars cannot sustain large rates of dinitrogen fixation during the period of rapid seed growth (IITA 1977a, b, c), especially in warmer (daytime) environments and with the relatively inefficient distribution of nitrogen to seeds (compared with soybean) shown by cultivars examined in detail hitherto (Table 5; Eaglesham et al 1977, IITA 1977c). Indeterminate cultivars, which bear most of their fruits on branches, increase their vegetative dry weights longer into the reproductive period than more or less determinate types but, again, individual fruits fill very rapidly (Wien 1973). Since only two or three fruits are produced on each inflorescence, then unless the number of nodes which become and remain reproductive can be increased, a larger number of nodes, and hence more dry matter, must be produced if more fruits are to be harvested (Wien and Ackah 1978). Whether or not the efficiency of seed yield production (harvest index), already small in indeterminate types, was to decline further would depend on the relative success of fruit growth later in the season (fruits do not ripen simultaneously as they do in indeterminate soybeans; Koller 1971) when crops typically experience progressively more severe heat and water stress.

Many estimates of the respective rates and durations of carbon and nitrogen assimilation and distribution have been made for cowpea crops producing relatively small yields. Studies on the spatial and temporal relationships between carbon metabolism. dinitrogen fixation, and phenological development of field crops grown at optimum population densities for particular growth habits and producing large yields are needed. Certainly, we need to identify the sources of carbon and nitrogen available to fruits and to understand how effectively assimilates are involved in transport of these elements and their incorporation into seeds. However, the potential importance of attributes such as CO_2 uptake by fruit walls and seeds, mechanisms which facilitate the rapid flux of fixed nitrogen through vegetative structures into fruits, larger amounts of dinitrogen fixation before flowering, greater mobilization to seeds of nitrogen from stems, branches, peduncles, and fruit walls and/ or less mobilization from leaves, and other alternative strategies to maximize total photosynthate production and the efficiency of subsequent utilization (IITA 1977a, c; Pate and Minchin 1980; Summerfield 1980) can only be meaningfully assessed for productive symbiotic combinations in a range of crop environments.

Carbon exchange rate

If a large, healthy leaf area can be produced early in the season and maintained well into the reproductive period so that a large amount of radiation is absorbed, then

growth efficiency (amount of dry matter produced per unit of radiation absorbed) will depend on the rate of leaf photosynthesis and on the fraction of assimilated carbon which is lost by respiration (Elston et a1 1975).

Genotypic differences in foliar carbon exchange rates (CER) have been reported for several legumes, including cowpea, but the extent by which net photosynthesis rate can be advanced by breeding is only speculative (Nasyrov 1978, Ozbun 1978, Kueneman et a1 1979).

Individual cowpea leaves have maximum rates of photosynthesis at full expansion; the intensity of photosynthetically active radiation at which leaves are light-saturated declines from about 66 to about 33% of full sunlight as leaves age, and photosynthetic rate declines precipitously as leaves lose nitrogen and senesce. Both fruits and leaves commonly reach temperatures (warmer than 30°C) at which photosynthesis would be reduced. Green fruits have a net loss of CO_2 even in full sunlight; they respire much more rapidly than leaves which, in the dark, evolve CO_2 at rates which are typically equivalent to between 5 and 10% of maximum photosynthesis rate. The large rates of fruit respiration mean that temperature effects become progressively more important at light intensities less than full sunlight (IITA 1975, 1976; Wien and Littleton 1975).

Area of origin and degree of domestication have no influence on peak rates of photosynthesis in young cowpea leaves (Lush and Rawson 1979); differences in photosynthetic duration and total leaf area are most likely to account for differences in carbon accumulation between elite and wild lines. The photosynthetic capacity of cowpea leaves seems neither greater nor less than that of other grain legumes, is equally variable, and presents the same problems with respect to measurement and interpretation of comparative data (Evans 1974). Selection for photosynthetic rate *per se* or some related attribute (Sinha 1977) may not be a worthwhile objective, as it presents very great problems with little surety of return. One major problem is that an enormous range of values is often reported for the same genotype. Moreover, CER values have sometimes been measured at the seedling or early vegetative stage when, in fact, photosynthetic productivity during the period of seed fill is most likely the major source of carbon for cowpea seeds (Enyi 1973, Stewart et a1 1978, Wien and Tayo 1979, Pate and Minchin 1980), although some translocation of previously stored assimilates can occur (IITA 1976, Littleton et al 1979b), depending on reproductive load and the rate and synchrony of fruit growth.

Ignorance about the way in which rates of respiration are related to the contemporary rates of photosynthesis and to the accumulated dry weight of a crop stand (Monteith 1972); large variations in respiratory activity between organs at different times which cannot be explained by any one general theory (Elston et al 1975, Evans 1974, Tanaka 1977); and the paucity of information on differences in carbon and nitrogen economy which are due to the host, to strain of *Rhizobium*, or to the environment (Pate and Minchin 1980, Schubert and Ryle 1980) limit the ability of models to predict crop growth reliably, especially after flowering. Until more precise data are available these factors must preclude attributes of respiration from among the selection criteria of cowpea breeders.

Crop growth rate, harvest index, and economic yield

Cowpea crops grow most rapidly when canopies are closed and complete light interception is achieved; subsequent increases in LAI do not appear to be detrimental to total dry matter production (Wien 1973). Although in the savanna zone of West Mrica mean monthly solar radiation during the growing season (May to October) is 42% greater than in the growing season in the forest zone (March to November), there is no evidence that cowpea crops grow faster at the former site. Kassam and Kowal(l973) present data which suggest that average crop growth rates (CGR) might be expected to range between 18.3 and 2 1.2 and between 24.8 and 28.7 g/ m^2 per day in the forest and savanna zones, respectively, if the maximum rate of photosynthesis of individual cowpea leaves is taken to be 40-50 mg CO_2/dm^2 per hour (IITA 1975, 1976). However, their value of 15 g/m^2 per day for maximum CGR of cowpea grown in experiment plots in the savanna zone corresponds to a maximum rate of leaf photosynthesis of just 13 mg CO_2/dm^2 per hour. Thus, the 25% increase in average yields of cowpea crops grown in experiment plots in the sunny north (Kassam and Kowal 1973) seems not to be due to the effects of differences in insolation on CGR in the two zones.

Cowpea and soybean crops seem somewhat inferior to other nonlegume C-3 species in terms of CGR; of course, both of these legume crops achieve full light interception at a LAI of about 3 whereas the crops cited by Monteith (1978) typically achieve it at much larger values (6-9), and then partition a larger portion of dry matter into economic yield than do many, especially indeterminate, cowpeas.

If, as seems likely, cowpea yields are often limited by the poor ability of genotypes to assimilate carbon and nitrogen during the reproductive period and/ or to partition large amounts of their daily gains of these two elements into fruits (Wien 1973, IITA 1977a, b, Pate and Minchin 1980). then it would be useful to evaluate reliably not only economic yield but also harvest index (HI), and then not just for seed dry weight but also for nitrogen if potentially productive symbiotic associations are to be identified with confidence; but these data are seldom available. If belowground dry matter production is neglected, HI (seeds) is simple to measure for cereals (Donald and Hamblin 1976). A large proportion of dead leaves remain attached to the stems of cereals, but in cowpea most leaves die and fall off. We have no way of knowing for most trials with cowpeas whether HIs include belowground dry matter or recoverable dry matter (Holliday 1976) or are based on standing dry weight at harvest only; the exceptions are notable (Littleton et al 1979a).

We can make few generalizations except that sole crop cowpea grown with adequate crop protection can produce an excellent yield of protein-rich food per hectare per day by any standards; shorter crop durations and more or less determinate growth habits may be correlated with large HIs (although ‘‘cause” and “effect” are difficult to identify); longer crop durations in indeterminate types can compensate for smaller rates of yield production but, again, we cannot be precise. Cultivars may contain large amounts of nitrogen but yield poorly, and vice versa; large yielding cultivars may or may not apportion most of their nitrogen into fruits, and if they do, large seed yields and benefit to succeeding crops in terms of nitrogen in crop

residues or minimizing depletion of inorganic nitrogen from soils (Nair et a1 1979) are unlikely to be compatible objectives.

The "self-destructive" hypothesis proposed by Sinclair and de Wit (1976) postulates that fruiting induces monocarpic senescence by depleting nutrients essential for photosynthesis from leaves. This idea was supported by the dramatic positive effects on soybean yields of foliar fertilization with N, P, K, and S in proportions characteristic of mature seeds (Garcia and Hanway 1976). However, the crops grown by Garcia and Hanway experienced what appears to have been a remarkable combination of adverse weather. Furthermore, many subsequent data do not support the theoretical analysis of Sinclair and de Wit (IITA 1977 a, b, Sesay and Shibles 1980).

COMPONENTS OF ECONOMIC YIELD

Adams (1967) has stressed that a useful understanding of yield requires detailed investigation and analysis — genetical, physiological, and phenological — of the initiation and interrelations of yield component characteristics and of mineral nutrition and the assimilation of organic compounds by the plant.

For cowpea there is considerable evidence that yield is principally a function of the number of seeds which mature (Sinha 1977). Variations in yield between cultivars (Doku 1970) indifferent environments (Stewart et al 1980), in various crop mixtures (Wien and Smithson 1979), because of edaphic or other stresses including depradations by pests (Adams and Pipoly 1980), and between plants dependent on symbiotic dinitrogen fixation or on inorganic nitrogen (Summerfield et a1 1977b) are strongly correlated with the number of fruits which reach maturity. In general, significant negative correlations between either the number of seeds per fruit or the dry weight of individual seeds and the number of fruits per plant are much less common; hence the number of mature seeds harvested per plant or per unit area of land usually determines economic yield.

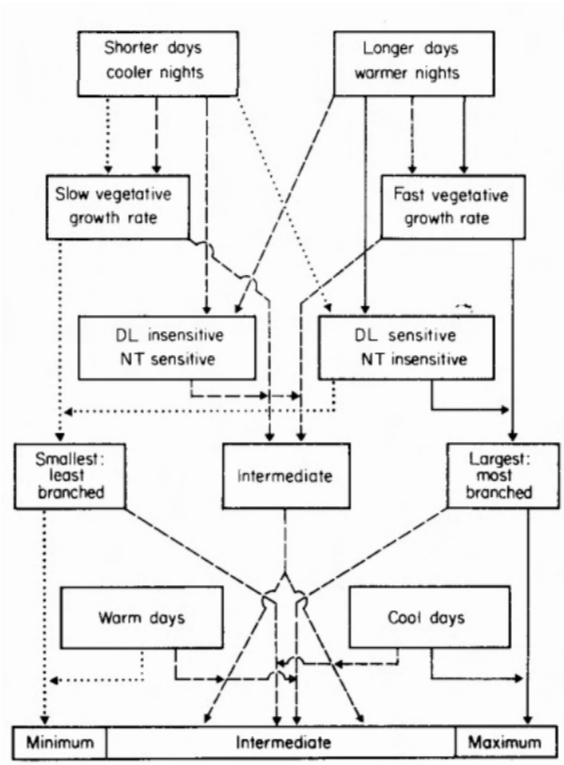
It is perhaps surprising then that traditional components-of-yield analyses equate seed yield in cowpea with the product of just three components (the number of fruits that reach maturity, the average number of seeds in them, and the mean weight of individual seeds), two of which are relatively homeostatic and seldom contribute substantially to variations in seed yield of any particular genotype. These aggregated data fail to provide any direct understanding of why yield or any particular component of it varies; they do not provide any knowledge about the processes by which components of yield are determined, nor how these processes are related to plant growth and development or to the environment. Furthermore, since biological yields are recorded only infrequently, the relative investment of dry matter into fruits cannot be quantified. To classify as equal two genotypes which yield 100 units of seed without knowing their respective biomass is unacceptable (Bunting 1971a); to neglect root (and nodule) weight, both notoriously difficult and time-consuming to estimate in the field, could be a serious omission since the ratio between dry matter production above and belowground changes with time, with the environment, and with the genotype (Holliday 1976); and to test progeny materials at only one "standard" density presupposes that large yielding cultivars at that particular density will outyield all other combinations of plant type and density — which is patently

invalid (Donald and Hamblin 1976, IITA 1975, Nangju et al 1976). We have used a more detailed components-of-yield analysis, not only to identify those plant attributes and responses which seem likely to most influence adaptability to the aerial environment but also to predict the optimum environment for maximum yield and to identify characters which best suit specific genotypes for particular situations (Summerfield 1975). It would seem prudent to devote greater attention to factors responsible for variations in the number of fruiting nodes and to the spatial and temporal relationships between carbon metabolism and nitrogen nutrition, not only with respect to fruit load *per se* but also to the rate and synchrony of fruit growth (IITA 1977a, b, Summerfield 1980).

ADAPTATION TO THE AERIAL ENVIRONMENT

It seems appropriate to consider the growth and development of an annual legume as a number of consecutive phases: vegetative (including juvenility), mature (ripeness-to-flower), reproductive (flowering and setting of fruits), and senescent (including ripening of fruits). In indeterminate cowpea, the last three of these phases can occur simultaneously on the same plant. Of course, the amount and distribution of dry matter produced during successive stages of development are often determined or limited by those environmental factors which also initiate phase changes (Summerfield and Wien 1980).

The rate of reproductive development, yield potential, and seed yield per se in cowpeas are notoriously sensitive to the vagaries of weather and climate (Erskine and Khan 1977). Despite numerous studies in artificial environments and in the field, the literature contains apparently contradictory conclusions with respect to those characters and responses with which genotypes should be endowed so as to be well adapted to specific environments (Summerfield and Wien 1980, Summerfield 1980). A greater understanding is needed not only of the genetic factors which control crop duration but also of the environmental factors that react with them. Cowpea breeders have usually selected for “adaptation” to particular sites, supposedly chosen to represent particular regions, rather than to specific conditions of, for example, photoperiod and temperature. Thus, they often have to select genotypes suitable for local environments, knowing only their response in a different one. Even after selections have been grown and tested for a number of seasons — perhaps as many as 10 or 15—at a particular site the results can, at best, be usefully indicative; they can never be decisive. Furthermore, the possibility of using statistical procedures to account for the effects of weather on yield adaptation trials seems remote. The statistical approach has very restricted objectives and has almost invariably been unrewarding; attempts to correlate seasonal changes in compound quantities such as net assimilation rate and relative growth rate throughout the life of a crop with the state of the environment are one of the least productive exercises of traditional crop ecology (Monteith 1975). A simple predictive scheme (Fig. 3), developed after extensive research in controlled environments with substantiating field observations (Table 7), coupled with an appropriate integrated screening technique which uses both the field and a precisely regulated glasshouse environment (Fig. 4), provides an opportunity for the cowpea breeder to better ensure that



3. Generalized scheme for predicting adaptability of more or less determinate cowpea genotypes to the tropical aerial environment (day length [DL], day and night temperature [NT]). Plants were well-watered throughout growth and dependent either on inorganic N or on dinitrogen fixation. Solid line: route to maximum seed yields; dashed Line: route to intermediate seed yields: dotted line: route to minimum seed yield.

his progeny genotypes or populations are well adapted to particular environments. Even when the main objective of breeding is to lessen the effects of pests and diseases, the major requirement in cowpea (Singh and Allen 1980, Smithson et a1 1980), such a policy can only be effective if the resistance attributes are incorporated into progeny material which is well adapted to the environment.

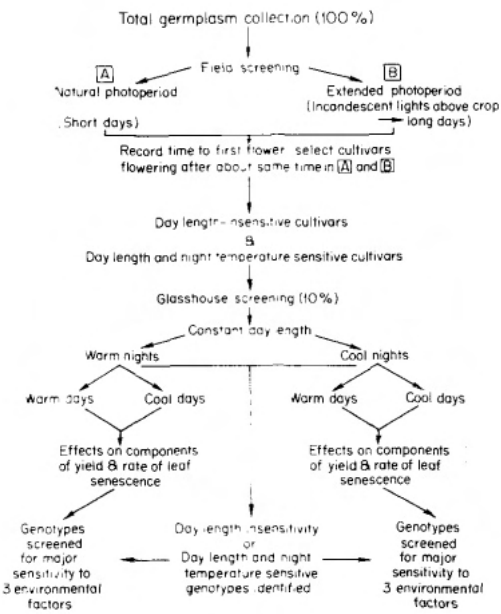
Well-watered plants grown in pots in controlled environments with appropriate cultural methods, husbandry, and rigorously evaluated technology can closely resemble their counterparts grown as spaced individuals in the field (Table 8). They also respond to a range of factors in substantially similar vein to plants grown in the field (Table 7), and they allocate and redistribute nitrogen to seeds in comparable proportions (Table 9). It seems that knowing only the seasonal march of mean weekly maximum and minimum air temperatures, of photoperiods based on a minimum light intensity of 5 f.c. (Francis 1972, IITA 1973), and the sensitivity or otherwise of genotypes not only to photoperiod (Njoku 1958, Wienk 1963, Ojehomon 1967) but also to temperature with respect to the onset of flowering, it is possible to predict relative yield in specific environments (Fig. 3).

These climatological data are readily available for most locations and the integrated screen provides a rapid technique for the breeder to evaluate not only the flowering response of a large number of progeny lines (Summerfield et a1 1979; Fig. 4) but also the ability of genotypes to yield well in supra-optimal day temperatures (and perhaps to screen indirectly for the ability to withstand drought; Table 6).

Table 7. Extrapolation from controlled environments[a] to the feld: a comparison of the responses of cowpea genotypes[b] grown in various photothermal regimes and different nitrogen nutrition in controlled environments, with plants grown at crop densities in the field.

Field responses predicted from experiments in controlled environments
Rate of leaf initiation a mean air temperature (D).
Rate of leaf expansion a mean minimum air temperature (D).
Onset of flowering (absolute values and relative sensitivity) a photoperiod (D and I)
Onset of flowering a mean air temperature (D and I).
Partition of dry matter into leaves; absolute values and ontogeny (D).
Variations in leaf thickness (SLA) with temperature and time (D).
Dominant effect of fruit number on economic yield (D and I).
Partition of dry matter into fruits; absolute values and ontogeny (D).
Correlation between fruit number and dry weight per plant (D).
Importance of green leaf area postanthesis (D).
Variations in leaf nitrate reductase activity; absolute values and ontogeny (D).
Allocation and redistribution of N to seeds (D).
Responses to ephemeral waterlogging (D).
Atypical photoperiodic effects on the onset of flowering (D and I).
Dominant effect of mean maximum air temperature on crop duration and realization of yield potential (D).
Ability of nodule-dependent plants to produce large yields (D and I).
Temperature effects on rate and duration of seed fill (D).

[a] Using appropriate plant culture and management techniques and with a technology developed for the species investigated (see Table 8). [b] Cultivars are more or less determinate (D) or indeterminate (I).



4. Diagrammatic representation of an integrated strategy for day length, day and night temperature sensitivity screening of cowpea (Summerfield et a1 1979).

Table 8. Selected morphological attributes of TVu 4552 grown with appropriate plant husbandry and management techniques (Summerfield et al 1977c) in controlled environment cabinets with specific lamp types, and in the field in Nigeria (Summerfield et al 1977a).

Location[a]	Days from sowing to first flower	Plant height (cm)	Branches (no./plant)	Main stem nodes (no.)	Terminal leaflet Length (cm)	Terminal leaflet Width (cm)
Field (IITA)	38	53	3.5	12.4	13.5	10.2
Cabinets a)	37	62	3.3	10.3	12.0	8.5
b)	31	52	3.3	10.0	12.0	8.5

[a]a, b denote 2 different lamp types from the 6 combinations tested; the remaining lamps produced unwanted photomorphogenetic effects so that plants did not resemble those in the field.

Table 9. Comparison of the sources contributing to the total reduced N content (TRN) of mature seeds in more or less determinate cowpea grown in controlled environments and in the field (Eaglesham et al 1977).[a]

Attribute	K2809 plants in controlled environment (1973)	TVu 4552 plants in the field at Ibadan (1976)
TRN in seeds[b] (%)	63.2	63.7 (75.4-80.2)
Sources of seed N:		
Remobilized[c] (%) from		
Leaves	34.4	39.7
Stem + branches	13.0	8.6
Peduncles	2.9	4.3
Roots + nodules	2.9	ND[d]
Total remobilized	53.2	52.6
Assimilated[a] (%)during reproductive period	46.8	47.4 (56.3-71.9)
TRN in nonseed components[b] (%)	36.8	36.3 (19.8-24.6)
Emergence to first flower (days)	43	35
Emergence to final harvest (days)	85	56
TRN in plant (mg)	4318	1321 (1057-1071)

[a]Both sets of plants depended primarily on dinitrogen fixation for their N supply. Figures in parentheses are ranges for 2 soybean cultivars studied in the same investigation (IITA 1977a,b,c). [b] and [c] denote % TRN in plant and seeds, respectively. [d]Not determined.

Populations of West African cowpea are exceptionally well adapted so that they start to flower at the end of rains at a particular location; the initiation of reproductive primordia and the expansion of visible buds into open flowers require two distinct photoperiodic triggers, longer and shorter, respectively (Wien and Summerfield 1980). Thus, in the shortening day lengths the plants can accumulate several floral initials, which commence development when the photoperiod is sufficiently short to allow expansion of floral parts (Bunting 1975). Lush and Evans (1980) have proposed an alternative regulatory mechanism: they noted that only 2 to 4 inductive cycles were required for floral initiation compared with about 20 for development to open flowers. Of course, either mechanism will result in the timely adaptive development shown by cowpea in West Africa, and both will depend on the sensitivity of individual genotypes (rate of advance in flowering per unit change in photoperiod)

and on the difference between the experienced and critical day length. Variations in altitude in this part of the tropics are not large; hence small differences in night temperature are probably inconsequential. Elsewhere in the tropics, topographical variations cause much larger variations in night temperature (and so in mean temperature), which are likely to have important effects on adaptation.

Although the cultivars grown by traditional farmers have only a small potential for seed production (Rachie and Rawal 1976), they seem better adapted for fruit production in the warming days of the dry season than many cultivars selected from breeders' plots in cooler tropical environments.

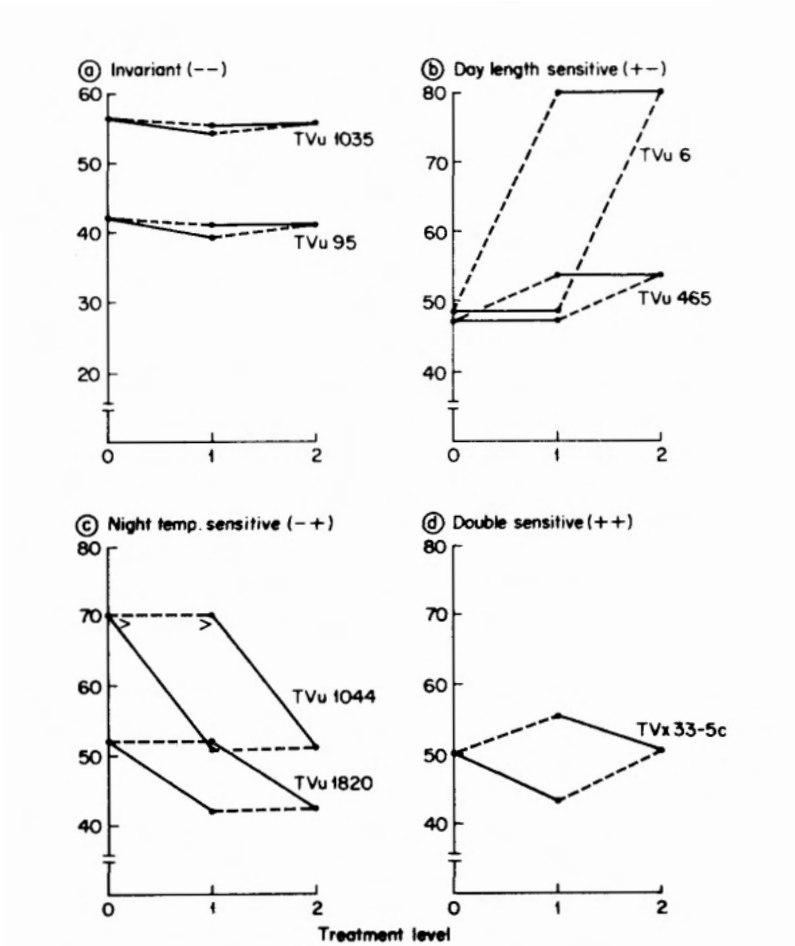
The flowering responses shown in Figure 5, and which have been used in the predictive scheme (Fig. 3), can probably accommodate the majority of cowpea genotypes. Both Wienk (1963) and Ojehomon (1967) have described some genotypes as "ambiphotoperiodic" (i.e. there are two photoperiods in which flowers are initiated after more or less the same number of inductive cycles), but neither was able to control temperatures precisely so that not only were fluctuations a confounding factor but probably there were also complex interactions between temperature and the methods used to regulate photoperiod, and so their interpretations are open to question.

Some cultivars can flower sooner in longer (15 hours) than in shorter (10 hours) days. Such cultivars appear to show a quantitative long day response but, in fact, they are insensitive to photoperiod, and their rate of reproductive development is modulated strongly by average temperature (Hadley et al, in preparation). Furthermore, we now know that the critical photoperiod becomes shorter as temperatures become warmer, which could explain why some cultivars brought from Senegal and Upper Volta to Ibadan (07° 30' N), where the day lengths are shorter but temperatures are warmer, come into flower much later than expected (P. R. Goldsworthy, pers. comm. 1980).

A single combination of factors is not optimal for all successive stages of development of the cowpea crop, and there seems little point indescribing the response of cultivars to individual factors which inevitably interact as they change with time in the natural environment. It is necessary for plant breeders, together with crop physiologists, to assess the advantages and disadvantages of photothermal responsiveness for particular environments at different latitudes and altitudes (Wien and Summerfield 1980).

PROSPECTS

There seems little doubt that increased protein supplies from grain legume crops, including cowpea, will most likely result from larger and stabilized seed yields rather than from attempts to improve seed biochemical efficiency (Boulter 1980). However, since the energy required is about the same for synthesizing proteins with good or poor amino acid profiles (Boulter 1977), improvements in protein quality seem distinctly possible. Unfortunately, early attempts to apply traditional knowledge of temperate *Rhizobium*-legume systems to improve protein production by tropical legumes met with discouraging failures (Graham and Hubbell 1975), and it now seems clear that concepts adopted for cereals may have little relevance to legume



5. Effects of photoperiod (13 h 20 min vs 11 h 40 min) and night temperature (24° vs 19°C) on flowering (days from sowing) in cowpea. Typical responses from the 200 or so genotypes screened so far are shown: a) invariant cultivars, b) variously sensitive to day length, c) variously sensitive to night temperature, and d) sensitive to both factors. Note that the consequences of opposing responses can result in identical durations of vegetative growth in long and short days depending on whether the nights are warm or cool.
Treatment levels are 0, short days and cool nights; 1, long days and cool nights or short days and warm nights; 2, long days and warm nights.- - - - and —— denote the effects of increase in day length and night temperature, respectively.

breeding (TAC 1975). If crop physiologists are to contribute significantly to increases in productivity of pest-and disease-resistant cowpea, they must understand better the dynamic spatial and temporal relationships between carbon metabolism and dinitrogen fixation (Atkins et a1 1979, La Rue 1978, Rawsthome et a1 1980), and determine what proportion of the variation found is due to genetic differences; they must also seek to explain rather than be content to describe the

responses of genotypes to their environments, not only for sole crops but also for crop mixtures (Summerfield 1980). Established techniques now incommon use may provide information less useful than considered hitherto, e.g. the enthusiastic use of various controlled environments for diverse experiments can hardly be justified unless the plants grown in artificial climates closely resemble those in the field (Summerfield and Wien 1980). Then again, it is desirable to supplement estimates of dinitrogen fixation activity based on the reduction by nitrogenase of acetylene to ethylene with other, though more laborious and time-consuming, methods (Gaskins and Carter 1976, Zary et al 1978). The problem is not one of generating data but of ensuring that some of them might be sufficiently useful so that breeders can adopt more critical selection criteria. Such knowledge can permit greater emphasis on specific crosses and so allow the breeder to work with larger populations of fewer crosses, to select more intensively, and hence to become more efficient. If useful genetic variation does exist for even some of the many attributes of the nodulated cowpea, the breeder will probably require selection techniques that are reliable, rapid, inexpensive, applicable to large numbers of plants and to the field situation, require a minimum of labor and, perhaps, are nondestructive.

Because grain legumes have been poorly researched compared with cereal crops, and since soybeans have probably received far more attention than all other grain legumes combined, there is an inevitable temptation to extrapolate from research on graminaceous crops or soybeans, or from data recorded in temperate environments, in the hope that some scenario will be forthcoming; it will not. It is even possible that the nitrogen nutrition of soybean is not very typical of grain legumes in general (Sprent 1979). Research intended to adapt to a new situation a technology previously developed elsewhere has not been an unqualified success. "The outstanding achievements have come from research which uses pure and applied *science* (both imported and locally won), plus an informed understanding of the local *environment,* to synthesize new *technology* which meets local needs and is both wanted and usable by local people" (Bunting 1971b).

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CHICKPEA, PIGEONPEA, AND GROUNDNUT

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Of the grain legumes, chickpea, pigeonpea, and groundnut are some of the most important crops in the semiarid tropics. Groundnut has received considerable research attention in developed and developing countries but chickpea and pigeonpea have been neglected crops until recently. Even now they receive little attention. Therefore, information relating to the physiological aspects of growth and yield of these two crops is fragmentary. This paper reviews work on the growth, development, and yield of these three crops in relation to management and environmental factors.

CHICKPEA

Cicer arietinum L. (*Leguminosae*, Papilionoideae, tribe Vicieae) is commonly known as chickpea, gram, Bengal gram, garbanzo, or pois chiche. Chickpea is distinguished in the Indian subcontinent as desi (generally brown seed coat) and kabuli (generaliy white seed coat). Kabulis are preferred and are better adapted to East Asian regions, including the Indian subcontinent. Ninety percent of the world's chickpea area is in the Indian subcontinent — 79% in India and 11% in Pakistan (Anonymous 1977).

Chickpea is essentially a subtropical crop adapted to warm dry conditions. Excessive moisture, cloudy weather, and high humidity reduce flowering, pod set, and yield. A diurnal sequence of cool nights and warm days is optimum for crop growth and yield. It is quantitatively a long day length plant but it flowers in all photoperiods. Chickpea responds to rhizobium inoculation on virgin soils and, occasionally, on soils where it has been grown previously. It is particularly important in the Indian subcontinent between lat. 10° N and 35°N, where it is grown on the residual moisture of heavy, well-drained deep soils during the postmonsoon dry season. It grows as an irrigated crop during the dry season in Ethiopia and during spring and summer in the Mediterranean regions. It was recently introduced to Africa, Australia, and the Americas.

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In this paper the growth and yield of chickpea are illustrated by studies carried out in two contrasting environments: International Crops Research Institute for the Semiarid Tropics (ICRISAT) Center, Hyderabad (17° 32'N, 78° 16'E, altitude 542 m), and Hissar (29° 10'N, 75° 44'E, altitude 221 m). At Hyderabad the crop is grown on deep Vertisols, with pH values of 8.0-8.3, medium in available N, and low in available P. Winters are mild and growth is terminated by regularly rising temperatures and increasing atmospheric evaporative demand in late February. At Hissar the crop is grown on Entisols with a pH of 8.2 and medium availability of nitrogen and phosphorus. Precipitation is 300 mm in the rainy season plus another 80 mm during the crop growth period. Winters are long with lower long temperatures. Open pan evaporation is low during the crop growth period and the temperature rises later, resulting in a longer growth duration.

Photosynthetic rate

In common with other legumes, chickpea is classified as a C-3 plant (Sinha 1977). There is at least one report on a crassulacean acid metabolism (CAM)-like behavior in chickpea (Santakumari et al 1979).

Leaf photosynthetic rates in chickpea cultivars vary between 15 and 40 mg CO_2/dm^2 per hour. This rate compares favorably with photosynthetic rates in other C-3 crops such as wheat, cotton, and barley, but is poorer than in C-4 plants such as maize, sorghum, and millet. The photosynthetic rates in chickpea are better than those in soybean, lentil, drybean, cowpea, and red clover (Sinha 1977, van der Maesen 1972).

Large differences in relative rates of photosynthesis exist between chickpea cultivars. Pandey et al (1976) reported a difference of 124% between cultivars with the highest and lowest photosynthetic rates. A similar difference (1:14.5) was reported by Shantakumari and Sinha (1972). Cultivars of diverse geographic origin exhibited large differences in photosynthetic efficiency ranging between 200 and 400 µg CO_2/cm^2 per hour (van der Maesen 1972).

CO_2 fixation by leaves decreased from flowering to pod formation. Cultivars that had the highest photosynthetic rate at flowering had the lowest rate during pod filling (Shantakumari and Sinha 1972). Nitrogen applied in the form of 1% KNO_3 solution during pod development enhanced the rate of photosynthesis (Sinha 1973).

Both pods and stems contribute to total photosynthesis in chickpea (Pandey et al 1976, Khanna and Sinha 1973). Pod walls remain green for a considerable period and, because they are photosynthetically active, may contribute to grain yield. Differences in pod photosynthesis exist among cultivars; the ratio of lowest to highest was reported as 193.5 (Shantakumari and Sinha 1972). Chickpea pods normally subtend below the leaves and consequently are shaded. In field experiments pods were hooked on the adaxial leaf surface to expose them to greater illumination. The absence of increases in seed yield (Saxena and Sheldrake 1980) indicated that the light intensity requirement for maximum pod wall photosynthesis may be low.

Cultivars differed in photosynthetic rate with increasing illumination (Shantakumari and Sinha 1972), but leaves of most of the cultivars reached maximum photosynthetic rates at a light intensity of 0.5 cal/ cm^2 per minute. Leaf photosyn-

thetic rates were highest in 2-week-old leaves (van der Maesen 1972).

Prasad et al (1978) reported a significant positive correlation (0.56) between photosynthesis and grain yield but no other evidence of a relation between leaf photosynthetic rate and grain yield.

The translocation of photosynthates to the nodules generally stops at flowering and nodule disintegration begins (Shantakumari et al 1975). Roots always receive more photosynthates than the nodules. Under irrigation the translocation of photosynthates to roots and nodules is higher. The use of labeled carbon ^{14}C indicated that photosynthates are translocated to all plant parts including unfed branches (Shantakumari et al 1975). The developing pod receives most of the photosynthates from its subtending leaf (Pandey et al 1978). When there is no axillary pod the photosynthates are diverted to other actively growing sites such as the lower pods, which serve as strong sinks. During pod development, when stems are also growing fast, competition for photoassimilates may occur between these two sinks. Lower leaves supply 36% of their photoassimilates to stems and developing pods (Pandey et al 1978).

In general, the translocation of preflowering photoassimilates accumulated in stems to developing seeds is small in chickpea. Only 22-27% of the total photoassimilates in seeds are accounted for when estimates are from defoliation studies (Pandey et al, unpubl., quoted by R. J. Summerfield et al 1979) and around 7-20% when the relative loss in stem weight and gain in seed weight provide the basis for estimates (Saxena and Sheldrake, unpubl.).

Crop growth rate, leaf area index, leaf area duration, and dry matter production

The rate and duration of growth of chickpea are greatly influenced by climatic conditions, especially temperature, which strongly influences the adaptation of cultivars in different regions. In India, the adaptation of early cultivars at Hyderabad (where winters are short) and late cultivars at Hissar (where winters are long) is an example (Saxena and Sheldrake 1979). The growth and development patterns of cultivars adapted to these contrasting environments are illustrated by the changes in the crop growth rate (CGR), leaf area index (LAI), and dry matter accumulation of G-130 (Hissar) and JG-62 (Hyderabad) in 1977-78 under conditions of a gradually receding soil-moisture profile (Fig. 1).

CGR values in the early stages are higher at Hyderabad than at Hissar. At 50 days after sowing (DS), the CGR at Hyderabad was 9.0 g/m^2 per day compared with 2.0 g/m^2 per day at Hissar. Thereafter at Hissar the CGR increased exponentially until 150-160 DS, shortly after flowering and during pod set. During this period maximum CGR ranged from 20 to 34 g dry matter/m^2 per day. Then the crop abruptly stopped growing as the plants prematurely senesced because of the sudden rise in temperature, which normally occurs at this time of the year. A similar CGR (20 g dry matter/m^2 per day), sustained for a shorter period because of increasing temperatures, is reported for these environments by others (Sinha 1977).

In contrast, at Hyderabad the CGR increases gradually, reaches a maximum of 8-14 g dry matter/m^2 per day and then declines as gradually at later growth stages — a pattern somewhat similar to that observed at Pantnagar, India (Prasad et al 1978), where maximum values ranged from 8 to 12 g dry matter/m^2 per day. The CGR

values in irrigated chickpea at ICRISAT Center are as high as 20 g dry matter/m^2 per day, approaching the values in northern Indian environments such as at Hissar.

LAI followed a pattern close to that of CGR at both locations. At Hissar, 140-150 DS during the exponential phase of LAI increase, a sudden rise in temperatures normally occurs and the active leaf area abruptly declines from 6 to almost zero. In crops that received no presowing irrigation, maximum LAI values were between 3 and 4. At Hyderabad, the maximum LAI was between 1 and 2 at peak CGR values and only rarely exceeded 2. LAI values of 2-3 were recorded in irrigated chickpea.

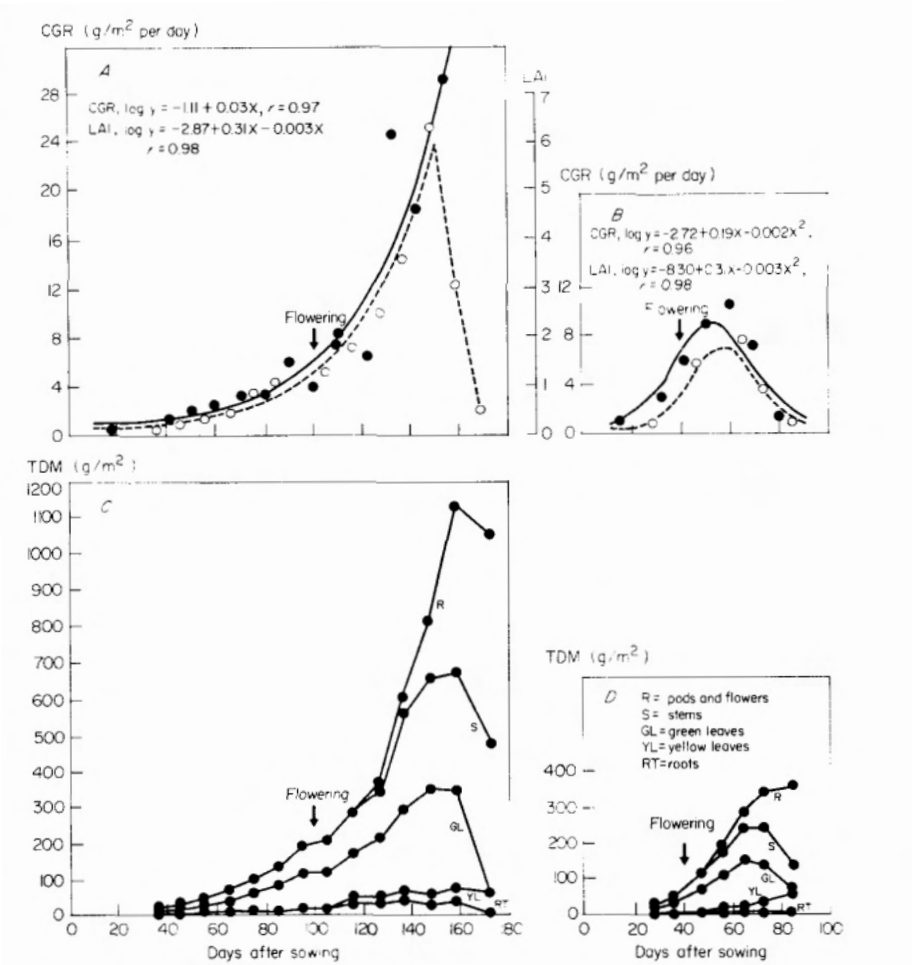
The accumulation and distribution of dry matter are also shown in Figure 1. In early growth stages the accumulation of dry matter at a given time was slower at Hissar than at Hyderabad. At Hyderabad the crop accumulates almost all of its dry matter by 85 DS and senesces, whereas at Hissar it accumulates only a fraction of the total dry matter at harvest. At both locations most of the dry matter accumulation in leaves, stems, or roots occurs after flowering, reflecting the indeterminate nature of the crop in which vegetative growth continues along with reproductive growth. Pod number increases simultaneously with LAI, but once the leaf area starts to decline there is no further increase in pod number (Sheldrake and Saxena 1979, Saxena and Sheldrake 1979). The addition of dry matter continues for a protracted period at Hissar because cooler temperatures prolong growth. Under such environmental conditions even the growth duration of early cultivars is extended because the flowers produced during the cool season do not set pods and the crop continues to grow vegetatively (Saxena, unpubl.). The period of ineffective flowering was around 60 days in early cultivars and was short in late cultivars (Table 1). At harvest, therefore, the total node numbers in early and late cultivars are similar. The rate of increase in dry matter during the linear phase of growth differs significantly between cultivars at Hyderabad (66.3-197 mg dry weight/day per plant) and is positively correlated with grain yield. At Hissar, cultivars do not differ significantly (350-450 mg dry weight/day per plant) and there is a negative trend in the relation to grain yield (-0.23) (Saxena and Krishnamurthy, unpubl.).

Green leaf area duration (LAD) showed trends similar to those described for rate of increase in dry matter. At Hyderabad, it ranged between 29 and 62.7 days and although it correlated positively with grain yield, the relation was not very close (r= 0.53*). In contrast, at Hissar, the LAD was very high and was positively correlated with average growth rates (0.79*) but was negatively correlated with grain yield (-0.63*).

Yield, yield components, and harvest index

In chickpea, average yields vary widely, from 0.2 t ha in Jordan to 1.7 t/ha in Egypt (Anonymous 1977). Average yields in India ranged from 0.4 to 0.8 t/ha.

Growth duration at Hissar is twice as great as at ICRISAT Center and so are the yields per hectare (Table 1). Under well-managed experiments, yields as high as 4 t/ha are obtained in Hissar and 3 t/ha with irrigation at Hyderabad. The potential yields of this crop are high. At ICRISAT Center, early-duration cultivars are better adapted and yield more than the late cultivars, which perform very poorly. At Hissar, the late cultivars yield more, but the early cultivars also give relatively higher



1. Crop growth rate (CGR), leaf area index (LAI). and dry matter accumulation (TDM) of 2 chickpea cultivars: G-130 grown at Hissar (A, C) and JG-62 grown at Hyderabad (B, D).

Table 1. Growth duration, total dry matter, yield, and yield components of chickpea at International Crops Research Institute for Semi-Arid Tropia, Hyderabad, and Hissar, India.

Character[a]	Hyderabad	Hissar
Total growth duration (days)	75-100	165-180
Vegetative period (days)	35-50	60- 100
Period of ineffective flowering (days)	–	30-60
Duration of podding (days)	40-50	45-50
Nodes (no./plant)	150-180	300-400
TDM (t/ha)	2.0-2.6	5.5-6.8
TDM (kg/ha per day)	20-30	30-40
Yield (t/ha)	.95-1.4	2.2-3.0
Yield (kg/ha per day)	10-20	15-20
Harvest index (%)	40-60	35-40

[a] TDM = total dry matter.

yields than at ICRISAT Center because growth duration is extended. The per-day productivity of dry matter is higher at Hissar than at ICRISAT Center, but the per-day yield is similar (Table 1). The duration of podding ranges from 40 to 50 days. Extending podding duration by 30 to 35 days with irrigation increases chickpea yields at Hyderabad. Podding duration at Hissar cannot be extended with current cultivars because cool temperatures during early flowering inhibit pod set and high temperatures in late reproductive stages of growth cause premature senescence. It may be possible to extend the duration of podding at Hissar by the selection of cultivars that tolerate low and high temperatures during these crucial growth stages.

In chickpea, the number of pods per plant has the highest correlation with yield. Pod number per plant is closely correlated with the number of secondary branches (Gowda and Pandya 1975; Sandhu and Singh 1972; Saxena and Sheldrake, unpubl.). Grain yield has a low positive correlation with 100-grain weight but is negatively correlated with the number of grains per pod. The 100-grain weight has highly significant negative correlations with seeds per pod and pods per plant (Gowda and Pandya 1975).

Harvest index (HI) values are higher at Hyderabad than at Hissar (Table 2) because of greater vegetative growth at Hissar. Also at Hissar, the HI is higher in late-sown crops, which produce less dry matter and yield than crops sown at the normal time. Pinnae fall begins fairly early in the season, especially at Hyderabad. This results in inaccurate computation of the HI. At Hyderabad the HI is overestimated by 10% due to pinnae fall (Saxena and Sheldrake 1979), but the cultivar ranking for HI does not change even if the HI values used have been corrected for pinnae fall. HI values observed with a number of cultivars ranged from 20 to 47%, the highest being from the best adapted local cultivar (Dahiya et al 1976, Lal 1976).

Response to irrigation

Chickpea can draw water from depths of 150- 180 cm (Sardar et a1 unpubl.; Sandhu et al 1978) and grow and yield well without supplemental irrigation provided:

- there is adequate soil moisture in the profile at seeding in regions where the temperatures remain low for a fairly long time after planting, and
- open pan evaporation is low and humidity is high, such as at Hissar in India.

On a deep Vertisol at ICRISAT Center where crop growth duration is short, the yields of the best adapted chickpea Annigeri were doubled by frequent irrigation with the soil water profile fully saturated at planting (depth of the profile, 187 cm; water-holding capacity, 840 mm; available water. 230 mm) (Table 2). The long-term average precipitation in the rainy season is around 700 mm for this region and winter rains add another 150 mm. Chickpea responded to irrigation because in the surface soil layer, where most of the roots were concentrated, moisture was depleted rapidly (Gupta and Agarwal 1977). The irrigated plant maintained a higher leaf water potential, greater LAI, longer LAD, and the crop growth duration was extended by about 35 days. The average net assimilation rates of the irrigated plants were high during the first 52 days. Both pods per plant and seeds per pod increased and contributed to yield (Table 2). The response in total dry matter was greater than that in yield and so the HI is lower in the irrigated treatment. Leaves of the nonirrigated plants showed no rolling of the pinnae or drooping of the compound leaf. The

Table 2. Effect of irrigation on yield, total dry matter, harvest index, and yield components of Annigeri on a deep Vertisol at International Crops Research Institute for Semi-Arid Tropics, Hyderabad, India, 1978-79.

Treatment[a]	Yield (t/ha)	Total dry matter (t/ha)	Harvest index (%)	Pods (no /plant)	Seeds no./pod)	100-seed weight (g)
Nonirrigated	1.3	2.3	59.3	35.4	1.12	17.2
Irrigated 2 times – 31,43 DS	2.1	3.6	59.8	44.6	1.20	16.2
Irrigated 4 times – 31,43,65, and 92 DS	3.0	6.0	50.8	63.7	1.32	15.1
LSD (0.05)	0.59	2.0	–	21.1	0.07	1.59
CV (a)	20.7	38.7	15.2	19.5	2.5	4.3

[a]DS = days after sowing.

nonirrigated plants had fewer leaves with smaller pinnae, fewer internodes, and fewer branches.

At Hissar, on an Entisol with 220 mm stored soil moisture from the 320 cm preplanting rains and 80 mm rainfall during crop growth period, a heavy presowing irrigation reduced yields by 9-12% (Saxena and Sheldrake, unpubl.). The excessive vegetative growth encouraged lodging. The LAI values in irrigated chickpea ranged from 7 to 8, compared with 3 to 4 in the nonirrigated crop. At Ludhiana in northern India, an irrigation during podfill increased yield when early crop growth was well supported by conserved moisture; irrigation also encouraged excessive growth in those experiments (Sandhu et al 1978).

Responses to supplemental irrigation in chickpea occurred in the absence of' enough stored water in the soil profile or where winter rains were negligible or absent. Two irrigations, one during vegetative growth and the other during podfill, generally gave the best yield response (Saxena and Yadav 1975, Sharma et al 1974) at a number of locations in India. The highest yield increase in northern India was 32%.

The average water use by chickpea crops at Dehradun, India, ranged from 110 to 210 mm as the yields varied from 0.9 to 1.8 t ha (Singh and Bhushan 1979-80). The water-use efficiency was around 8.6 kg grain mm per ha. Application of P_2O_5 increased the water-use efficiency. At ICRISAT Center, water-use efficiencies of rainfed chickpea and of those receiving irrigation only during the early stages of growth (31 and 43 DS) were around 8.1 kg grain/ mm per ha, whereas that of a crop receiving frequent irrigation (31, 43, 65, and 92 DS) was 7.8 kg grain/mm per ha (Sardar Singh and Saxena, unpubl.). Nonirrigated chickpea extracted water from a depth of 142 cm and fully irrigated chickpea from a relatively shallow depth of 127 mm.

Photoperiod response

Chickpea is grown at a wide range of latitudes at which photoperiods vary as well as planting time. It is under increasing photoperiods in the Mediterranean region, under decreasing photoperiods in India and Pakistan, and under constant photoperiods in Ethiopia (van der Maesen 1972). Chickpea has been variously described as long-day length plants (Nanda and Chinoy 1960a, b; Eshel 1968; Pandey et a1 1977), quantitative long-day length plants (Sandhu and Hodges 1971, and van der

Maesen 1972), and short-day length plants (Bhardwaj 1975). Cultivars that are early to late in flowering and maturity under normal field conditions all flower more rapidly in longer (15-hour) days. Temperature can modify the photoperiod response. Cooler temperatures with short days delay flowering further whereas warmer days with longer photoperiods hasten flowering. These two opposing effects can exactly offset each other (Summerfield et al 1979). The response of chickpea to longer photoperiods is being used in the ICRISAT breeding programs for accelerated generation turnover to speed advancement of breeding material (Sethi et al, unpubl.).

Potential yields of chickpea, though fairly high, are not realized in farmers' fields because of constraints such as water, salinity, and nutrient deficiencies. The yield potential can be further increased by breeding cultivars tolerant of salinity and drought, developing input (water and nutrient)-responsive cultivars, and extending the podding duration by identifying cultivars tolerant of cooler temperatures.

PIGEONPEA

Cajanus cajan (L.) Millsp (*Leguminosae,* Papilionoideae, tribe Phaseoleae), commonly known as pigeonpea and redgram, is a grain legume of considerable importance in India and is grown in many other tropical countries from 30° N to 30° S.

Most of the improved and local cultivars of pigeonpea are short-day length plants, but day-neutral and intermediate forms also exist. Flowering periods are often long and second flushes are common.

Pigeonpea is tolerant of drought, but sensitive to waterlogging. It grows well on all kinds of well-drained soils. Wet weather during vegetative growth followed by dry conditions during reproductive growth favors high yields. Pigeonpea also grows well in humid areas.

Leaf photosynthetic rate

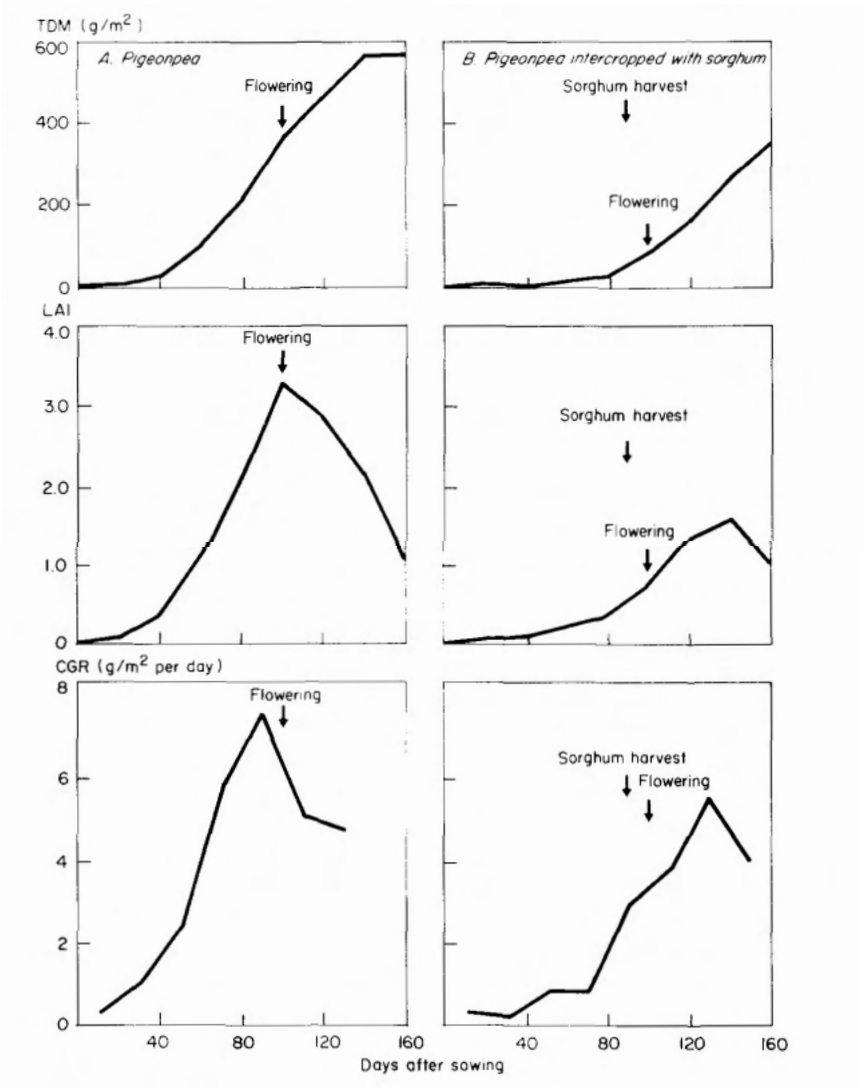
Like all food legumes, pigeonpea is a C-3 plant. Low amounts of phosphoenol pyruate carboxylase (PEP) enzyme (activity ranging from 0.04 to 0.11 µmol CO_2/dm^2 per minute) have been reported but it is doubtful whether such low levels of activity can be involved in photosynthesis (Sinha 1977). No direct measurement of absolute photosynthetic rate of pigeonpea leaves is available, but genotypic differences in the relative rates of photosynthesis of pigeonpea leaves measured by ^{14}C fixation have been reported (Pandey et al 1976). In 12 genotypes tested, the relative photosynthetic rates varied from 100 to 126%.

Without direct measurement of leaf photosynthesis, net assimilation rate (NAR) is the best measure of photosynthetic efficiency. For a medium-duration cultivar (ICP-1) at ICRISAT Center, NAR was about 75 g/m^2 per week at the time of flower bud initiation (Sheldrake and Narayanan 1979).

Crop growth rate

A typical growth pattern of a medium duration cultivar (ICP-1) grown on a mediumdeep Vertisol at ICRISAT Center over 3 years is illustrated in Figure 2. Dry matter production and CGR in the earlier stage of growth were very slow. The peak

CGR of 7.65 g/m^2 per day was attained between 80 and 100 DS. The CGR values in later stages of growth were underestimated because no correction was made for the fallen leaves and other organs. Although the pods continued to fill beyond 140 days and new flowers and buds were formed, they were not reflected in total dry matter because of the continuous loss of dry matter by leaf fall. Sheldrake and Narayanan (1979) estimated that the fallen material constituted 25% of total dry matter production of 8.4 t/ha for this cultivar grown on a Vertisol.



2. Crop growth rate (CGR), leaf area index (LAI), and total dry matter (TDM) of medium-duration pigeonpea. ICP-1 grown alone (A) and intercropped (B) with sorghum on medium-deep Vertisol at International Crops Research Institute for the Semi-And Tropics, Hyderabad, India (M. Natarajan. unpubl.)

Work in Australia with longer growth duration pigeonpea showed three distinct growth phases: an initial lag phase up to day 84, a very rapid growth phase lasting until day 168, and a final slow phase of dry matter accumulation. In this study the maximum CGR for one of three accessions reached as high as 18 g/m^2 per day (Wallis et al 1975).

Differences in maximum CGR have been reported for different cultivars. At ICRISAT Center, early cultivars T-21 and Pusa ageti had a maximum CGR of 6.8 and 5.1 g/m^2 per day whereas the medium duration cultivars ST-1, ICP-1, and HY-3C produced 8.9, 13.7, and 7.5 g/m^2 per day (Sheldrake and Narayanan 1979). The slow growth rate during the first 2 months is typical of all cultivars. That may be a disadvantage in a pure crop but not in a mixed crop. Pigeonpea is generally intercropped in India (Pathak 1970), West Indies (Ariyanayagam 1975), and Africa (Acland 1971) with a variety of other crops such as cereals, low-growing legumes, and root crops, but notably with the cereals sorghum, maize, and millet. The effect of these associated crops on the growth and development of pigeonpea is discussed later.

Dry matter production

Dry matter yield as high as 23 t/ha has been reported from Australia for a long-duration pigeonpea UQ1 (Akinola and Whiteman 1974b). When pigeonpea was grown in the normal season at ICRISAT Center, the aboveground dry matter production generally ranged between 6 and 8 t/ha for medium-duration cultivars and between 3 and 5 t/ha for early cultivars (Sheldrake and Narayanan 1979, ICRISAT unpubl. data). The dry matter production of the determinate and indeterminate cultivars in each of the three growth duration classes was studied. The indeterminate types outyielded the determinate types in all cases (ICRISAT 1978).

Because of pigeonpea's photoperiod sensitivity, its dry matter production is greatly influenced by the time of planting. Akinola and Whiteman (1974a) observed a range of photoperiod responses over a broad group of accessions, but the maximum dry matter yield of all the accessions declined with a delay in sowing beyond September. At ICRISAT, when cultivars belonging to early-, medium-, and later-duration classes were planted in October instead of the normal planting time in July, plants flowered earlier and were shorter (0.5-1 m) than normal (1.5-2.5 m) (ICRISAT 1978). In Puerto Rico, when the normal April-May planting time of indeterminate cultivars was delayed to September-October, the plants also flowered earlier and were appreciably shorter (Abrams and Julia 1973).

Dry matter production has been studied in relation to population density. Akinola and Whiteman (1974b) found that the dry matter yield-density relation described a parabolic curve over a wide range of plant population densities. Increasing plant production favored vegetative growth, particularly of the stem, and reduced seed yields. Thus, the optimum density for dry matter production (107,639 plants/ ha) was much higher than that for seed yield (17,940 plants/ha). For a medium-duration cultivar (ICP-I) tested at ICRISAT Center with population densities ranging from 15,000 to 130,000 plants/ ha, dry matter accumulation increased up to the highest population density. Seed yield response to a population density of about 100,000 plants/ha remained low and then decreased (ICRISAT unpubl. data).

Partition of dry matter and harvest index

In pigeonpea, dry matter accumulation in the vegetative structures continues unabated after the onset of reproductive growth. At ICRISAT Center dry weight of the stem increased after flower bud initiation, reflecting continued production of new branches and continued thickening of existing stems (Narayanan and Sheldrake 1976). The early cultivars produced 73-86% of their total stem dry weight after flower bud initiation and the medium-duration cultivars about 35–55%. Production of secondary branches continued during the reproductive phase in all the cultivars.

During the initial slow growth phase, the leaf fraction constituted a greater portion of the dry matter than the stem, but thereafter decreased progressively. The stem, however, continued to be the major constituent of the total dry matter until harvest.

Pigeonpea has one of the poorest HI values among the grain legumes. At ICRISAT Center, mean HI values of 34% for the early cultivars and 24% for medium-duration cultivars have been recorded (Sheldrake and Narayanan 1979). These values, however, overestimated the partitioning efficiency of the crop because the enormous loss of dry matter through leaf fall was not considered in the calculations. The mean HI for the medium cultivars was reduced from 24 to 17% when correction for leaf fall was made. In Trinidad, the HI of pigeonpea has been reported to range between 12 and 30% for early- and medium-duration cultivars (Ariyanayagam 1975).

Cultivar differences in HI may be influenced by the relative duration of the vegetative phase and by the dry matter partitioned into seeds in the reproductive phase. The higher HI of early cultivars might be due in part to the relatively higher portion of their whole growth period that was occupied by the reproductive phase (Narayananand Sheldrake 1976). Further studies at ICRISAT Center revealed that HI did not differ appreciably between determinate and indeterminate cultivars in early and medium groups, but in the late-maturity group the mean HI was higher in determinate cultivars (31.5%) than in indeterminate cultivars (19.2%) (Venkataratnam and Green 1979).

As in most food legumes, HI in pigeonpea is strongly influenced by environment and can be manipulated agronomically by planting density, irrigation, and fertilization. Striking changes in HI caused by intercropping and change in the time of planting were also reported.

As mentioned earlier, pigeonpea is grown mostly in association with other crops and this can greatly change the growth and development pattern of the crop. Figure 2 compares the dry matter accumulation pattern in a medium-duration pigeonpea cultivar (ICP-1) grown alone or in an intercrop system at the same population density. Sorghum, the other component in the system, severely depressed the growth of the intercropped pigeonpea, and the growth rate of the intercropped pigeonpea did not exceed 0.8 g/m^2 per day until the sorghum was harvested. After the sorghum harvest the pigeonpea CGR rose sharply, peaking at 5.5 g/m^2 per day between 120 and 140 DS. Intercropped pigeonpea was shown to have great compensating ability after the harvest of sorghum (Natarajan and Wiky 1980a). The dry matter production of intercropped pigeonpea at the time of sorghum harvest (85 DS) was only 14.5% that of pigeonpea grown alone. Three

months later, at maturity, the total dry matter yield of intercropped pigeonpea was 41% of the maximum that pigeonpea alone produced. Severtheless, the HI of intercropped pigeonpea was 31.6% compared with 18.8% for pigeonpea grown alone. This was due not to a change in the partitioning efficiency of the intercropped pigeonpea per se but to the greater dry matter production that occurred after the crop had entered the reproductive phase. Intercropping pigeonpea with less aggressive, low-growing legumes such as groundnut is practiced to some extent in India and these intercrops may have less effect on pigeonpea growth.

Pigeonpea is normally planted in India in June-July when the day length is maximum. Late plantings, which produce smaller plants with less vegetative growth, result in high HI (ICRISAT 1978). Thus, with high plant populations to compensate for the smaller plant size, pigeonpea has good potential as a winter crop in areas of India where winter temperatures are not too low (Narayanan and Sheldrake 1979).

Economic yield and yield components

At ICRISAT Center pigeonpea seed yield normally ranges between 1 and 2 t/ha for a medium-duration cultivar, depending upon the rainfall and soil type. It is approximately 6-12 kg/ha per day in the normal crop season. Yield can be much higher. Under favorable growing conditions, dry seed yields of 1.6-2.5 t/ha can be realized and an exceptional yield of 5 t/ha was reported from India (Rachie and Roberts 1974). Akinola and Whiteman (1972) reported the highest annual dry seed yield of 7.6 t/ha, based on 2 major harvests from a single planting of UQ 50 — a per-plant yield of 2.5 kg with plants spaced at 1.83 × 1.83 m. Wallis et al (1979) reported that a photoperiod-insensitive, short-duration variety (112 days to first harvest) had a yield potential of 3 t/ha or 27 kg/ha per day.

A strong association found between total annual seed yield and the total number of pod-producing branches per plant suggested that seed yield was influenced by the number of sites available for pod production (Akinola and Whiteman 1974a). There was no significant direct relation between seed yield and other yield components such as number of seeds per pod, weight of 100 seeds, and ratio of seed weight to pod weight. Work at ICRISAT Center and in Puerto Rico also indicated that grain yield differences in pigeonpea resulting from agronomic manipulation were largely manifested through differences in the pod number and pod-bearing branches per plant rather than in the seed number per pod and 100-grain weight (ICRISAT, unpubl. data; Abrams and Julia 1973).

Canopy development and light use

Canopy development in pigeonpea is very slow. A typical leaf area development pattern for a medium-duration cultivar showed that after the first 30 days of growth, LAI was barely 0.5 (Fig. 2). Therefore, a large portion of the incident sunlight reaches the ground unintercepted. A crop of the same cultivar intercepted as little as 10% of the total incoming radiation (Natarajan and Willey 1980b) 1 month after sowing. A peak interception level of 77% was reached at about 100 DS.

Figure 2 shows that the maximum LAI of 3.28 nearly coincided with the attainment of peak CGR. Although this maximum LAI is typical of a medium-duration cultivar, higher values have been reported under more favorable conditions (Shel-

drake and Narayanan 1979). Leaf area development in pigeonpea is influenced by such factors as variety, fertility, density, and moisture availability. Keatinge and Hughes (1980) reported peak LAI values ranging from 0.34 to 12.5 in 24 situations resulting from site, variety, and moisture level combinations. Maximum LAI values ranging from 13 to 16 have been reported from Australia for 4 pigeonpea cultivars (Wallis et al 1975).

Rachie and Roberts (1974) suggested that the erect *Cajanus* plant, with comparatively small lanceolate leaves, should have higher photosynthetic efficiency than other legumes. They believed that LAI values of 7.0 and higher should be considered optimum compared with LAI values of 3.0 and 4.0 for other large-leaved legumes. This opinion was contradicted by Hughes et al (1980) because the values were higher than for other tropical legumes and higher than those normally achieved by the pigeonpea varieties in their trials. Studies at ICRISAT with early and medium-duration cultivars also showed that the maximum LAI values were mostly below 4.0 when pigeonpea was grown at optimum population density and exceeded 4.0 only when the season was abnormally wet. The maximum LAI was normally achieved after flower bud initiation and nearly coincided with the time of maximum CGR (Sheldrake and Narayanan 1979, Natarajan and Willey 1980a).

Pigeonpea intercepts about 95% of the incident radiation when the LAI is about 4.4 (Hughes et al 1980; Natarajan and Willey, unpubl.), and virtually all the light at LAI values greater than 6.0 (Wallis et al 1975).

Pigeonpea, besides being slow in canopy development, inefficiently uses intercepted radiation for dry matter production. A mean intercepted light-use efficiency of 0.9 1% and 1.08% for the period up to maximum dry matter accumulation was obtained with a short-duration pigeonpea at Trinidad (Hughes et al 1980) and a medium-duration cultivar at ICRISAT Center (Natarajan and Willey 1979). The relation between the accumulated dry matter and accumulated intercepted radiation was approximately linear in both studies, at least during vegetative growth.

Response to major climatic factors

Temperature. A temperature range of 25 to 30° C is optimal for pigeonpea, but it can survive temperatures up to 45° C if soil moisture is adequate (Sinha 1977). Pigeonpea is extremely sensitive to frost but it can survive, though with poor growth rates, when temperature goes as low as 5-10°C. Pigeonpea cultivars differ in degree of cold tolerance (Chi-Chu Wang 1979).

Water. Pigeonpea has a deep taproot system and is highly drought resistant (Gooding 1962). Root development is extensive and deep, enabling the plant to tap moisture and nutrients at greater depths than the more herbaceous tropical grain legumes. Once established, pigeonpea grows exceptionally well on residual moisture. On upland soils in southern Nigeria the crop grows vigorously and fruits profusely 75 days after rains stop (Rachie and Roberts 1974). In India, where the crop is almost entirely rainfed, the medium- and long-duration cultivars flower at the end of the rainy season and grow for long periods on residual soil moisture. Notwithstanding its high drought tolerance, pigeonpea responded to irrigation in dry seasons (Saxena and Yadav 1975, Keatinge and Hughes 1980).

Day length. Most pigeonpeas are photoperiod sensitive and are quantitative

short-day plants (Wallis et al 1979). But a range of photoperiod responses has been found by investigators working with a broad group of genotypes. Early-maturing types did not seem to show a typical short-day reaction as did the medium types (ICRISAT 1975). Akinola and Whiteman (1974a), in an experiment with two early- and two late-maturing cultivars, showed that the late-maturing cultivars were quantitative short-day types, one of the early-maturing cultivars was day-neutral or nearly day-neutral with a quantitative response to low temperature, and the other was intermediate. Four photoperiod response groups were identified among 21 cultivars tested by monthly planting (ICRISAT 1976). Interactions between the photoperiod responses of pigeonpea and climatic factors such as temperature were found at ICRISAT (ICRISAT 1976) and in Australia (Akinola and Whiteman 1974a).

Perennial character. Gooding (1962) described pigeonpea as a short-lived perennial that is often cultivated as an annual. This is especially so in India where pigeonpea is normally cut and harvested when the pods mature. If the plants are left standing, the reproductive phase is followed by a second flush of growth and flowering (Sheldrake and Narayanan 1979). The second crop is produced during the hot dry season when the fields cannot be used for any other crop: the well-established root system of the pigeonpea exploits water that is still available in the soil (ICRISAT 1977).

According to Sheldrake and Narayanan (1979), the perennial nature of pigeonpea means that during the reproductive phase, sufficient assimilants and other nutrients must be retained for the survival and continued growth of the vegetative structures. They think that the plants set fewer pods than they can fill because the pods do not set when the assimilants supply falls below a threshold. The feasibility of exploiting the perennial nature of pigeonpea to produce more than one crop from a single planting has been demonstrated at ICRISAT and the University of Queensland, Australia (ICRISAT 1977, 1978; Sharma et al 1978; Sheldrake and Narayanan 1979: Wallis et al 1979).

Two physiological factors seem to limit the seed yield in pigeonpea:

1) a prolonged phase of slow growth in the early growth stages, and
2) poor partitioning of dry matter into seed.

Farmers use the first limitation to their advantage by intercropping pigeonpea with fast-growing, early-maturing crops. The second limitation is more important and further study is needed to understand the physiological constraints that govern it.

GROUNDNUT

Arachis hypogaea L. (*Leguminosae,* Papilionoideae, tribe Aeschynomeneae) commonly known as groundnut, peanut, earthnut, or monkeynut, is usually grown as an annual crop. Groundnut is of South American origin, most likely from Eastern Bolivia, and is now grown throughout the tropics and subtropics to 40 N and S lat, where rainfall during the growing season exceeds 500 mm. It is very important in semiarid tropics, where about 2/3 of the world's groundnut is produced. Groundnut performs well in the dry temperature range between 24 and 33° C but can survive up to 45° C if adequate soil moisture is maintained. The most suitable soils for ground-

nut are well-drained, light, sandy loams. Groundnut does not tolerate waterlogging and harvesting is difficult in heavy soils because the soil sticks to the pods. Groundnut is generally considered a day-neutral plant although some work suggests that the sensitivity of growth parameters to day length is modified by temperature (Wynne et a1 1973). However, normal day length is not a critical factor influencing yields. Provided that the correct strain of *Rhizobium* is present in the soil, or the seeds are inoculated with it before they are sown, root nodules are abundant on the main and lateral roots. The nodules are globular and never lobed.

Photosynthetic rate

Groundnut has the C-3 photosynthetic pathway, but the observed rates of photosynthesis at high light intensities are comparable with those of C-4 plants. There is no evidence of light saturation in this crop as in other C-3 species at relatively low light levels (Pallas and Samish 1974, Hesketh and Moss 1963).

Photosynthetic response of groundnut helps to explain its adaptation to the wide range of light conditions in humid, semihumid, and and regions. Its high rate of photosynthesis at any light level indicates that it is one of the more efficient species in converting solar energy to fixed carbon. Genotypic variation in photosynthetic rate ranging from 16 to 30 mg CO_2/dm^2 per hour at a given light intensity seems to exist (Pallas 1973). Leaf photosynthetic rates in groundnut genotypes varied between 24 and 37 mg CO_2/dm^2 per hour (Bhagsari and Brown 1976a). Photosynthetic rate was positively, though weakly, correlated with percentage nitrogen and chlorophyll content of leaves. Stomatal frequency and photosynthetic rates were negatively correlated. A significant correlation was obtained (r = +0.79) between the rates of translocation and photosynthesis for 9 groundnut genotypes studied (Bhagsari and Brown 1976b).

The highest apparent photosynthesis (AP) was observed for leaf 3, the youngest fully expanded leaf on the branch, and the lowest AP for leaf 8. Leaf 5 exhibited an intermediate AP rate (Henning et al 1979). AP decreased with plantage; the decrease was 21% from day 80 to 110 and 58% from day 100 to 140. Leaves near the periphery of the groundnut plant contribute most during pod filling and the photosynthetic capacity of all leaves decreases during this period. There was a linear increase in net photosynthesis (Pn) for 4 out of the 5 genotypes tested when atmospheric CO_2 concentration was increased from 50 to 600 ppm (Bhagsari and Brown 1976c). Net photosynthesis of leaves of all the five genotypes was not closely related to boundary layer resistance nor leaf characteristics including chlorophyll content, stomatal frequency, leaf nitrogen content, or specific leaf weight.

The indeterminate nature of groundnut permits stem growth to absorb any surplus photosynthate; thus photosynthate utilization is not considered a good measure of photosynthetic rate (Williams et a1 1976). Cool temperature restricts vegetative growth and reduces photosynthesis. In warmer conditions, the development of the reproductive sinks does nor appear to alter photosynthesis (Williams et a11975a).

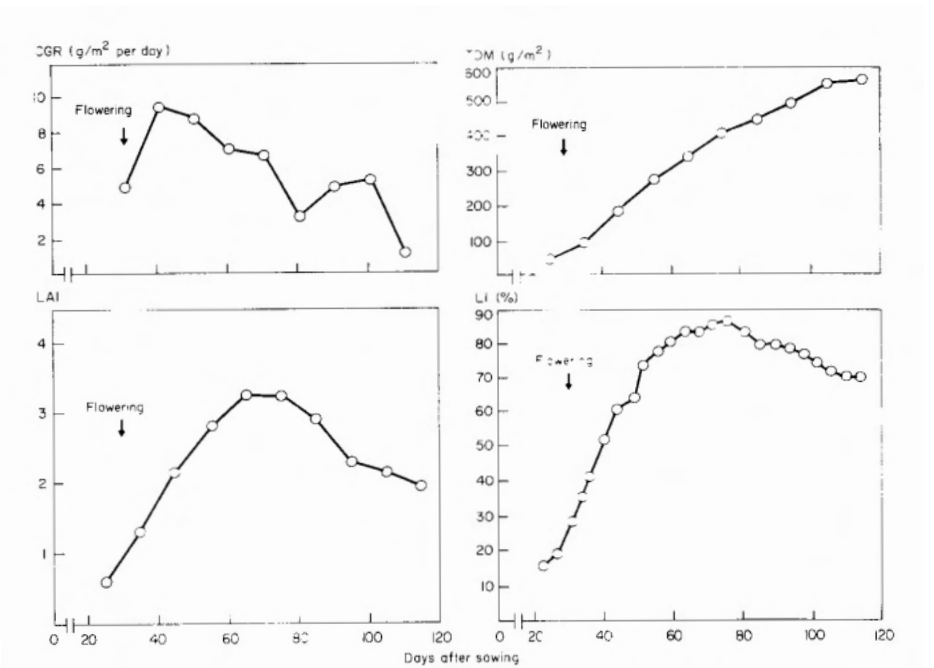
Khan and Akosu (1971) used ^{14}C to trace carbon transport in groundnut during the vegetative growth stage. Developing leaves assimilated most of the carbon while fully expanded leaves exported most of their carbon to developing apices of young

leaves and roots. Immediately following peg formation, the developing pods become the main sinks. At this stage assimilates are translocated mainly from the leaves of a branch to pods of the same branch.

Crop growth rate and dry matter production

Maximum CGR of groundnut are similar to those of other C-3 crop species (Enyi 1977, Williams et al 1975). Maximum CGR values ranging from 13 to 20 g dry matter/m² per day were obtained for four groundnut cultivars in Rhodesia (Williams et al 1975b). Samaru 61, a groundnut of about 125 days duration, grown at Samaru, Nigeria, produced 845 g dry matter/m^2. The maximum CGR value was 20.7 g dry matter/m^2 per day at about 60 DS (Kassam et al 1975). Dodoma Edible, another groundnut of about 125 days duration when grown in Morogoro, Tanzania, produced 1,550 g total dry matter/m^2, a mean CGR of 12.5 g dry matter/m^2 per day (Enyi 1977). The CGR of 5 groundnut cultivars grown in Florida, USA, did not differ significantly; their pooled CGR was 19.1 g dry matter/m^2 per day (Duncan et al 1978).

At ICRISAT Robut 33-1, a groundnut of about 115-day duration, produced 568 g total dry matter/m^2. The maximum CGR was 9.5 g dry matter/m^2 per day (Fig. 3). In this cultivar flower initiation occurs at about 30 DS and abundant flowering continues until 70 DS. Initial CGR increased rapidly, reached a maximum at about 35 DS, and then gradually declined. This pattern was complicated to some extent by



3. Crop growth rate (CGR), leaf area index (LAI), total dry matter (TDM), and percent light interception (LI) in groundnut Robut 33-1 on a medium-deep Alfisol at ICRISAT, Hyderabad, India (M. S. Reddy, unpubl.).

leaf losses of unknown magnitude that lowered apparent CGR values late in the season. CGR also declined because of vegetative growth rate reductions. The rate at which the kernel component continued to contribute to CGR appeared unaffected by the decline in the leaf area.

A close and positive relation between CGR and grain yield - GY = 34.37, CGR = 306.93, and r = 0.982 - was reported by Enyi (1977). The relation between the CGR and LAI was linear; CGR increased with increasing LAI between LAI of 1 and 4.2 (CGR - 43.86, LAI - 9.75, and r = 0.881). Williams et al (1975a) found a poor relation between the yield and CGR, total dry matter, or LAI presumably because of variable growth distribution between vegetative and reproductive components.

Duncan et al (1978) concluded that selection for higher yield in groundnut has not resulted in corresponding increases in CGR. A large part of the yield differences in groundnut cultivars with nearly the same CGR values is associated with differences in partitioning of daily photosynthate to fruits. The duration of the transition from vegetative to reproductive growth, and the proportion of growth going to reproductive components vary considerably with temperature and variety (Williams et al 1975a,b). The distribution of assimilates between vegetative and reproductive components is important because any change in this distribution that favors reproductive growth under the same growth conditions may result in greater total pod growth rate and, therefore, higher yields. This greater pod growth rate should also allow a greater pod initiation rate, and decrease the losses of yield and quality that usually occur as a result of the indeterminate pod production pattern.

Leaf area index

The LAI of Robut 33-1 increased gradually. reached a maximum of 3.3 around 65-75 DS, and then declined gradually to 2.0 at harvest (Fig. 3). Maximum LAI values ranging from 4.5 to 6.2 were achieved with 4 groundnut cultivars in Rhodesia (Williams et a1 1975b). The development of leaf area differed considerably and appeared to be independent of branching habit. Kassam et a1 (1975) observed a maximum LAI of 5.5 at about 70 DS in Samaru 61 (125 days duration) grown at Samaru, Nigeria. The LAI decreased to 1.5 at harvest. Duncan et a1 (1978) reported that the LAI continued to increase to more than 7.0 in some cultivars, but because light interception appeared complete at about LAI 3.0, further increase in LAI was assumed to have no measurable effect on CGR. Dodoma Edible, grown at Morogoro, Tanzania, attained a maximum LAI of 5.6 about 80 DS and decreased to 0.6 LAI at harvest (Enyi 1977). There was a positive and linear relation between LAD and grain yield (GY = 33.97, D = 458.03. and r = 0.853).

Florigiant groundnut in growth chambers has larger leaf area for the 34/30° C and 30/26°C day night temperatures than for the 26/22°, 28/22°, and 18/14°C (Cox 1979). The optimum average temperature for the maximum leaf was about 30° C—slightly higher than that of flowering and about 2°C above that for dry weight accumulation.

Yield and other yield components

Groundnut pod yield per unit area depends on the number of pods per unit area and weight per pod. The number of pods depends on the number of pegs and pods

produced within the time available for filling. The pod growth rate and development to mature kernel depends on the supply of carbon and on temperature. Pod yield in groundnut is also affected by variety, spacing, fertilizer, soil moisture, and soil type.

Groundnut yields are reasonably high considering the conditions under which the crop is grown. Worldwide average yields are 0.9 t unshelled nuts ha and are as high as 5.5 t/ha for the United States. Yields exceeding 9.6 t/ha have been obtained (Rachie and Roberts 1974, Hilderbrand and Smartt 1980). The shelling percentage is about 80% for early-maturing, bunch types compared with 60-75% for spreading cultivars.

Robut 33-1 at ICRISAT produced 2.21 t dry pods/ha (Table 3). Samaru 61 at Samaru, Nigeria, produced 1.6 t kernel/ha at the rate of 2.6 g/m^2 per day; the HI was 62.5% (Kassam et al 1975). Dodoma Edible at Morogoro, Tanzania, produced seed yield up to 2.72 t/ha (Enyi 1977). Pod yields ranging from 2.47 to 5.38 t/ha for 4 Florida cultivars in the US were reported by Duncan et al (1978). Groundnut's great ability to recover from adverse conditions such as drought and waterlogging gives the crop considerable performance stability.

Temperatureresponse

The effect of temperature on groundnut flowering and fruiting has been studied by several workers (Wood 1968, Cox 1979, Carlson et al 1975. Wynne et al 1973). Wood (1968) subjected a Spanish type, at early flowering, to 12 days of varying temperatures. Fruit production was greatest for plants held at a constant day/night temperature of 25° C. Plants were exposed to 30/25° C day night temperature regime before and after the 12-day treatment. The total dry matter accumulation of the Makulu Red cultivar grown in Rhodesia increased with increasing mean temperatures over a range from 17.9 to 23.3° C, but the yield of kernels was greatest at 20.1° C (Williams et al 1975). In phytotron studies, maximum dry matter accumulation of NC4 groundnut was achieved at 28° C during early growth, whereas older plants had maximum dry matter accumulation at 32° C (Carlson et al 1975). Cox (1979) conducted two studies in growth chambers to evaluate the effects of temperature on the vegetative and reproductive growth phases of the Florigiant cultivar. Day/night temperature regimes ranged from 34/30° to 18/14°C in the first study and from 34/30° to 22/18° C in the second. Early growth, determined by accumulation of top dry weight, was optimum at a weighted mean temperature of 27.5° C; essentially no growth occurred at 15.5° C. Rate of increase in pod weight, individual pod weight, and total fruit weight were greatest at 23.5° C. During early growth, the optimum temperatures for leaf area development and for flowering were above 28°C. In later stages the optimum temperature for flowering decreased to about 26°C.

Photoperiodism and day length response

Flowering induction in groundnut is generally independent of photoperiod and cannot be regulated by photoperiodic treatment. Tatenyi (1957) reported that groundnut is photoperiod sensitive, but only during the first 6 days after germination. The growth of groundnut plants of both subspecies of *A. hypogaea* responded to the effect of day length (Wynne et al 1973). Plants grown under short days (9 hours) produced pegs but only 31.2% of the flowers produced pegs when the plants

Table 3. Growth duration, yield, and yield components of Robut 33-1 groundnut cultivar grown on a mediumdeep Alfisol at International Crops Research Institute for Semi-Arid Tropics, Hyderabad, India (av of 3 seasons).[a]

Days to initial flowering	30
Initial flowering to pod formation (days)	40
Pod development and maturity (days)	45
Total growth duration (days)	115
Total dry matter (t/ha)	5.7
Pod yield (t/ha)	2.2
Total dry matter (kg/ha per day)	50
Pod yield (kg/ha per day)	19
Harvest index (%)	39
Shelling percentage	58

[a] M. S. Reddy, unpubl.

were grown under long days. Three groundnut lines and three F_1 hybrids grown under a 9-hour day were smaller but produced more fruit than when they were grown under a long-day treatment (9 hours of light plus a 3-hour interruption of the dark period). Most hybrids showed greater heterotic response for fruit yield under short days than under long days (Wynne and Emery 1974).

Solar radiation

Light interception in Robut 33-1 at ICRISAT was measured by tube solarimeters throughout the growing season. Interception increased gradually and reached a maximum of 87% by about 75 DS and declined gradually to 70% at harvest (Fig. 3). The total light energy intercepted by this crop was 29.04 kcall cm^2, and 1.9 mg of dry matter per kilocalorie was produced (Reddy and Willey 1979). Seasonal energy conversion of groundnut grown at Samaru, Nigeria, was 0.6% of the total incoming radiation (Kassam et a1 1975).

Solar radiation during early growth is an important yield determinant. Plants that were shaded to 80% reduction in direct solar radiation from emergence to beginning of flowering (4 weeks) had slower leaf development and lower CGR and reproductive development. At ICRISAT, artificial shade (70% reduction in solar radiation) 55 DS until final harvest did not produce any noticeable reduction in total dry matter or leaf area development; however, the study was conducted during the summer dry season when solar radiation values are especially high.

Water relations

Little research has been conducted on the water relations of groundnut, but the crop appears comparatively resistant to drought and is able to extract soil moisture under extreme conditions. In the sandy soils of Senegal, yields are reduced when soil moisture reaches 70% of its retention capacity. The permanent wilting point is estimated at 40% of that level (Dancette 1970). Moisture deficiency has a direct effect on yields, particularly when it occurs during flowering. Water requirements for groundnut grown on dry lands have been estimated as 500-600 mm/ season. During the first months of growth, daily requirements increase from 1.5 to 4 mm/day, reach 5-7 mm/day during peak growth, decrease to 4 mm by the 1st month of the

Table 4. Effect of moisture stress on yield, total dry matter, harvest index, and other yield components of Robut 33-1 on a medium-deep Alfisol at International Crops Research Institute for Semi-And Tropics, Hyderabad, India, 1980 summer.[a]

Treatment	Pod yield (t/ha)	Total dry matter (t/ha)	Harvest index (%)	Pods (no./plant)	100-kernel weight (g)
No stress (irrigated every 10 days)	2.7	5.9	45	16.2	35.92
Stress (irrigated every 20 days)	0.8	2.4	34	6.5	13.28

[a]M. S. Reddy, unpubl.

vegetative cycle, and finally drop to 2 mm daily during ripening (Ochs and Wormer 1959, Mantez and Goldin 1964). Crop water use of 120-day Samaru 61 in the Northern Guinea Savanna was reported at about 440 mm, corresponding to a crop water efficiency of about 520 g water/g total dry matter (Kassam et al 1975).

Robut 33-1, grown on a medium-deep Alfisol at ICRISAT during 1980 summer, produced 2.7 t dry pods/ha when the crop was irrigated every 10 days compared with 0.8 t dry pods/ ha from a stressed crop irrigated every 20 days (Table 4). During the 1978 rainy season crop water use of Robut 33-1 was 368 mm, corresponding to a crop water-use efficiency of 134 kg dry matter/ ha per cm water (Ready and Willey 1980).

Florunner groundnut, when subjected to a 70-day drought by rainfall-controlled shelters (from 36 to 105 days in a 140-day crop), produced only 1.4 t pod yield/ha compared with 5.2 t/ha in the no-drought treatment (Stansell and Pallas 1979). It seems that water stress does not reduce photosynthesis in groundnut as drastically as it does in some other crops (Klepper 1973). Transpiration rates of groundnut plants drought-stressed to wilting were 66% of maximum, and stomata were only partially open (Wormer and Ochs 1959). Diffusive resistance, determined with a porometer or from transpiration rates, vaned between 0.5 and 2.5 seconds/cm for control plants, while the diffusive resistance of stressed plants reached maximum values of 18-20 seconds/cm. Under a given degree of water stress, as indicated by relative leaf water content, leaf diffusive resistance and net photosynthesis were similar in five groundnut genotypes tested (Bhagsari et al 1976).

Yields in the semiarid tropics are lower (about 0.9 t/ha) than the yields (about 3 t/ha) in the developed world. The reasons for these large disparities in yields include pests, diseases, unreliable rainfall, and poor agronomic practices. Yields can be further improved by breeding for disease resistance because diseases are the greatest yield reducers. The crying need of the semiarid tropics farmers is for high-yielding varieties tolerant of various stress situations.

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POTATO

H. E. Haeder and H. Beringer

The actual maximum tuber yields (world record in the Netherlands of 40 t/ ha) remain far behind the yield potential, which is estimated at 100 t/ha. Attempts to increase tuber yield in the future should focus on improvement of storage capacity for photosynthates, i.e. number of tubers and tuber growth rate.

Present evidence suggests that endogenous phytohormones participate in tuber initiation and tuber growth. Nitrogen stress has been shown to decrease the gibberellin-to-abscisic acid ratio in stolon apices and to favor tuber initiation. Starch synthesis and starch accumulation might also be hormonally controlled; auxins and cytokinins appear to be primarily involved. Ample potassium nutrition, especially in the form of potassium sulfate, promotes the transport of photosynthates to the tubers and, hence, tuber growth. Sulfate application improves the attractiveness of tubers for assimilates and consequently favors the tuber-to-shoot ratio.

The activity of starch-synthesizing enzymes depends highly on tuber growth rate and differs between the apical and basal parts of the tuber. From the data now available it is impossible to decide if manipulation of enzyme activities will be a step toward the improvement of the harvest index of potato.

In 1978, the area under potato — 18.2 million ha throughout the world — corresponded to 1.3% of the total arable land. Ten years earlier, it was 1.5% (Table 1). The yield data are rough estimates of actual yields.

The cultivated potato *(Solanum tuberosum)* is grown all over the world. The highest average yields are obtained in countries with a moderate climate (Bodlaender 1963). In these countries day length is 13 to 17 hours during the growing season, average temperatures around 15°-18° C prevail, and rainfall or irrigation provides ample water supply. Under such conditions and the use of modern cultivation techniques, tuber yields of 40 t/ ha are now obtained on well-drained soils. But these actual yields are far behind the highest possible yields, calculated to be about 100 t marketable tubers/ha (Sibma 1977).

Such yields have in fact been recorded over several years at an experimental station in England (Evans 1977, Fig. 1). During all the years indicated, tuber yields were three times higher than the average national yield. Inputs in that experiment were high, and it is questionable whether those high inputs are economic. Neverthe-

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Table 1. Potato area and tuber yield in 1978 (FAO 1979).

Location	Area		Tuber yield (t/ha)
	Thousand ha	Arable land (%)	
World	18,167	1.3	15 0
Africa	514	0.3	8.7
North + Central America	759	0.3	26.3
South America	1,020	1.2	9.6
Asia	2,932	0.7	10.9
Europe	5,857	4.6	20.5
USSR	7,042	3.1	12.2
Oceania	44	0.1	22.6

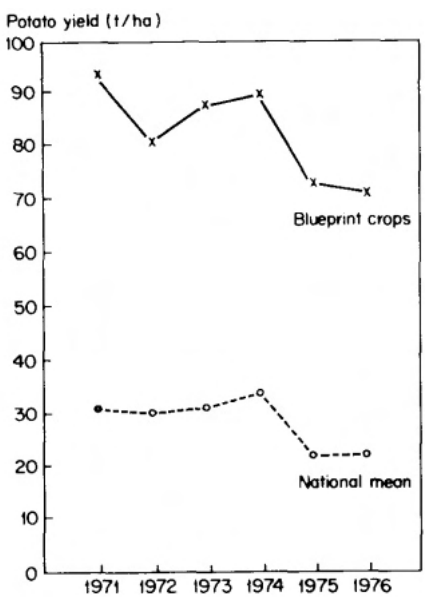
less the tuber yields prove that the estimated yield potential of 100 t/ ha is realistic.

Van den Zaag and Burton (1978) classify potato yields into three categories: actual (obtained normally), attainable (obtained with the best available growing (techniques), and potential (calculated yield maximum).

They suggest raising actual yield step by step. Better education and instruction to growers could probably increase yield 10-20% in a relatively short time. A quick breakthrough to the level of potential yield is, however, hardly possible. Long-term research is needed for a high realization of potential yield. The following section discusses three important factors that could diminish the gap between actual and potential yield.

ENCOURAGING CULM GROWTH

An important prerequisite for optimal light interception and consequently higher yields is early development of a full leaf cover. Presprouting of seed tubers is useful for reducing the time between planting and flowering. Growth regulation has also



1. Yields of blueprint potato crops at Stockbridge House experimental horticulture station (Evans 1977). Blueprint means "producing the yield of a crop at its maximum potential."

Table 2. Effect on potato yield of presprouting in light and of gibberellic acid (GA)[a] spray of seed tubers at planting (Marinus and Bodlaender 1978).

Treatment	No presprouting			Presprouting in light		
	Stems (no./10 m^2)	Tubers (no./10 m^2)	Tuber yield (t/ha)	Stems (no./10 m^2)	Tubers (no./10 m^2)	Tuber yield (t/ha)
Without GA	214	650	25.2	210	688	36.3
With GA	238	758	25.2	340	959	31.5

[a]GA concentration 22.5 mg/liter.

been tested and seed tubers have been sprayed, for instance, with gibberellic acid (GA) (Marinus and Bodlaender 1978) to accelerate early development (Table 2). The data demonstrate the beneficial effect of presprouting on tuber yield and tuber setting. GA treatment of seed potato increased the number of tubers and stems, especially in the presprouting treatment, and thus established a higher storage capacity for assimilates. Tuber yield, however, was less. Obviously other factors prevailed and limited growth of the individual tubers. The results of this experiment cannot of course be generalized.

Effects of exogenous growth regulators are dependent on the concentration used as well as on the phytohormonal balance within the tissue. Consequently the response to such a treatment varies between cultivars and between conditions of growth. Generally the correlation between tuber yield and number of stems per area is higher than that between tuber yield and number of plants/area (Dambroth 1977, Caesar et a1 1978). Carls (1978), when growing potato at different locations in Sri Lanka, observed a remarkable influence of temperature on stem number but no correlation between tuber yield and stem number (Table 3).

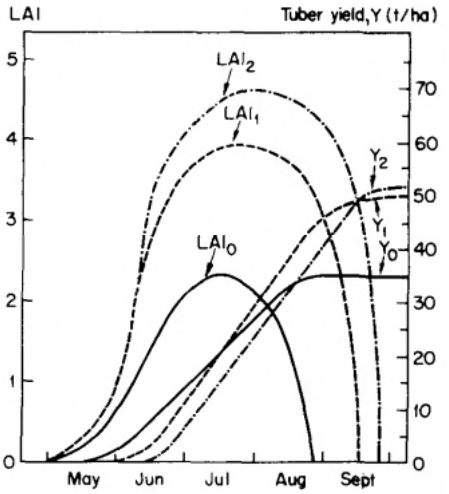
Culm growth can be stimulated by nutrient supply, which again favors leaf growth and a rapid attainment of an optimal leaf area index. Ivins and Bremner (1964) had already observed: the more extended the leaf area at the time of tuber initiation, the faster the rate of bulking and the higher the final yield (Fig. 2). About 6-8 weeks after emergence is the time of highest leaf growth.

For the grower, nitrogen application is the most practicable tool for regulating culm and leaf growth. Under temperate conditions of northwestern Europe it is

Table 3. Stem number and tuber yield at different locations in Sri Lanka (Carls 1978).[a]

Location	Stems (no./m^2)	Tuber yield (t/ha)
1900 m NN 10.7°-19.9°C min max	27.0	15.1
1200 m NN 15.7°-24.6°C min max	20.1	15.7
0 m NN 25.1°-30.°C min max	17.9	15.4

[a] Av of 4 varieties.



2. Correlation between leaf area index (LAI) and tuber yield (Ivins and Bremner 1964).

recommended that all fertilizer nitrogen needed by the crop be applied before planting (Hunnius et al 1978). According to Hunnius and Munzert (1979) up to 80% of the total nitrogen needed is taken up in the first 4 weeks after emergence. At the time of tuberization, the pool of inorganic nitrogen in the soil should be small. Then shoot growth would be diminished and most of the photosynthates produced could be used for tuber growth.

Generally a leaf area index of 4-5 might be sufficient for high tuber yields. Farmers try to achieve it by proper spacings and plant populations, which of course are affected by the environmental conditions. In field experiments done on 6 locations between 71° N. lat. with long days (Norway), and 36° N. lat. with short days (Tunis), Caesar et al (1978) examined the effect of 2 spacings (40,000 and 80,000 plants/ha) on the performance of early- and late-maturing varieties. Under short-day conditions in Northern Africa, a higher number of plants/ha was necessary to fully utilize incident light. Generally, narrow spacing yielded more tubers than wide spacing but less marketable tubers.

Under northwest European conditions about 0.4 kg culm dry matter per m^2 should be available in July to be sure that sufficient foliage is present in September for tuber production (Van den Zaag and Burton 1978). An extended productivity of the canopy in autumn is as important as the vigorous growth in spring. Generally, potato varieties possess only one of these desirable features. But now clones with both characteristics could be selected by Swiezynski et al (1978).

ENHANCING TUBER SETTING

The most critical and complex step in improving yield of potato is the setting of tubers. Generally, the older the plant the more prone it is to form tubers. Superimposed on the effect of age, the changes which occur in the stolon tip giving rise to tubers are hastened by low temperatures in the range 10-20° C, high light intensity, low nitrogen supply and short days. The requirement for short days is not strict.

Table 4. Number of stolons and tubers per stem (Wurr 1977).

Variety	Total		First node		Second node	
	Stolons (no.)	Tubers (no.)	Stolons (no.)	Tubers (no.)	Stolons (no.)	Tubers (no.)
Desiree	9.6	8.0	5.2	5.0	0.8	0.8
Pentland Crown	10.0	3.0	5.4	2.4	1.2	0.3
Maris Piper	9.6	4.8	4.7	2.3	1.2	0.7
S.E. mean	±0.25	±0.22	±0.17	±0.16	±0.04	±0.05

Generally early varieties show less response to photoperiod than late season varieties (Moorby and Milthorpe 1975).

With regard to physiological age, data by Wurr (1977) on tuber formation at different nodes of potato stems of three varieties are informative (Table 4). All test varieties had similar numbers of stolons per stem but different numbers of tubers. The range of nodes at which tubers are formed seems to control tuber distribution. More stolons were formed at the first node than at any other one of eight nodes. In the cultivar Desiree, practically each stolon had one tuber; in the two others, tuber numbers were half that of stolons.

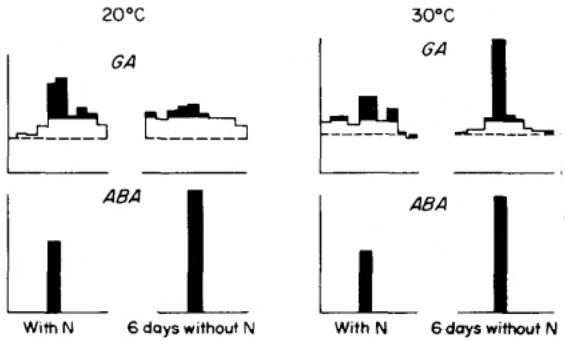
The physiology of tuber initiation is hardly understood. Nevertheless the analysis of phytohormones in plants during the last decade has contributed to a better understanding of environmental factors which might affect tuber setting. High temperatures as well as high nitrogen supply have been observed to inhibit tuber initiation.

This was verified in an experiment by Krauss and Marschner (1971). Use of only 5 liters nutrient solution per plant caused a faster depletion of nitrogen in the medium (Table 5). Consequently, growth was less, but tubers were initiated 45 days after the experiment started. In the other treatment no tubers set even within 100 days. This effect of nitrogen stress was assumed to be of hormonal character. In a subsequent experiment, the authors grew potato at 200 and 300 C, and withheld nitrogen supply in the nutrient solution for 6 days (Krauss 1978). Tuber setting was observed only in the nitrogen-stressed plants grown at 200 C. Unfortunately the original paper contains neither the units for hormone contents on the ordinate, nor the R_f *values* of the TLC plates on the abscissa (Fig. 3). Nitrogen stress increased ABA content at both temperature treatments. GA content dropped at 20°, but increased at 30° C because of interrupted nitrogen supply. High ABA contents and low GA-to-ABA ratios favored tuber initiation (Krauss 1978).

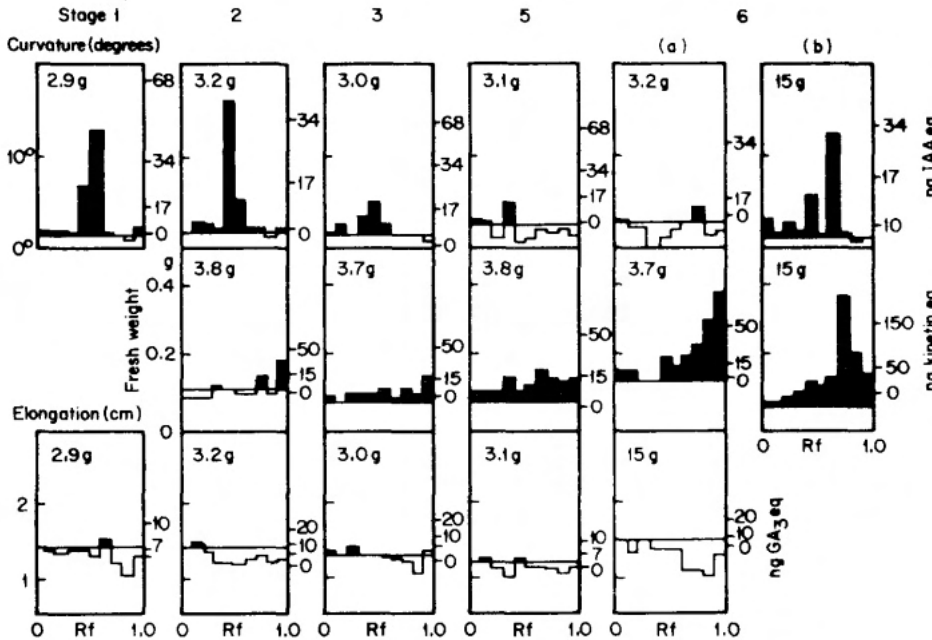
The interactions between phytohormones in tuber setting and tuber growth are definitely more complex than they might look. Obata-Sasamoto and Suzuki (1979),

Table 5. Influence of nitrate supply on growth and tuber setting (Krauss and Marschner 1971).

Nutrient solution		N uptake	Dry matter per plant		Days till tuber initiation
mM NO_3	liters/plants	(meq/plant)	Shoot	Root	
3.5	25	205	53.7	4.43	>100
3.5	5	144	26.5	2.23	45



3. Effect of nitrogen supply and temperature on abscisic acid and gibberellic acid contents in shoots of *S. tuberosum* (after Krauss 1978).



4. Progressive changes in contentsof auxin (IAA eq.), cytokinin (kinetin eq.), and gibberellin (GA_3 eq.) in stolon tips just before (stage 1), during swelling (stage 2), and in young tubers of different diameters: 0.2-0.5 cm (stage 3), 2.5 cm (stage 5), and 3.5 cm (stage 6) (Obata-Sasamoro and Suzuki 1979).

who covered auxins and cytokinins, observed a particularly high auxin content in the swelling stolon tips (stage 1 and 2) and a low one at later stages of tuber growth. The histograms (Fig, 4) are subdivided into R_f fractions. The cytokinin activity was initially low but increased as the tuber continued to grow. GA could not be detected. According to the same authors, the subsequent decrease in auxin level and the rapid increase in cytokinin level promote the activities of starch synthesizing enzymes. All these results on endogenous hormones and their involvement in tuber setting need further corroboration.

ENHANCING AND EXTENDING TUBER GROWTH

The main cause of the great gap between actual and potential yield seems to be water shortage during tuber growth (Van den Zaag and Burton 1978). Interaction between

water supply and tuber yield was observed by Roztropowicz (1978) (Table 6). Yield increased up to 300 mm rainfall. But more important than the amount is equal distribution. During tuber growth, potato needs 20-30 mm rainfall/ week and for maximal growth rates rainfall interruptions should not be longer than 2 weeks (Hunnius 1972). Therefore the recommendation is to breed potato cultivars with deep and widespread root systems (Van den Wal et al 1978).

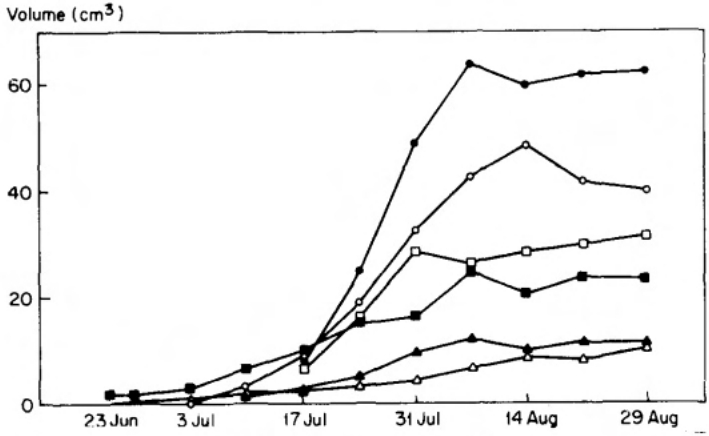
Moorby and Milthorpe (1975) calculated maximal tuber growth rates of 25 g/m^2 per day. Van den Zaag and Burton (1978) reported an average growth rate of 7.2 g/m^2 per day. These authors emphasize that daily tuber growth rate is far below optimal for much of the growing season. When studying the growth rates of several individual tubers in a single plant, Wurr (1977) measured average growth rates of 1.0 to 3.3 ml/day, but the growth patterns of the individual tubers were very different (Fig. 5). Some tubers followed a sigmoid growth curve, some grew linearly, and some showed periods of interrupted growth. This difference between individual tubers, which might be due to competition for assimilates or to hormonal influences, is the most serious difficulty in studying yield physiology in potato. For efficient conversion of light into chemical energy during photophosphorylation, for CO_2 assimilation as well as for translocation of assimilates in the phloem, potassium is an important nutrient (Pfluger and Mengel 1972, Peoples and Kock 1979, Mengel and Haeder 1977). This has also been demonstrated with potato (Fig. 6). In a water culture experiment, plants with different potassium levels were supplied with $^{14}CO_2$ for 24 hours at 6 weeks after flowering (Haeder et al 1973). There was an increase in harvest index expressed by the tuber-to-shoot ratio with increasing potassium nutrition. This effect was also reflected in the pattern of ^{14}C distribution. In plants supplied with 10 meq k liter, 80% of the ^{14}C assimilated during 24 hours was translocated to the tubers, whereas in plants with the lowest K supply only 40% was deposited in the tubers. The high percentage of ^{14}C in tubers with highest K supply might not only be a result of the higher harvest index or sink but also an indication that potassium stimulates the flow of assimilates into the storage tissue.

Apart from yield the nutritive quality of tubers is also important. Potato is basically a major source of starch. In countries where it is a staple food, it was, in former times, a source of Vitamin C. Ascorbic acid as well as citric acid and malic acid can be increased by ample potassium nutrition (Muller 1965).

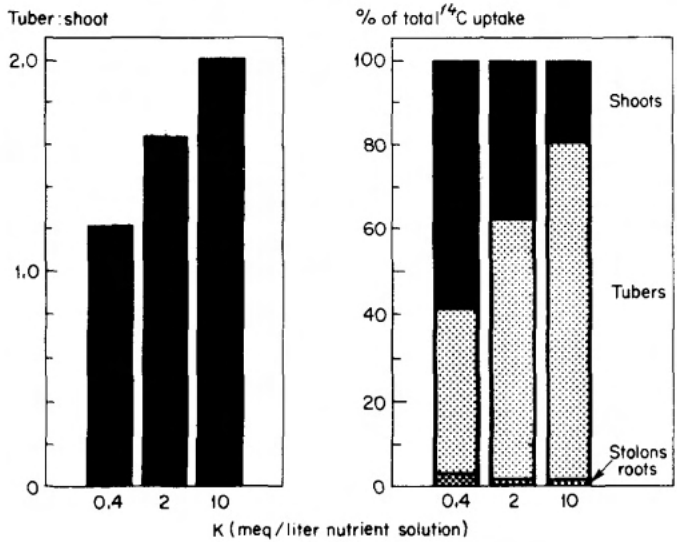
Many field experiments have demonstrated a beneficial effect of sulfate of potassium as compared to muriate of potash (Table 7). The high starch content in the sulfate treatment could be due to a higher dry matter percentage of tubers or to

Table 6. Total rainfall during vegetation period and potato yield (Roztropowicz 1978), av of 350 experiments during 3 years.

Total rainfall (mm)	Tuber yield (t/ha)
<150	23.9
150-200	25.9
200-250	21.8
250-300	28.3
300-350	26.3



5. Growth of some tubers on a single plant (Wurr 1977).



6. Effect of different K supply on tuber-to-shoot ratio and total uptake of ^{14}C during 24 hours and percentage distribution of ^{14}C in the plants 6 weeks after flowering (Haeder et al 1973).

stimulating effects of potassium sulfate on assimilate translocation and on starch synthesis in the tubers. To test the effect of potassium sulfate on assimilate translocation (Haeder 1975), potato was grown in nutrient solutions containing potassium either as Cl^- or SO_4^-. Six weeks after flowering $^{14}CO_2$ was applied and its distribution within 24 hours was determined (Table 8). Plants of both treatments assimilated nearly the same amount of $^{14}CO_2$. In the sulfate treatment, however, 39% of the label was translocated to the tubers. In the Cl^- treatment, only 21% was deposited in the storage tissue. Replacing KCl by K_2SO_4 generally leads to higher organic acid content in plant dry matter. For starch synthetase from maize kernels a

Table 7. Effect of potassium sulfate and potassium chloride on yield and starch content of potato tubers (Terman 1950).

Treatment	Tuber yield (t/ha)	starch (%)
KCl	28.1	13.3
K_2SO_4	28.3	14.6
1/2 KCl + 1/2 K_2SO_4	28.7	13.8

Table 8. Influence of Cl^- and $SO4^{--}$ nutrition of potato on tuber yield and distribution of assimilated $^{14}CO_2$ [a] (Haeder 1975).

	K (4 meq/liter) +Mg (6 meq/iter) offered as	
	Cl^-	SO_4^{--}
Tuber yield (g dry matter/plant)	153	194
Starch (% fresh tuber)	12.4	13.3
Total ^{14}C (µCi/Pl.)	124	133
^{14}C-distribution (% of ^{14}C)		
Leaves	37	34
Stems	38	23
Tubers	21	39
Roots	4	4

[a] $^{14}CO_2$ applied at 6 weeks after flowering and distributed within 24 h after $^{14}CO_2$ exposure.

requirement of >0.1 M citric or malic acid in the incubation mixture has been reported (Boyer and Preiss 1979). E trapolating this result on maize to the situation in potato tuber, it remains a speculation if SO_4 nutrition might improve starch content via higher concentrations of organic anions within the tuber and higher rates of starch synthesis.

Starch synthesis in tubers is corroborated by several enzymes. ADPG-pyrophosphorylase, ADPG-starch synthetase and phosphorylase have all been found to be stimulated by 100 mM K (Hawker et al 1979). But to what extent might enzyme activities control or even limit tuber growth, i.e. sink capacity? Enzyme activities in tubers vary between different parts of a tuber and are related to tuber growth rate (Mares and Marschner 1980, Tsay and Kuo 1980). But growth rates of tubers again differ from each other as already mentioned, and this question remains unanswered.

CONCLUSION

The data in this paper are sufficient evidence that there is a great chance for improving tuber yield of potato. Farmers should be trained to use the best husbandry techniques suitable to the prevailing conditions of the locations to reach attainable yield. Quick attainment of a sufficient leaf area index, high tuber setting, and higher tuber growth rates are the objectives.

More scientific effort is necessary to reduce the gap between the attainable and the potential yield.

Whether source or sink is more important for improving tuber yield still remains to be elucidated. The fundamental processes for tuber setting and tuber growth need more attention, especially the involvement and participation of phytohormones. Results from physiological studies will eventually lead to the application of synthetic growth regulators and supplement the efforts of plant breeders to obtain cultivars with high yields and good quality.

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SWEET POTATO AND YAM

S. K. Hahn and Y. Hozyo

Sweet potato *Ipomoea batatas* (L.) Lam. is a dicotyledonous plant native to Central America. It is a perennial plant but is treated as any annual with a normal growing period of 3 to 7 months, depending on growing areas and cultivars. The major economic part is the tuberous root (tuber). Sweet potato plants are propagated in temperate areas by slips or shoot cuttings from the tuberous roots and in the tropics by slips from the growing plants.

Sweet potato is grown over a wide range of environmental conditions between 40° N and 40° S lat., and from sea level to 2,300 m altitude (Hahn 1977a). Yields are reasonable even in soils of low fertility and pH. Although sweet potato is grown in relatively high rainfall areas, it has good drought tolerance. Average yields of about 20 t fresh weight/ha (6 t dry yield) in 4 to 5 months have been recorded in several countries. About two-thirds of the world production is in Asia.

Yams are monocotyledonous plants in the genus *Dioscorea,* which contains between 300-600 species (Coursey 1967, Ayensu and Coursey 1972). The most important edible species from Africa are *D. rotundata* Poir (white yam, white guinea yam), *D. cayenensis* Lam. (yellow yam, yellow guinea yam), and *D. dumetorum* (Kunth) (trifoliate yam, bitter yam). Edible species from Asia are *D. alata* L. (water yam, white Lisbon yam), *D. bulbifera* L. (aerial yam), and *D. esculenta* (Lour.) Burk (Chinese yam, lesser yam). *D. trifida* L. (cush-cush yam) is from the Americas. About two–thirds of the world's production comes from Africa (West Africa particularly).

Yams are adapted to areas of fairly high rainfall and with a distinct dry season of not more than 5 months. Because their growing period exceeds 5 months, yams are not grown in areas with rainy periods of less than 5 months.

The phenology of yam species shows an annually repeated growth cycle of 5 to 10 months and dormancy for 2 to 4 months. These two phases correspond approximately to the wet and dry seasons (Coursey 1967). The underground stem tuber is the economically important part of the plant and propagation is by means of these tubers (300-600 g/set). Cultivated yams produce vines 2-7 m long, depending on the species. The vines are supported by poles 2-4 m long.

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In sweet potato and yams, the plant part that is of economic importance is vegetative, asexually reproduced, and grows underground (except *D. bulbifera*), but some yam species may bear bulblets. Yield-forming processes are rather simple compared to those in cereals. The yield-forming period is about 100-180 days for sweet potato and 180-240 days for yam. The economic yield is predominantly starch.

This review aims to identify the physiological characters that determine yield potential of sweet potato and yam, examine how they are interrelated and how they interact with the environment, and consider how the information can be used in drawing up specifications for improved cultural practices and cultivars.

SWEET POTATO

The caloric production per hectare from the edible part of sweet potato in Japan is 2.94×10^7 kcal/ha for an average fresh yield of 21 t/ha. This is 1.9 times that of rice with an average yield of 4.5 t/ha (Murata et al 1976). Caloric production depends mainly on the photosynthetic capacity of the crop after tuber initiation, the duration of that capacity, the amount of assimilates available for tuber growth, the speed of translocation and amount of photosynthates translocated, and the ability of the roots to store the carbohydrate.

Crop growth rate

Crop growth rate (CGR) of sweet potato in the natural population is lower than that of other crops and with a C-3 photosynthetic pathway (Murata et al 1976) because of low photosynthetic activity per unit leaf area and poor light interception by the thin layer of horizontally displayed leaves.

The maximum dry matter yield of 120 g/m^2 per week obtained in Japan (Tsuno and Fujise 1963) is rather low. Dry matter yield production can be expressed as a product of net assimilation rate (NAR) and leaf area index (LAI). Here, NAR and LAI are called components of dry matter yield production. Each will be discussed in relation to dry matter yield production.

Source-sink relation

The total dry matter yield of the sweet potato tuber depends on photosynthetic activity of the leaf canopy source, the capacity of the plant to translocate assimilates from the source to the tubers sink, and the capacity of the tubers to accommodate or capture assimilates. Increasing those activities and maintaining them for longer periods would lead to higher economic yield. Wilson (1972) reported that source and sink strength each consist of two major components — size and activity. Clarification of the relative importance and relation of these source-sink characteristics is the first priority in analyzing the physiology of yield.

With the use of reciprocal grafts between an inherently high yielding sweet potato cultivar and a related species (*I. trifida*) that produces virtually no tuber yield, the speed and rate of growth of tubers and the relation of photosynthetic activity with starch synthesis and with total dry matter yield production were studied on the basis of differences in amount and ability of tuber development, photosynthetic activity, dry matter production procedures, and tissue-chemical properties (Hozyo and Park

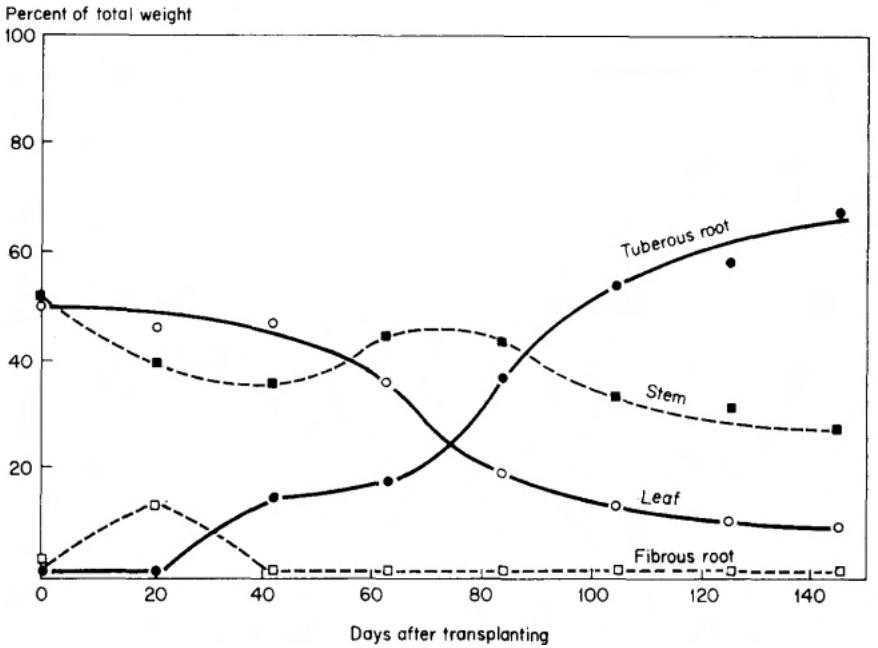
1971; Hozyo and Kato 1973, 1976a; Kato and Hozyo 1974, 1978). Dry matter yield production of the stock cultivar with good sink was much higher than that of the related species with poor sink irrespective of source, and photosynthetic activity decreased when the related species was used as stock. Tissue-chemical examination showed that the scion did not significantly affect the starch synthesis in the tuber. This indicates that the tuber sink affects photosynthetic activity in the source (leaf blade) and ultimately affects dry matter production.

The reciprocal graft experiment with five sweet potato cultivars showed that early and late tuber developing abilities of the cultivars were determined by their stocks (sinks) because of their genetic characteristics, but not by scions (sources) (Hozyo et al 1971). A series of reciprocal graft experiments between *Ipomoea* species (Hozyo and Park 1971; Hozyo and Kato 1973) and closely related *Ipomoea* species (Hozyo and Kato 1973), and an experiment on the physiology of tuber development (Hozyo 1973) revealed that tuber developing ability affects the photosynthetic activity in the source. Cultivars with large sink capacities showed greater sink responses to source than cultivars with poor sink capacities. Cultivars with the greater source potential showed the greatest source response to sink (Hahn 1977b).

The question then arises: "Does sink affect only photosynthetic activity of source. or does it also affect translocation of photosynthates?" Graft experiments showed that the tuber developing ability affects translocation speed (Hozyo and Kato 1976b). As that ability decreased in the graft with *I. trifida* stock. the translocation speed was reduced by one-third, and the translocation coefficient decreased 43 times compared with the graft with a cultivar as stock (Kato and Hozyo 1978). These results suggest that sink has a regulatory mechanism in dry matter yield production. Sink capacity in sweet potato affects yield more than the potential source (Hahn 1977b).

Dry matter accumulation provides some indication of the competitive ability of a sink to *attract* assimilates relative to other sink regions. *Mobilizing ability* seems a more applicable term to describe the resultant accumulation of dry matter by a sink within the competitive framework of a whole plant system. The various growth and storage centers of the plant activity compete for assimilates. Each center has a competitive or mobilizing ability whereby it competes with other centers to attract assimilates. The mobilizing ability of a sink is a measure of its ability to import assimilates and is expressed by the absolute growth rate of the whole plant or plant part being investigated (Wareing and Patrick 1975).

In sweet potato, which is morphologically vegetative, the accumulation of dry matter in storage organs (sink), and continuous internal competition for assimilates and other essential nutrients between the vegetative and the economically important parts complicate the description (Bunting 1971). When there is keen competition between shoot and root for assimilates, the shoot system has the advantage (Wareing and Patrick 1975). In sweet potato, growth of both tubers and shoot is parallel for a long period; therefore, there is keen competition between them during almost all of the growth period (Fig. 1). To reduce internal competition, a rapid shoot development to obtain full photosynthetic structure at an early growth stage, before tubers develop, is desired. Further growth of fully developed shoots should be minimized so they do not have an unnecessary competitive advantage over the tubers. After

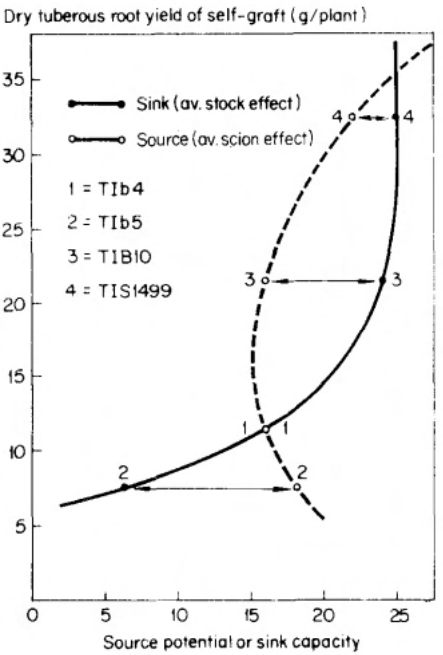


1. Relative changes in dry matter of plant parts of sweet potato.

formation of storage organs, competition should be in favor of tubers without reducing too much the size and activity of shoots, particularly leaves. After obvious tuber development, there was compensatory correlation (= -0.89 to -1.00) or stress (Thomas et al 1971b) between leaf and tubers, in which a decrease in leaf dry weight followed an increase in tuberous root dry weight. This negative relation indicates competitive inhibition of leaf structure development as storage roots further develop. As the tubers increase in size, branch and leaf production gradually cease and the existing leaves senesce, decreasing the total leaf area. Leaf senescence results mainly from lack of the substrate supply to potential growing parts of shoot and absorbing roots. This in turn probably results in decreasing potential rates of photosynthesis and of tuber growth. Eventually tuber growth stops.

High stem-leaf ratio at a later growth stage is an indication of excessive nonproductive shoot growth, which results in lower light interception, lower NAR, undesirable partitioning of photosynthates, and death of lower leaves (Tsuno and Fujise 1963). There should be no more stems and petioles than are required to support the adequate leaves in an efficient arrangement and to supply sufficient minerals, nutrients, and water.

Physiological and morphological initiatives are interdependent; they change with stage of growth. At the early growth stage of sweet potato, shoots (including leaves and stems) take the physiological and morphological initiatives from the tuberous roots, but at the later growth stage (from 80 days after planting) tubers begin growing appreciably and may take the initiative from the shoots. Early transfer of the morphological initiative from shoots to tuberous root, before shoots develop to their full capacity, results in lower tuber yield.



2. Relation between source potential and sink capacity reflected in dry tuberous root yield of self grafts.

In the reciprocal graft experiment, the dry tuber yield of the self-graft was plotted against source potential (mean scion effect) and sink capacity (mean stock effect) to examine the source-sink relation, the effect of source potential and sink capacity on yield, and the balance between source potential and sink capacity (Hahn 1977b). Sink capacity appeared more important than potential source in determining dry tuber yield only within certain limits (Fig. 2). It seems that an active source coupled with a large tuberous root sink capacity is desirable, and that there must be a balance between source potential and sink capacity at a higher level to obtain higher economic yield. The balance between source potential and sink capacity will certainly change with changes in the growth stage and environmental conditions. The balance needs to be maintained longer after appreciable tuber growth by minimizing undesirable competition.

Source

Leaf area. Variation in the total leaf area of a plant depends on changes in leaf number and leaf size. Leaf number depends on the number of growing points, the length of time they produce leaves, the rate of leaf production during the period, and the lifetime of the leaves. Variation in leaf size may arise from environmental effects on cell division or on cell expansion (Watson 1952). The result is change in leaf area and leaf area duration.

In sweet potato, the developmental sequence that gives rise to changes in leaf area with time is much simpler than in cereals. Sweet potato plants continue to produce new leaves until harvest. The change in leaf area thus depends almost entirely on the activity of apical meristems and on the growth and longevity of the leaves they

produce. To maintain the necessary leaf area for maximum rate of dry matter production within the plant as a whole, as high a proportion of assimilates as possible should be plowed back into the apical meristem and leaf tissue.

Leaf area index. The optimum LAI of sweet potato in the natural population is lower than that of cereals because the creeping shoots crowd the leaves in a thin layer, resulting in more mutual shading. In Japan, the optimum LAI was reported as 3.2 m^2/m^2 at average solar radiation of 430 gcal/cm^2 per day; maximum dry matter yield production was 120 g/m^2 per week (Tsuno and Fujise 1963). In the West Indies, the maximum LAI of a cultivar was 4.0 with fertilizers and 3.0 when none were applied. During the early dry season in Nigeria, the maximum LAI was 2.9 with no fertilizer.

LAI was twice as high for plants grown on rich soils, especially those high in nitrogen, than for those grown on poor soils throughout the growth stage (Tsuno and Fujise 1963). Sweet potato cultivars showed different LAI responses to nitrogen application. The cultivars that showed a low response to nitrogen had high areas; those with high response had low leaf areas. In the low-response cultivars the application of nitrogen raised the leaf area above the optimum level, with resulting mutual shading of leaves and reduced photosynthetic activity (Haynes et a1 1967).

Variation in plant spacing also influences LAI. Cultivars with high leaf area grown at close spacing experience mutual shading and low yield results. On the other hand, the cultivars with low leaf area may be grown at a closer spacing and still be expected to produce a higher yield (Haynes et a1 1967). The cultivars adapted to the high altitude (2,000 m) and poor soils in Rwanda, Africa, and Peru and Central America where sweet potato is grown at a high plant density (6-8 plants/m^2) have small leaf area. Such cultivars may have the advantages of drought and cold tolerance in addition to better light interception and less plant competition. LAI varies with cultivar under the same environmental conditions.

Net assimilation rate. The extent to which dry matter production could be increased by increase in leaf area depends on whether NAR is affected by increase in LAI. The NAR of plants grown on fertile soil was low although their LAI was increased compared to that of plants grown on poor soil. The low NAR was due to reduced light interception rate because of mutual shading of leaves (Tsuno and Fujise 1963).

In Japan, the maximum photosynthetic activity was 20 mg CO_2/dm^2 per hour (Fujise and Tsuno 1962). Photosynthetic activity increases linearly up to the light saturation point of 0.8-0.9 g cal/cm^2 per minute but does not increase substantially at higher light intensity. The light saturation point for each individual leaf was around 30 klux. This is expected to increase in the natural population because of decreased light interception due to the reduced light transmission rate with increasing LAI.

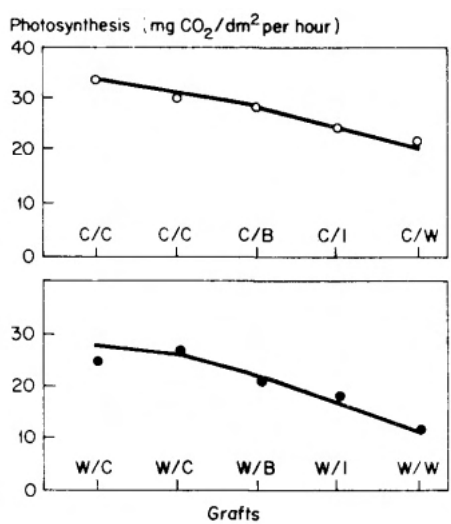
Leaf orientation influences the light transmission rate and thus the light interception rate. When LAI is large, erect leaves should be an advantage. Tsunoda (1959 cf. Wallace et a1 1972) found that sweet potato cultivars with good fertilizer response had relatively thick, small leaves.

Potassium ion (K^g) increased photosynthesis and translocation of photosynthates. The optimum temperature for photosynthesis was 23° -33° C, relatively high for a C-3 plant. Cultivars did not differ much in photosynthetic activity.

Respiration in the leaf is necessary for dry matter yield production, but respiration in the stem, which is nonproductive, should be as small as possible. The average respiration rate of leaves during the growing period was 50% of that of the whole plant; that for the tubers was 20-30% (Tsuno and Fujise 1964d). The respiratory rate per unit dry matter was 50-80% for the stem and 10-20% for the tubers (Tsuno and Fujise 1963).

Photosynthetic activity and CO_2 diffusion resistance. The photosynthetic activity and CO_2 diffusion resistance of leaf blades also relate to dry matter yield production. The photosynthetic activity referred to is apparent photosynthetic activity. The measurement of photosynthetic activity is affected by airflow rate, form and structure of the assimilation chamber used, leaf area, temperature, relative humidity, and light intensity. Because those factors affect CO_2 amount, CO_2 diffusion resistance, and stomatal opening and closing, photosynthetic activity must be measured with extreme care. Taking into account such factors Hozyo and Kato (1978) measured photosynthetic activity by using a specially made instrument (Fig. 3). At 25° C, 50% relative humidity, light intensity of 0.482 cal/cmo per minute, and airflow of 8 liters/minute, the photosynthetic activity was 30-35 mg CO_2/dm^2 per hour at the initial tuber development stage (early growth stage), and 25-30 mg CO_2/dm^2 per hour at the advanced (late growth stage) tuber development stage (Hozyo et al 1979, 1980). The effect of stomatal resistance on photosynthetic activity was less than that of methophyll resistance (Hozyo et al 1979, 1980). Photosynthetic activity and CO_2 diffusion resistance are closely related to nitrogen content and carbohydrate concentration in the leaf blade. The photosynthetic activity of sweet potato appears to be similar to that of other C-3 crop plants.

Leaf area duration. The leaf area duration (LAD) of a crop is a measure of leaf area produced per unit land area throughout its life, hence of its opportunity for assimilation. At constant NAR, dry matter production of different crops would be proportional to LAD (Watson 1952). The LAD of a cultivar in Japan was 54 weeks. High fertilizer application reduced LAD.



3. Photosynthetic activity in grafts of sweet potato. W = wild type (related *Ipomoea* species), C = cultivar, B = first back cross of interspecific hybrid of cultivar × wild type to cultivar, I = interspecific hybrid, cultivar × wild type.

Table 1. Translocation rate of ^{14}C-photosynthate toward shoot apex and underground organ in different graft types.[a]

	Translocation rate (cm/h)			
	C/C	C/W	W/C	W/W
Toward shoot apex	48	42	46	31
Toward underground organ	128	31	31	21

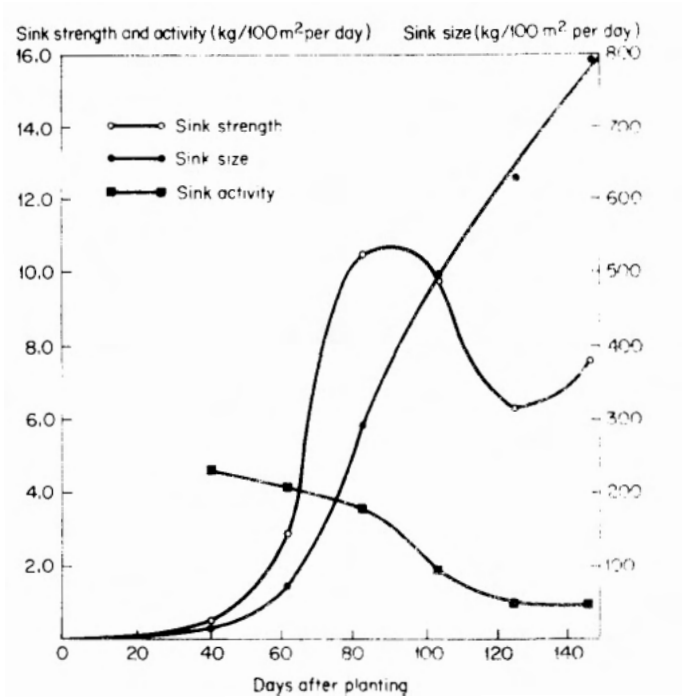
[a]C/C = cultivar on cultivar, C/W = cultivar on wild type, W/C = wild type on cultivar, and W/W = wild type on wild type.

Translocation of photosynthates. The partitioning of photosynthates into the organs is of economic interest. The primary factor affecting such partitioning is translocation. A radioactive tracer experiment with ^{14}C showed 1) a translocation polarity of the photosynthates toward underground parts as early as the tuberous root initiation stage, 2) accelerated translocation speed, and 3) an increase in the amount of photosynthate translocated as tuber development advanced (Kato and Hozyo 1974). The cultivar Okinawa 100 showed a translocation speed of 48 cm/hour toward the shoot apex and 128 cm/hour toward the tuber (Kato and Hozyo 1978). The translocation coefficient was $2.81 \times 10^2/cm^2$ per second toward the shoot apex and $57.62 \times 10^2/cm^2$ per second toward the tuberous roots (Table 1, Kato and Hozyo 1978).

Sink

The ability of the sink to accept assimilates is a major factor leading to high economic yield; the major aim, therefore, would be to maximize the relative growth rate of the sink (Wilson 1972). The physiological basis of the sink is a frontier for understanding yield formation (Watson 1968). Watson (197 1) defined sink capacity as the integral of sink strength over the period of its activity. Wilson (1972) proposed the approximation: sink strength = sink size × sink activity. That, in turn, could be related in terms of total dry matter to absolute growth rate= dry weight × relative growth rate (Fig. 4). Strength is the absolute rate of change in weight of a substance for a plant part, and size is measured by weight, area, or some other appropriate characteristic. Waering and Patrick (1975) define sink activity as the rate of uptake or incorporation of assimilates per unit weight of sink tissue, and sink size as total dry weight.

Morphological components of yield. The morphological components of sweet potato yield are the number and size of tubers. The size component could be further divided into either volume (fresh weight) or density (dry matter percent or content). The physiological and morphogenic processes involved in differentiation and development of the tuber components must be clearly understood in relation to sink development, which leads to yield. The size of an organ is proportional to the size of the meristem from which it develops (Simnott 1921, cf. Grafius 1978). Tuberous roots are differentiated from the adventitious root primordia in the planting shoots. The primordia initiate at a very early stage of ontogeny on the nodes around the first fully expanded leaf of the young shoots (Togari 1950). Therefore, the internal state or physiological conditions of the young shoots and the environmental conditions they encounter are important for subsequent tuberous root differentiation and



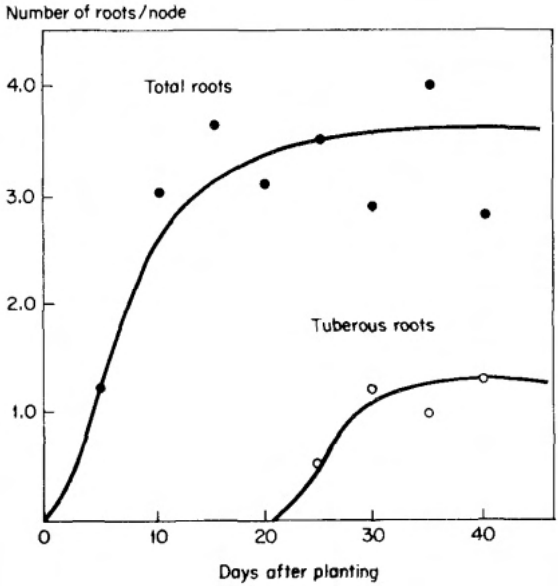
4. Relation among sink strength (absolute growth rate), sink size (dry weight), and sink activity (relative growth rate) of sweet potato.

development. The adventitious roots differentiated in the nodes are classified as 1) young, 2) fibrous, 3) pencil-like, and 4) tuberous. The young root becomes either tuberous, pencil-like, or fibrous depending on the primary cambial activity, the degree of lignification of stele cells, and the environmental conditions at the early growth stage. The young roots develop into tuberous roots when the primary cambial activity is high and the degree of lignification of stele cells is low, particularly at low temperature (22-24° C) and high potassium supply (Togari 1950).

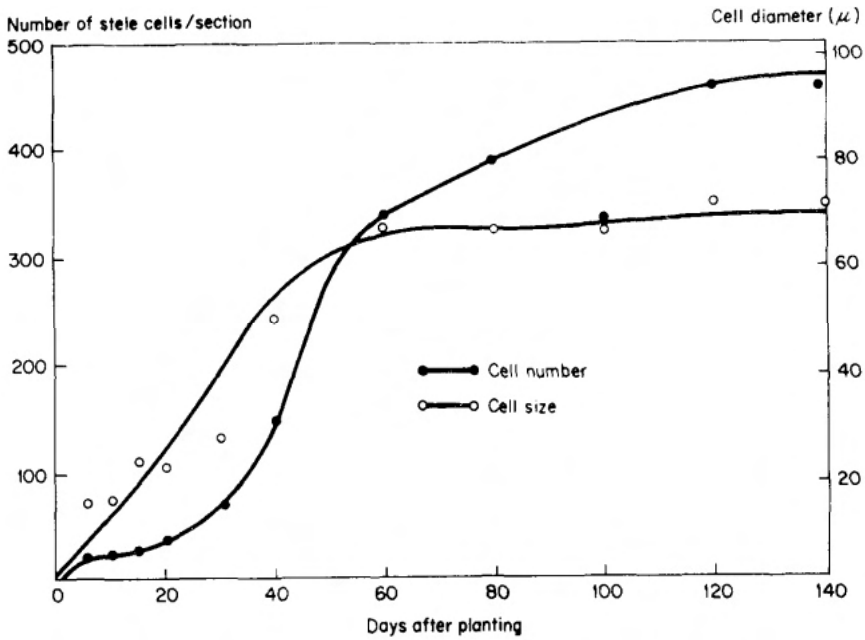
Tuberous root development depends on increase in number of cells and on starch accumulation (synthesis) in the cells (Tsuno and Fujise 1964d). The number of sweet potato roots reaches the maximum at 10-15 days after planting, and root length is greatest at 30 days (Fig. 5). Tuberous root numbers are determined as early as 30 days after planting. Stele cells constitute the storage tissue of tuberous roots The multiplication and growth of stele cells are shown in Figure 6 (Togari 1950)

Starch granules are first observed in the stele cells of the tuberous roots 20 days after planting. The gradual rate of starch granule multiplication and growth is shown in Figure 7. The lengthwise integral of (cell number × cell size) × (starch granules ×, granule size) per section determines the size of a tuber (Fig. 8). The approximate times of onset and the magnitude and duration of activity of the yield components in a normal genotype of sweet potato can be represented as shown in Figure 9. The developmental pattern of sweet potato yield components (root number, volume. and density) is sequential from the initiation of tuberous roots to final tuber size, A variation in root number (first in the sequence) causes a corresponding variation in root volume (second in the sequence) resulting in a compensatory relation or stress between them (Adams 1967, Thomas et al 1971a). A similar relation can be expected

in root density (the third component). Individual yield components make up the complex phenomenon of economic yield. The nature of interrelations among the components needs to be studied to gain a better understanding of how to combine them (Bunting 1971).

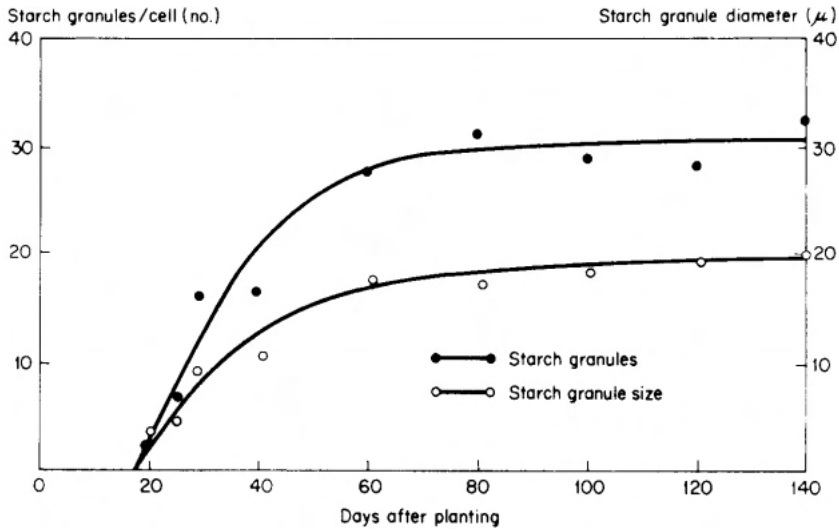


5. Changes in number of roots per node and number of tuberous roots of sweet potato as plant growth progresses (after Togari 1950).



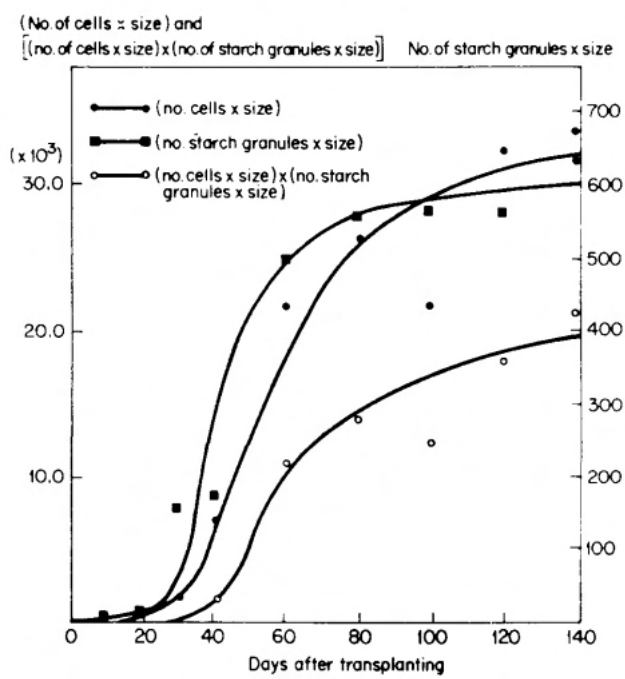
6. Changes in number of storage cells per section and size of cells in sweet potato as plant growth progresses (after Togari 1950).

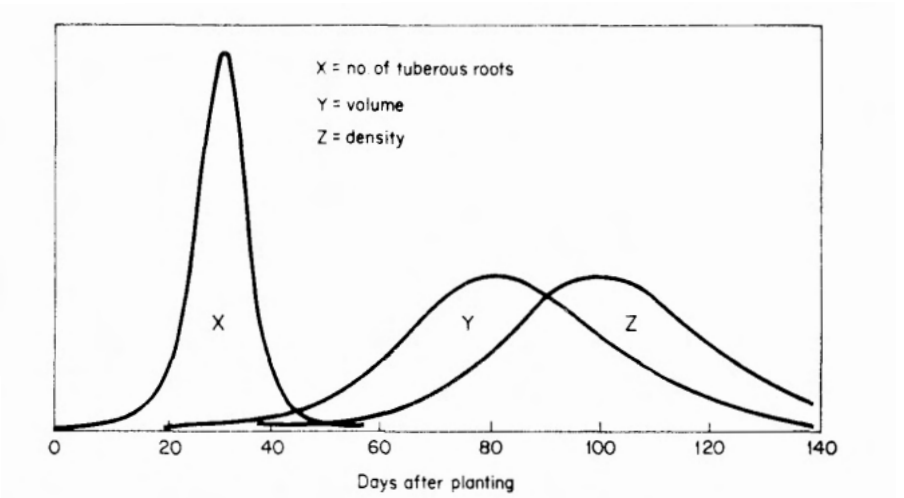
Factors affecting tuberous root differentiation and development. Tuberous root differentiation and development in the field may be limited by various external factors. The prevailing environmental conditions during the first 20 days after planting the slips are critical.



7. Changes in starch granules per cell and starch granule size as sweet potato plant growth progresses (after Togari 1950).

8. Changes in *A)* product of number of cells and cell size, *B)* product of starch granules and starch granule size, and *C)* product of *(A)* and *(B)* as sweet potato growth progresses (afterTogari 1950).





9. Approximate time of onset and the magnitude and duration of activity of the yield components of tuberous roots of sweet potato.

Soil aeration increases cell division and expansion. Under normal conditions the tuberous roots at early development stage have a high respiration rate amounting to about 25% of the whole plant. The lack of oxygen as a result of poor aeration often checks tuberous root initiation and development. High soil moisture content gives good shoot growth but poor tuberization, primarily because of poor soil aeration (Kodama et al 1965, Watanabe et al 1966).

Potassium accelerates the cambial activity in the tuberous roots in which starch is accumulated as the primary substance. K^+ addition increased the activity of starch synthetase in tuberous roots. Without added K^+, the enzyme activity often decreased by 7 to 8 times. When ADPG (adenosine diphosphate glucose) was used as a glucose donor, near to maximum or maximum enzyme activity was attained (Murata and Akazawa 1968, 1969).

Low temperature increases cambial activity and reduces lignification of stele cells in the internal tissue of roots. Dry and compact soil increases both cambial activity and root lignification. Low light intensity decreases cambial activity and lignification, and delays the development of tuberous roots. High nitrogen in the reduced soil decreases cambial activity, increases lignification. and causes root tendency to develop into nontuberous roots (Togari 1950). Lou night temperature (20° C) and long days seem to be critical for tuberous root initiation and development in sweet potato (Kim 1961). Tuberous root development was more rapid at 25°C than at 30° C, but no tuberous roots were formed at 10° C and 15° C (Spence and Humphries 1972). If tuberous roots are exposed to light at an early growth stage, they will stop developing (Hozyo and Kato 1976b). Investigations of tissues of tuberous roots exposed to light showed no obvious cambial activity or starch accumulation. When the exposed tuberous roots were again covered with soil, they resumed development; meristematic tissue was reactivated in cell division and expansion, and starch accumulation followed. This indicates that light inhibits tuberous root development.

When sweet potato plants in the field were exposed to stress (drought), tuberous roots developed slowly, but resumed growth when stress was removed.

It may be possible to estimate sink strength if it can be established that sinks depends on certain growth substances. Cytokinin content in the tuberous root significantly increased as the root developed; the increase paralleled the increase in average tuberous root weight. Cytokinin thus appears to play a role in tuberous root development by accelerating cell division and expansion (Hozyo 1973).

The highest dry matter production

In Southern Kyushu, Japan, total dry matter yield of 20 t/ ha was obtained from whole plants planted on *25* May and harvested on 18 November (Kodama et a1 1970). In Papua, New Guinea, *26* t/ha was obtained from the whole plants of 9 cultivars planted on 4 January and harvested on 11 July (Enyi 1977). More dry matter per day was produced in Papua, New Guinea, than in Japan. Dry tuber yield was 14 t/ ha in Japan and the whole plants were examined at appropriate growth stages for total dry matter yield and dry tuber yield. Tuber development was highest on 2 September, one and a half times as high as at harvest. The highest CGR of 150 g/ m^2 per week was recorded 10-14 weeks after planting when the LAI was *5.5.* Therefore, optimum LAI could be 5.5 if LAI at peak CGR is considered optimum. In Papua, New Guinea, the dry tuber yield of 17 t/ha was obtained during the growing period; the highest CGR for the highest yielding variety was 163 g/m^2 per week and the optimum LAI was 8.

The dry matter partitioning ratio on harvest index (HI), calculated as dry tuberous root weight over total dry weight, was 70% in Southern Kyushu and 72% in New Guinea. Although HI are almost equal to about 70% in both places, LAD was remarkably different — 88 weeks in Sew Guinea and 58 weeks in Japan. Dry tuberous root yield at both sites depended on LAI and HI. High HI and total dry matter yield production with longer LAD are key factors for higher tuber yield.

YAM

Many different species with different morphological characteristics make it difficult to gain a general picture of yam physiology.

Growth

Sobulo (1972) divided the growth cycle of white yam into four stages. The first stage is the dormant set. The second stage is the growth of the primary shoot and root. Tuber initiation followed by rapid tuber development is the third stage (late in this stage roots and shoots senesce). The fourth stage is the loss of tuber dry matter after the maximum is reached.

When dormancy ends environmental conditions are favorable. The layer of meristematic cells just beneath the tuber surface begins active cell division. Then the mass of cells becomes organized and a shoot apex differentiates. Soon the growing point begins to push through the surface and becomes visible as a small bud (the period from the onset of cell division until the appearance of the bud is 7-14 days).

When the bud has elongated to become a vine, its junction with the roots and old tuber remains stout and massive. New tubers develop from this region (Onwueme 1973). Ferguson (1973) noted in water yam four distinct phases of tuber development that may also be applied to white yam. The first phase extends from emergence to formation of the primary nodal complex (110-170 days after planting). The primary nodal complex is considered an integral part of the tuber because the two seem to grow as a single organ. The number of marketable tubers is determined (reaches a maximum at around 140 days after planting) during this first phase. The second phase is the period of rapid cell division and some cell expansion in which many of the cells involved in subsequent tuber development are formed (130-230 days after planting). The external and internal factors that affect the second phase are important in the determination of final yield. The third phase is the period of rapid accumulation of dry matter in tubers (170-290 days after planting). In the fourth phase, the accumulation of dry matter is greatly reduced and finally stops 290-310 days after planting (Fig. 10).

Morphological and physiological factors affecting yield

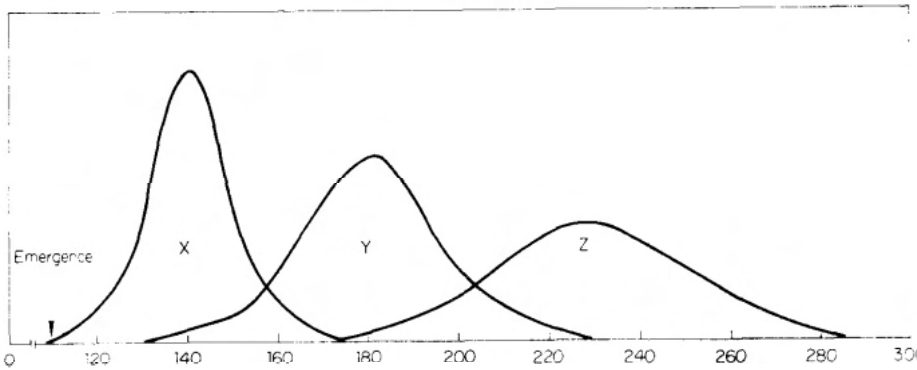
The morphological and physiological factors that affect yam tuber yield are, as in sweet potato, LAI, NAR, LAD, and number and size of tubers. They are influenced by the size of the set, age, time of planting, and staking (Enyi 1973). Certainly the supply of assimilates as determined by LAI, NAR, and LAD is an important factor in determining yield of yams (Chapman 1965, Enyi 1972, Ferguson 1973).

A yield-limiting factor is the low competitive ability or mobilizing ability of the slowly-developing tubers (sink) to attract assimilates during the early stages of crop growth after tuber initiation. Enyi (1972) reported that in Chinese yam, the accumulation of dry matter in the tubers is determined by the amount of assimilates available for tuber growth. He also reported that the pattern of dry matter distribution was dominated by the movement of photosynthetic products into the tubers shortly after they begin growing. This suggests that sink strength affects translocation and is important in determining dry matter yield of tubers.

Source

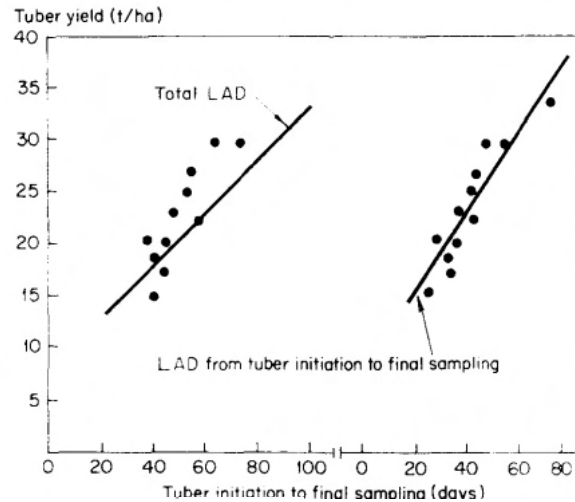
Leaf area index. In Trinidad, water yam shoots attained maximum development 6 months after planting (Haynes et al 1967). Sobulo (1972) reported that shoot development of white yam in Nigeria reached a maximum 7 months after planting — 4 months after leaf emergence. Leaf senescence occurred toward the end of 8 months after planting; of final harvest 10 months after planting and all the leaves had fallen and dried. 'The maximum LAI obtained for a water yam cultivar in Trinidad was about 4.0 (Chapman 1965). LAI for the same cultivar was 2.7 in Barbados (Gooding and Hoad 1967). The maximum LAI of white yam in Nigeria ranged from 1.91-2.53 at 6 to 7 months after planting (Sobulo 1972). Maximum LAI of a Chinese yam cultivar was from 5.0 to 8.0 6 months after planting (Enyi 1972).

LAI of a Chinese yam cultivar increased with set size and plant density (Enyi 1972). There are four kinds of planting sets: the small whole tuber or seed yam and sets from top, middle, and bottom portion of a whole tuber. A whole tuber is cut into sets if seed yams are not available. The sets from the top of the tuber are the oldest.



10. Approximate time of onset and the magnitude and duration of activity of the yield components of tuberous yam.

11. Tuber yield as a function of total leaf area duration and leaf area duration between tuber initiation and final sampling (after Enyi 1972)



Usually they germinate earlier and produce more vigorous shoots than sets from other parts of the tuber. Heavier sets of the same kind germinate earlier, have longer shoots, and yield more (Waitt 1963). In water yam, tuber initiation and development were slower as set weight decreased, which may be partly responsible for the lower tuber yield (Ferguson 1973, Onwueme 1978). Studies of Chinese yam showed that tuber yield increase with larger set size resulted from increases in LAI, LAD, the number of tubers, a higher growth rate, and a longer duration of tuber development (Enyi 1973). LAI was reduced under intercropping (IITA 1976). Nitrogen application increased LAI, LAD, tuber number per plant. and enhanced tuber development in Chinese yam (Enyi 1973).

Net assimilation rate (NAR). For a major part of white yam growth period, NAR was between 0.30 to 0.47 g/gper week. This low SAR may be due to mutual shading of lower leaves, which becomes more pronounced as leaf growth increases. Higher NAR values were observed in the late growth phase, probably because substantial

leaf fall reduced mutual shading (Sobulo 1972). The NAR value was 0.17 g/ dm^2 per week, about the same (0.16 g/ dm^2 per week) as that Chapman (1965) obtained for a water yam cultivar in Trinidad. Staking improves spatial display of leaves, minimizes mutual shading, and thus exposes the leaves to more sunlight, the combination of which probably increases NAR (Enyi 1973, Okigbo 1973). Imine (1940) reported that when vines were supported to a height of 2 m, their yield was almost double that of vines supported to a height of 1 m.

Leaf area duration. High correlation between tuber yield and LAD in water yam was reported by Chapman (1965). Tuber yield of Chinese yam was also positively correlated (r = 0.93-0.95) with LAD. Late planting of Chinese yam reduced LAD and, consequently, tuber yield (Enyi 1973). In Nigeria white yam leaf senesces much earlier when it is not slaked. To obtain high tuber yield, longer LAD is essential to achieve and maintain high leaf area during tuber development (Enyi 1972, Fig. 11).

LAD of Chinese yam increased from 56 to 100 weeks with increases in set size and at plant spacing of 90 cm X 60 cm (Enyi 1972). The increased LAD was ascribed mainly to earlier emergence and plant vigor as a result of planting larger sets. LAD decreased as planting space increased. Staking increased water yam LAD from 54 to 64 weeks (Chapman 1965).

Haynes et a1 (1967) reported no significant differences in LAD between white yam grown on 1-m and 2-m stakes in Trinidad. Unstaked water yam plants in Nigeria had longer LAD than the staked ones; resulting perhaps from a reduction in soil temperature and an increase in soil moisture brought about by the canopy covering the ground. However, unstaked white yam plants had shorter LAD because severe leaf diseases caused leaf senescence. Senescence was earlier in the intercrop than in the sole crop (IITA 1976). Short LAD was the major factor limiting yield of white and water yams.

Female plants of white yam have longer LAD than male plants and give higher tuber yields. The LAD is longer in yellow yam and Chinese yam than in other species.

Sink

Morphological yield components. The morphological components of tuber yield of yams consist of tuber number and tuber weight. Tuber weight depends on the species or cultivar, rate and duration of tuber growth, and number of tubers per hill.

In water yam, tuber initiation (invisible) has been suggested to be at or soon after emergence (at formation of the primary nodal complex) (Ferguson 1973). Once tubers are initiated, their development might follow a pattern similar to the one outlined for sweet potato. In Trinidad, noticeable water yam tuber development began about 5 months after planting (Haynes et a1 1967). The visible tuber initiation of Chinese yam began at about 5 months after planting (Enyi 1972). In white yam, it begins 3 to 4 months after planting, depending on the time of planting and emergence.

Tuber development in water yam was faster when larger sets were used, possibly because of earlier germination and rapid shoot growth accompanied by a rapid increase in leaf area. The application of potassium increased dry matter accumulation in Chinese yam tubers but had no effect on the other organs, and at final

sampling it increased the proportion of dry matter diverted into the tubers (Enyi 1973). Potassium had no significant positive effect on LAD but increased the rate of tuber development (Enyi 1972). It seems its effects on Chinese yam are similar to its effect on sweet potato. Short photoperiod encouraged tuber initiation in white yam (Njoku 1963) and Chinese yam (Enyi 1972). Day lengths of 12 hours or less favored tuber formation, but day lengths more than 12 hours favored shoot growth. Continuous exposure of the developing tubers to daylight reduced tuber yield and caused many small tubers to be produced (Gumbs and Ferguson 1976).

Tuber number of Chinese yam increased with an increase in leaf area, reaching the maximum at a leaf area of about 460 dm^2/plant (Enyi 1972). A high positive relation apparently existed between the maximum number of tubers initiated and the LAI at the time of initiation (Enyi 1973).

Staking increased the tuber number per plant in Chinese yam (Enyi 1973) and in white yam (Okigbo 1973). Plants grown on mounds and ridges had significantly higher tuber numbers than plants grown on level ground (Okigbo 1973). In white yam nonstaking reduced tuber size and yield by 40-60% but did not reduce the number of tubers (IITA 1973, 1974). Pruning white yam shoots to 50 cm significantly reduced tuber size and yield by 75% each but did not reduce the number of tubers (IITA 1973).

Tuber growth rate in Chinese yam increased with increase in leaf area, reaching a maximum at a leaf area of about 490 dm^2/plant. Further leaf area increases decreased the tuber growth rate (Enyi 1972).

Because tuber number is determined at a relatively early growth stage and there is little variation among cultivars in each yam species (except Chinese yam), the more important yield component that determines tuber yield appears to be tuber size. This depends upon rate and duration of growth, which in turn depends upon LAI, NAR, and LAD.

Source-sink relation

There is virtually no information on the source-sink relation in yams, but effects on tuber yield of staking and pruning vines give some idea. Results of staking and pruning show that source affects sink significantly in yams, but gave no idea how and why such treatments affect sink. Continuous exposure of yam tubers to daylight reduced tuber development. A well-planned experiment may give a better picture of the source-sink relation on the basis of shoot and tuber data. Because yams are monocotyledonous plants, the use of reciprocal grafts to investigate source-sink relation, as was done with sweet potato, will be difficult. Milking or removing developing tubers from growing yam plants is commonly practiced by farmers in West Africa. However, there is no published information on the effect of milking on tuber yield and shoots.

Yield potential

Fresh tuber yields of yams vary with species, cultivars, cultural practices, and environments. Average fresh, tuber yields of 10-20 t/ha can be attained in a 6- to 11-month growing period. But with good cultivars and good management, the potential fresh tuber yield could be 40 t/ha. Female white yam plants yield higher

than male plants. Production costs in traditional yam cultivation are high because of large labor requirements for planting, staking, harvesting, and storage. High storage loss of tubers due to tuber rot is caused primarily by fungal pathogens. Susceptibility to fungal pathogens is increased by nematode infestation or damage. Transporting tubers to market is difficult. Identification of a genotype with morphological and physiological characteristics suitable for nonstaking and mechanical harvesting can possibly reduce cost of production.

Despite serious production constraints and competition with other crops, yam production in West Africa may continue to be important because yams are closely bound with local tradition and culture.

USE OF PHYSIOLOGICAL INFORMATION

Cultivar improvement

Available physiological information should allow rational judgments on how to alter the form or development of the plant by breeding, and how to modify the environment by cultural practices to increase yield (Watson 1971). However, advances made so far in varietal improvement of sweet potato and yams have been obtained mainly by selecting directly for yield without taking into account physiological characteristics. It is difficult to use physiological information for integrated varietal improvement because yield is of a complex character; its expression depends on the functioning and interaction of many physiological processes. Genes for yield per se do not exist (Grafius 1959) and genetic control of yield is indirect through control of the physiological and developmental relations (Adams and Grafius 1971, Thomas et al 1971a, Grafius 1978). The most effective approach to breeding for high yield would be to identify physiological components that cause varietal differences in yield, and to acquire an understanding of their genetic control (Wallace et al 1972).

Varietal differences in LAI were observed by Tsuno and Fujise (1964c). Varietal differences in photosynthetic activity were noted at the later growth stage by Fujise and Tsuno (1962) and Tsuno and Fujise (1964c). Sadik (1973) screened 10,000 sweet potato seedlings and obtained a number of genotypes with high photosynthetic efficiency. However, a later report (IITA 1973) indicated no consistent differences in dry matter yield and its components between groups of high and low photosynthetic efficiency. The crosses of high to high photosynthetically efficient genotypes did not produce average progenies of high photosynthetic efficiency (Hahn 1977a). NAR variations between cultigens suggest that the NAR of existing cultivars can be increased through varietal improvement. But there appears to be little opportunity for increasing yield through increase of only NAR. There are tremendous sweet potato cultivar differences in tuber shape, number, size; in the orientation of leaves; and in canopy. These characters should also be incorporated into improved varieties.

Cultivar differences in source potential and sink capacity were reported from reciprocal grafts of sweet potato (Hozyo and Park 1971c, Hahn 1977a, Dahniya 1979). Hahn (1980), who screened 20 genotypes by grafting 1 of each on 4 tester cultivars, observed significant differences in source potentials among the tester genotypes. Dahniya (1979) reported that two high yielding varieties showed differences in source potential and sink capacity, one variety being good in source and the

other one in sink. He suggested combining the high source potential and high sink capacity of the varieties through crossing.

Source is a more complex character than sink (Wallace et al l972). It is affected by many other characters that interact among themselves and in turn are affected by and interact with environmental factors. Screening sweet potato for source potential is complicated and more difficult than screening for sink capacity (Hahn 1980). Because yield and sink capacity tend to increase simultaneously until they reach their limits set by photosynthetic capacity, yield improvement may be achieved much more easily by selecting for sink capacity alone. However, selection for sink and source individually could ultimately be misleading. It is advisable to select for both traits at the same time. Further progress will require both photosynthesis and sink capacities to increase in a more or less coordinated manner (Evans 1975).

It will be much easier to study in detail and to understand physiologically and genetically each physiological character that influences yield than to study yield per se. Interrelations among physiological characters need to be studied well before one plans to systematically combine the characters for higher yield. Selecting parents on the basis of complementarity of physiological components improves the probability of finding superior segregates (Wallace et al 1972).

Improved agronomic practices

For both sweet potato and yam, it is essential that cultivars used and agronomic practices adopted should enhance rapid leaf development soon after planting and subsequently the development of appreciable storage organs.

The primordia from which the storage organs of both crops differentiate are at some early stage initiated in the planted cuttings or sets (Togari 1950, Onwueme 1973). Therefore, the use of healthy planting material (slips, sets, or tuber cuttings) is of primary importance in determining to what extent subsequent normal initiation and development of storage organs readily occur. The number of sweet potato tubers is determined as early as 30 days after planting (Togari 1950); yam tubers also initiate storage root primordia soon after vine emergence (Ferguson 1973). Environmental conditions favorable to initiation of storage organs at this stage need to be provided through agronomic practices such as good soil aeration, and optimum and early fertilizer application.

The number and size of starch granules in the cells of sweet potato tubers reach their peak 60 days after planting (Togari 1950). Potassium ion (K^+) generally affects significantly the activity of the starch synthetase (Murataand Akazawa 1968, 1969). Application of potassium as a basal dressing at an early growth stage will increase activity of starch synthetase in the tubers and increase yield.

To achieve high yam yields, the environmental and agronomic factors that affect time of emergence, plant vigor, LAI, LAD. number of tubers, and rate duration of tuber development need to be provided through agronomic practices such as the use of optimum size of set, early planting, proper staking, right crop combination in intercropping, and optimum fertilizer application.

The key factors for success of sweet potato and yam production include the 1) maintenance of active source coupled with a large storage sink, and 2) existence of a favorable physiological source-sink relationship that triggers rapid and steady stor-

age root development. To tip the balance in favor of assimilate accumulation by the sink, all agronomic practices should be directed toward reducing the undesirable internal competition between shoot and storage organ. Undesirable competition between source and sink can be reduced by good soil aeration and adequate (not excessive) fertilizer application to enhance tuber development.

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CASSAVA

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Cassava is a C-3 plant that reaches maximal CGR values of 120-150 g/m^2 per week at LAI of 4 under solar radiation of about 450 g cal/cm^2 per day. Annual production of standing biomass at 40-50 t/ha is high for a C-3 crop, and these high figures are obtained by a long growth duration near maximal CGR rather than through very high CGR values.

Cassava forms new leaf and stem at the same time as it fills the economically useful part, the roots. This results in a delicate balance between top and root growth for maximum root yield, with the maximal root growth rate occurring at LAI values of 2.5-3.5. These LAI values can be most effectively maintained through most of the growing season by varieties that branch late (6 months after planting), and have large maximum leaf sire and a leaf life of 100 days or more.

Cassava grows and yields well at low fertility levels. Growth is reduced to maintain a high nutrient status in the leaves. Furthermore, as overall growth is restricted, a greater portion of the total dry matter is distributed to the roots. Under drought stress, the crop reduces water use and growth by reducing leaf area and closing the stomata. Leaves already on the plant are not shed any faster under stress and may become active after the stress period. Hence the cassava crop will readily survive a drought, but will produce very little during that period.

The cassava crop is grown in areas with mean annual temperatures above 20° C where annual temperature shows seasonal fluctuation, and 17° C where temperature is relatively constant. Germination is greatly delayed by lower temperatures and stops below 12° C. At higher temperatures, leaf area tends to be greater and low-vigor types are preferable: at low temperature the converse is true.

The true potential of cassava as a calorie source is realized under marginal conditions in areas where the crop's long growth cycle, ability to grow under low fertility conditions, and ability to survive long drought periods make it more productive than most alternative crops.

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The cassava crop has in the past received little attention from scientists in general and from plant physiologists in particular. As a result, there is relatively little information on the physiological basis of yield of the crop. Recently physiological studies in cassava were started in CIAT and cooperating agencies. Because these studies at first concentrated on the growth physiology of the crop under near ideal conditions, considerable data have been accumulated in this area. Only now is work starting on stress physiology of the crop. This paper therefore presents considerable hard data on the growth of cassava under good conditions. The data on stress physiology are both more superficial and more speculative.

ECOLOGICAL ADAPTATION

Temperature

Cassava is grown between lat. 30° N and 30° S at elevations up to 2,300 m above mean sea level. In Colombia, Peru, and Ecuador, specially selected clones are grown in the highland areas where the mean annual temperature is greater than 16°-17° C. Very small fluctuations in mean temperature characterize these areas. In areas with marked seasonal temperature changes, cassava is grown only when the annual mean temperature is greater than 20° C. Temperatures may reach 0° C with light frosts in cassava-growing areas. Frost causes necrosis of the expanded leaves and may kill the younger green stem tissue; however, with greater temperatures the axillary buds in the woody lower nodes form new shoots.

Rainfall and soil moisture

The cassava crop is found in areas with annual rainfall from as little as 750 mm/ year to more than 3,000 mm/year. Although yields are highest in areas with no pronounced dry season, the crop can be grown where there is no rainfall for up to 6 months. During the dry period, the crop stops producing new leaves and, as the older leaves senesce and abscise, becomes essentially dormant; at the onset of the rains, root reserves are used to produce new foliage (Cours 1951).

Although cassava will tolerate long periods with minimal amounts of water, it is extremely susceptible to excessive water. Standing water for as short as 24 hours may kill the crop; waterlogging greatly reduces growth. In areas with heavy rainfall and poor drainage, cassava is frequently planted on ridges or mounds.

Soil conditions

Cassava is grown on a vast array of soils throughout the tropics. It grows best and gives the highest yields under highly fertile conditions, but most often it is grown on the most depleted and eroded soils where other food crops cannot be cultivated. Low soil fertility status is frequently associated with extremely low soil pH and high levels of aluminum and manganese. Cassava grows better than most other crops at low pH and high levels of aluminum. On the other hand it is extremely susceptible to salinity and alkalinity; its growth is greatly reduced when conductivity of the soil solution is greater than 0.5 mmho/cm (Cock and Howeler 1978).

MAJOR PHYSICAL PARAMETERS

Leaf photosynthetic rate

Mahon et al (1977b) measured the photosynthetic rate of attached leaves of cassava and nine wild species of Manihot grown in growth chambers. The maximum photosynthetic rates ranged from 15 mg CO_2/dm^2 per hour in *M. quintiparta* to 29 mg CO_2/dm^2 per hour in *M. dichotoma.* Rates of all the cassava clones tested were within this range; however, they differed between clones, with that in clone M Col 22 being 29 mg CO_2/dm^2 per hour at saturation — 20% greater than that of any other clone tested.

At CIAT, plants grown outdoors in pots gave maximal rates of 33 mg CO_2/dm^2 per hour. M Col 22 had the second highest photosynthetic rate of 32 mg CO_2/dm^2 per hour (CIAT 1977). In general, the rates obtained at CIAT were higher than those reported by Mahon et al (1977b), the lowest rates of which at saturation light intensity were close to 27 mg/dm^2 per hour.

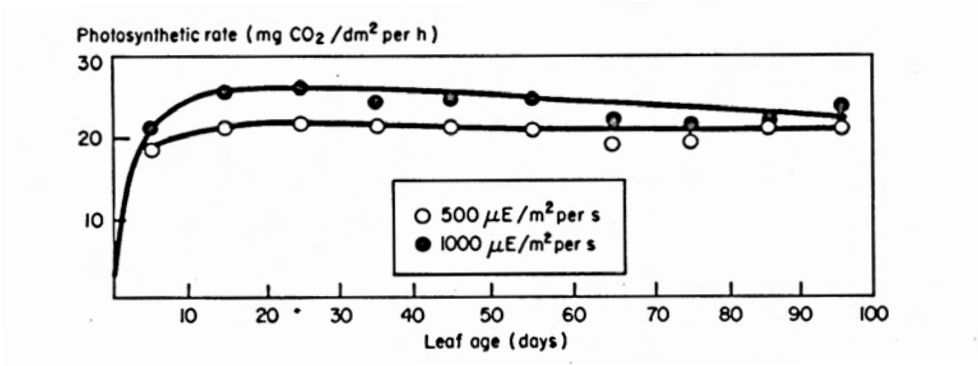
Mahon et al (1977a) found leaves had highest rates of photosynthesis at 25°C and more recent data obtained by the author suggest that the optimal temperature is 25-40°C. Young leaves of plants grown at 29°/26°C day/night temperature had much greater photosynthetic rates than leaves grown at 24°/19° C when measured at high photon flux densities.

Cassava leaves show a light saturation response typical of C-3 plants with little increase in photosynthetic rate above 1,200-1,500 µ Einsteins/m^2 per second (Mahon et a1 1977a, b; CIAT 1976,1978). Mahon et al (1977a) obtained a net efflux of CO_2 at 45 vpm CO_2 in all materials tested and Mahon et al (1977b) estimated the CO_2 compensation point as 68 vpm at 25°C. At CIAT we have obtained at 25°C similar values that increase rapidly with temperature to more than 100 vpm at 35° C. These data are all indicative of a C-3 photosynthetic pathway in cassava.

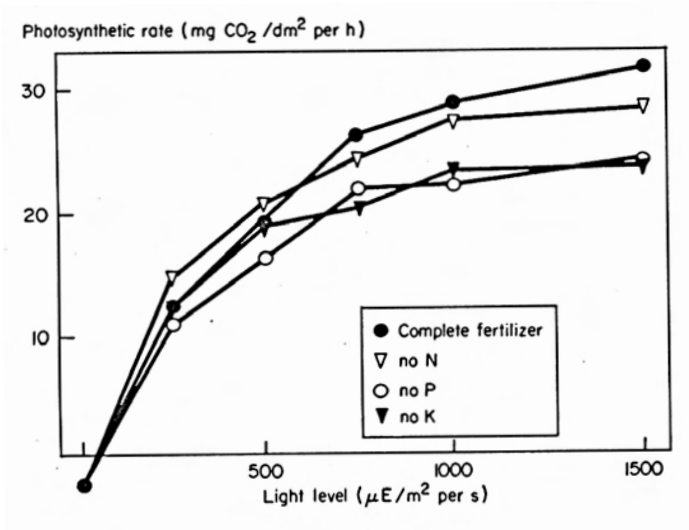
The photosynthetic rate of leaves of most crops decreases markedly with leaf age. Mahon et al (1977a) obtained much lower leaf photosynthetic rates in older than in younger leaves. Aslam et al (1977) also found large decreases in photosynthetic rate at high light intensity as leaves aged but found no such effect of plant age on photosynthesis. They suggested that the much smaller decline in photosynthetic rate in some of the clones tested may be important, particularly for screening purposes. Photosynthetic rate in plants grown in small pots outdoors markedly declined with plant age, but when two-thirds of the leaves were removed, the original rate (30 mg CO_2/dm^2 per hour) was restored and maintained until 100 days after planting if two out of every three leaves were removed as they formed (CIAT 1979).

In trials with plants grown in large plots with the clone M Col 72, the photosynthetic rate of individual leaves did not decrease up to 100 days after their appearance (Fig. 1). However, leaf photosynthetic rate in M Col 22 markedly decreased with plant age in the trials of Aslam et al (1977) while in trials at CIAT it remained high 50-60 days after leaf emergence. Although the data on photosynthetic rate as a function of leaf age are somewhat conflicting, it appears that in some clones photosynthetic rate declines slightly as the leaf ages.

The photosynthetic rate of leaves of cassava plants grown in sand culture decreased at lower nitrate levels in the culture solution (Mahon et al 1977a). The



1. Photosynthetic rate of leaves of cassava M Col 72 at 2 light levels.



2. Photosynthetic rate of individual leaves of cassava M Col 22 grown under different fertilization.

photosynthetic rate of individual leaves of plants grown in a very infertile Oxisol with and without fertilizer showed a relatively small reduction (Fig. 2) although the total dry weight per plant was markedly reduced.

Crop growth rate and leaf area index

Maximum reported crop growth rates. Enyi (1972a,b,c) reports crop growth rates (CGR) of 200-300 g/m^2 per week from trials in Sierra Leone. Zandstra (1979) states that cassava has a CGR of 210-280 g/m^2 per week but gives no details on how those figures were obtained. Williams (1972) estimated CGR of 315 g/m^2 per week for plants grown in polyethylene bags but a maximum CGR close to 150g/m^2 per week for field-grown plants. In a series of trials at CIAT and the surrounding area, I repeatedly obtained values of 100-120 g/m^2 per week with solar radiation of 400-500 cal/cm^2 per day and values up to 140 g/m^2 per week in one trial (CIAT 1972). The weight of the fallen leaves, which may reach 3 g/m^2 per day (Cock 1976), was included in the calculation. In other trials, reported data do not include fallen leaves and, hence, CGR is underestimated. Enyi (1973) obtained values of 100-120 g/m^2 per week and several authors report values of 80–100 g/m^2 per week (Cours 1951,

Holmes and Wilson 1977, Cock 1976, Cock et a1 1979). Unfortunately, comparison of the data is difficult as most reports do not give data on the solar radiation during the measuring period. Nevertheless, reported values above 200 g/m^2 per week are difficult to reconcile with the reported rather low photosynthetic rates of cassava leaves. I suggest that the maximum CGR under conditions of moderate insolation is from 100 to 150 g/ m^2 per week. Compared with those in other crops, these values are not high, but cassava can maintain rates close to the maximum for rather long periods. Holmes and Wilson (1977) reported an average CGR of 83 g/ m^2 per week over a 10.5-month period, and Cock (1976) obtained 98 g/m^2 per week over an 8-month period. In neither of these cases was leaf fall assessed; real values would have been even greater.

Crop growth rate as a function of leaf area index. The extinction coefficient of cassava is 0.7-0.86 (Veltkamp, pers. comm.), which corresponds to 95% light interception at leaf area index (LAI) 3.5-4.3. Hence, crop growth would be expected to increase with LAI values up to 34 and then level off. Enyi (1972a, b, c) found a fairly flat relation between CGR and LAI over the range of 3-6. In varieties CMC39 and CMC84, CGR increased with increasing LAI values up to 34, but after that did not change with increasing LAI value (CIAT 1972). Cock et al (1979) found a slight tendency for CGR to decrease above an optimum LAI of 4 in the clone M Col 113 at very high plant populations. The data from a series of trials in CIAT and its substation Quilichao have been used to compile Figure 3. Although there is considerable scattering of the data points, it is clear that CGR increases with LAI values up to 34 and then remains nearly constant as LAI further increases.

Williams and Ghazali (1969) measured large differences in leaf orientation between different clones. The upper leaves fold downward toward midday, thus assuring a more erect disposition, then throughout the afternoon gradually assume a more horizontal position (CIAT 1973). This change in leaf angle is most marked on bright sunny days. It does not appear to be associated with wilting as the stomata remain open throughout the process (CIAT 1973). Cock (1976) could not detect any difference between the CGR of clones with a large leaf angle change and that of clones with a little change. As most of these data were collected at LAI values of 2-4. when leaf angle theoretically has little effect on CGR (Duncan et al 1967), this result was not surprising. The changes in leaf angle could he useful to increase CGK at the highest LAI values attained by cassava. However, there is good reason to believe that this would not necessarily lead to higher yields of roots.

Maximum leaf area index. The LAI of most cassava clones increases rapidly in the first 4-6 months after planting and then declines (Cours 1951; Williams 1972: Enyi 1972a, b, c. 1973; CIAT 1972, 1977; Cock 1976; CIAT 1978, 1979). The maximum LAI values recorded are between 6 and 8 (Cours 1951; Enyi 1972a, b, c, 1973; Cock 1976; CIAT 1978, 1979). However, these levels are peaks normally observed over a very short time. Rosas et al (1976) found that shading the leaves reduced their life and that fully shaded leaves abicised 10 days after the treatment began. Cock et al (1979) found that up to 95% shading had little effect on life of leaves more than 30 days old, but when shading was greater, leaves abscised rapidly. Because 95% shading occurs when there is a leaf canopy of LAI 3.5-4.3, leaf production must be very high for larger LAI values to be maintained for any length

of time. Irikura et a1 (1979) obtained a mean LAI of 5.6 for 8 months with a variety that is heavily branched and has very large leaves. Although high LAI values are obtainable in cassava, they can be maintained only at the cost of very heavy leaf fall and very high leaf production rates.

Total dry matter production

Cours (1951), in a classic study of 41 clones grown over a period of 4 years, found an average total dry matter production of more than 40 t ha per year. Cock et a1 (1977) obtained harvestable dry matter yields of 45 t ha per year at very high plant populations. Enyi (1973) grew plants for nearly 15 months and obtained a total dry matter production of close to 47 t/ ha per year at very high plant populations. Holmes and Wilson (1977) after 46 weeks obtained the equivalent of 43 t/ ha per year. These data all underestimate the total dry matter produced because fallen leaf weight was not measured. Nevertheless, the reported dry matter yields fit well those estimated from CGR. If we allow 6 weeks for crop establishment and 46 weeks for growth close to the ceiling LAI of 3-4 with a CGR of 120 g/m^2 per week, the total dry matter yield would be approximately 52 t/ha per year. With average leaf life assumed to be 80 days and LAI to be 3 during the 46-week growth period the plant will lose 9 m^2 leaf/m^2 of land, which is equivalent to 6 t/ha. Hence the harvestable dry matter would be expected to be about 46 t/ha per year, which agrees very closely with the field data reported above. These data suggest that. although individual leaves have relatively low photosynthetic rates with ceiling LAI and maximal CGR also rather low, cassava has a rather high total productivity for a C-3 crop. Loomis and Gerakis (1975), from an extensive review of the literature. obtained maximal annual production values of the standing crop of close to 40 t ha per year for C-3 plants. More recently Loomis (in press) suggested that cassava is one of the most productive C-3 plants in annual production of standing biomass.

Harvest index

The harvest index (HI) is a crude measure of the distribution of biomass to the economically useful plant parts. In crops with a phasic growth cycle, where the vegetative phase essentially terminates before the filling period, HI is normally measured only at the end of the crop cycle. Crops such as cassava, sugar beets, and oil palms simultaneously develop the economically useful plant parts and their leaves and stems. Hence, in these plants HI is often measured during the growth cycle (CIAT 1973, Corley 1973). The growth difference in phasic and simultaneous development is of great importance; in phasic development, there is little competition between the development of the source and the filling of the economically useful sinks, while in the simultaneous development, there is normally competition for the development of source and sink. Thus in most phasic crops, a ceiling LAI for yield is expected while in the simultaneous development crops, the competition for available substrates between source and sink will lead to an optimum LAI for growth of the economically useful parts. Ceiling LAI values have been found in rice (Yoshida et al 1971) and optimal LAI values in cassava (Cock et a1 1979, Irikura et a1 1979) and oil palms (Corley 1973).

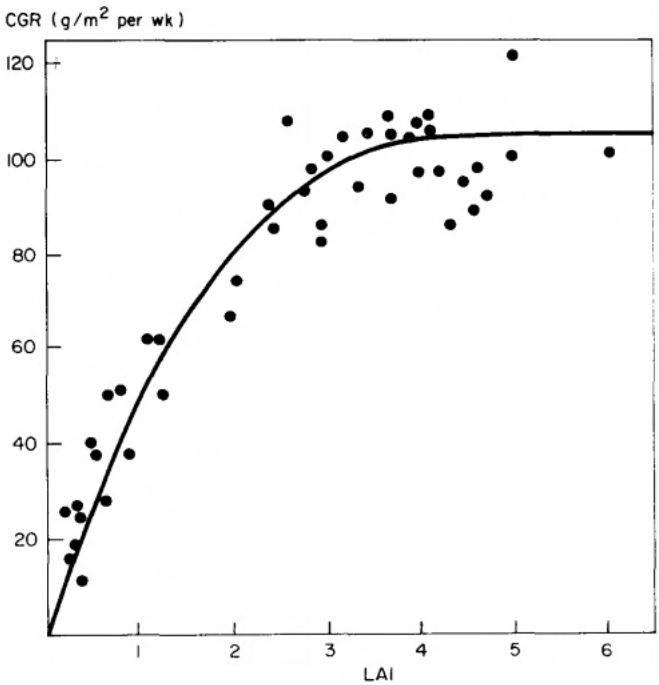
The HI can be determined on a fresh-weight or a dry-weight basis. Unless otherwise stated, HI as used in this paper refers to harvest index on a dry weight basis. In cassava, HI as measured in field experiments after a long growth cycle does not give an exact picture of the economic yield relative to the total biomass yield. The discrepancy is due to the large amount of biomass often present in fallen leaves and the exclusion of the fibrous roots. The fallen leaves may be equivalent to several tons per hectare of biomass. At very high plant populations, I have observed leaf fall of more than 30 g/m^2 per week. When leaf fall is allowed for in the estimate of HI, the term corrected HI is used.

Tan, while at CIAT, measured both HI and corrected HI index and found them closely related, with surprisingly little difference between the two measurements. When corrected HI was 0.50, HI was 0.52 (CIAT 1977). In these trials, LAI values never exceeded 3.7 and most were less than 3, hence leaf fall would not have been as large as in experiments with high LAI values. Simulation of cassava growth using a computer model (Cock et al 1979) has indicated that the corrected HI and measured HI can be very different in some cases. Care should therefore be taken in interpreting HI values.

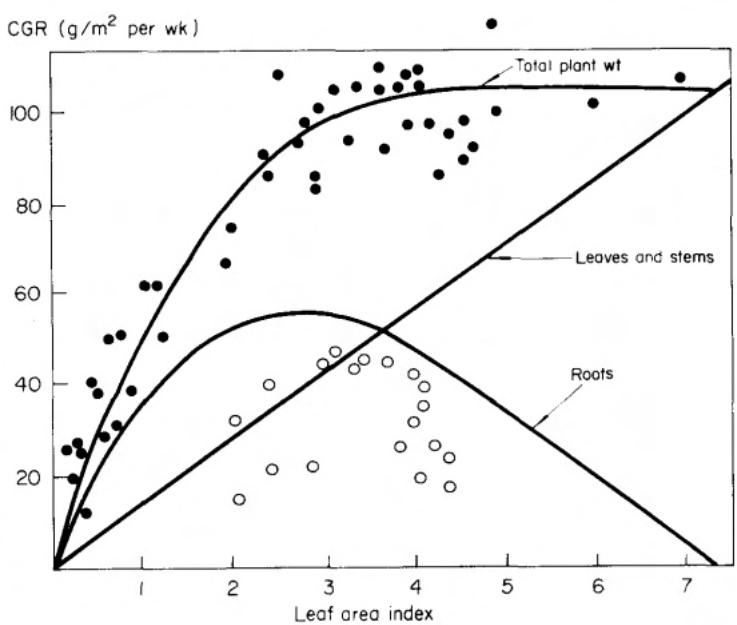
In single shoot plants, Enyi (1972b) found an average HI of about 0.55 with little effect of plant population. With multishoot plants, HI decreased from 0.45 to 0.37 as plant population was doubled from 6,000 to 12,000 plants/ha. Cock (1976) obtained HI values ranging from less than 0.30 to 0.57 for a number of clones with 20,000 plants/ha after 1 year. In one trial with M Col 22, HI values of more than 0.7 were obtained, but the HI decreased as population increased above 12,000 plants/ha (Cock et a1 1977). These high HI values agreed with the data of Hume (1975), who found up to 60% of assimilated ^{14}C in the thickened roots. Boerboom (1978) has suggested that after bulking begins, a constant portion of the new dry matter formed passes to the roots, and the portion depends on both the variety and the growing conditions. The reworked data of Tan and Cock (1979) supported this conclusion. When the simulation model (Cock et al 1979) was used, however, certain combinations of plant characters that resulted in high LAI values led to a poor fit to Boerboom's hypothesis although his conclusions were normally applicable. Irikura et al (1979) showed that at very high LAI values, which result in high CGR values, root growth rate was minimal. Similar conclusions are drawn by reanalysis of Enyi's data (1972a, b, c). This suggests that Boerboom's hypothesis may not hold at very high LAI values.

Cock et al (1979) found that shading had little effect on top growth but a marked effect on root growth rate. Tan and Cock (1979) showed that reduction of top growth by apex clipping or branch removal increased the root growth rate. They concluded that top growth has preference for available substrates and that root growth occurs when the available substrate is greater than that required for the tops to reach their growth potential.

CGR increases with LAI and then reaches a plateau (Fig. 3). When LAI does not change, the dry matter for leaf and stem growth required to maintain a given LAI would be expected to increase approximately linearly with LAI if leaf life is constant. This is shown schematically in Figure 4 (the CGR curve is the same as that shown in



3. Crop growth rate (CGR) of cassava as a function of leaf area index (LAI) in Valle, Colombia. Results are from several trials. Radiation levels average 400-450 cal/cm^2 per day.



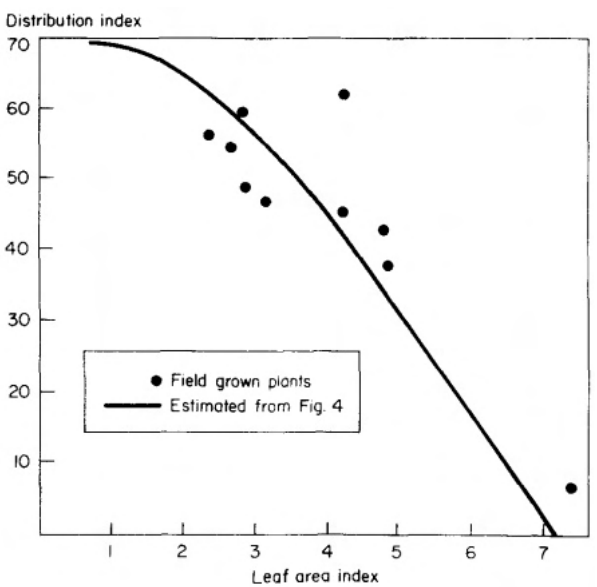
4. Crop growth rate (CGR) and dry matter used for stem and leaf and root growth at different constant leaf area indices.

Fig. 1). The root growth rate is obviously the difference between the dry matter required for leaf and stem growth and the total crop growth; it shows a marked optimum (Fig. 4). From this schematic relation, the distribution index (root growth rate divided by CGR) was estimated as a function of LAI and then compared with data from field experiments (Fig. 5). The close relation between the schematic representation and the field data suggest that the basic hypothesis is correct. Furthermore, maximum root growth rates occur at LAI values of 2.5-3 when the distribution index is close to 0.6. Cock et al (1979), Irikura et al (1979), and CIAT (1976) have all shown optimum LAI values of 2-3 for root growth rate.

The distribution index should be closely related to the HI. Recently, HI has been used as a selection tool by cassava breeders (Kawano 1978) and maximum yields under good conditions have been obtained at HI values (freshweight basis) of 0.5-0.7. The fresh-weight HI tends to be higher than corrected HI because leaf fall is not accounted for, but that is partially offset by the higher water content of leaves and young stems. Hence fresh-weight HI approximates the corrected HI. In one experiment the HI of M Col 22 was 0.52-0.54 and freshweight HI was 0.58 (D. J. Connor, pers. comm.).

Economic yield

De Vries et al (1967) estimated that among various food crops, cassava had the highest potential production of calories per hectare per year. The high potential economic yield of cassava is based on a long root-filling period rather than on a particularly rapid growth rate. The maximum root growth rates obtained over short time intervals at CIAT are between 40 and 50 g dry roots/m^2 per week (CIAT 1976, 1978; Cock et al 1979). From the data of Cours (1951), the maximum rate of starch accumulation in the roots is close to 50 g starch/m^2 per week. Kawano (1978) has



5. Distribution index as related to leaf area index of field grown plants and estimated from the schematic representation in Figure 4.

recently obtained a yield of 79.2 t/ha per year fresh weight at 0.375% dry matter — equivalent to 28 t dry roots/ha per year or 54 g/m^2 per week. The maximum root growth rate must have been somewhat greater than this figure as there is little root production in the first 2 months after replanting, suggesting the attainment of maxima of 60-70 g/m^2 per week.

RESPONSE TO MAJOR CLIMATIC FACTORS

Cassava is grown over a wide range of temperature and rainfall conditions between lat. 30° N and 30° S. Its response to water stress and temperature has been observed in major field studies but there is relatively little information on the effects of photoperiod or solar radiation.

Temperature effects

Germination. The germination of cassava cuttings is greatly delayed at low temperatures (Cock and Rosas 1975). Some varieties failed to germinate at temperatures of 16° –17°C. Keating and Evenson (1979) examined the germination response of two varieties at different soil temperatures and found that time to emergence decreased with increasing temperature up to 28.5° -30.0° C, depending on variety, and then increased at higher temperatures. Time to 50% shoot appearance was reasonably determined to be 210 degree days above a base of 13°C. The data showed that cassava would not germinate when soil temperature was less than 12° -17° C.

Growth and yield. Irikura et al (1979) did an exhaustive study of the growth and development of cassava at three nearly constant temperatures. The temperature regimes of 20°, 24°, and 28° C were obtained by growing plants at different altitudes. Site differences in fertility and rainfall were blanketed by raising fertility level and supplying irrigation at all sites. Differences in solar radiation may also have existed. However, these effects were probably small compared with those attributable to differences in temperature.

Vigor in the four varieties used in the experiment ranged from very high (Popayan), medium (M Mex 59 and M Col 113), to very low (M Col 22). At the lowest temperature the more vigorous line yielded most and at high temperature least; at high temperature, the trend was reversed (Table 1). LAI and vigor were closely related. A close relation was found between root dry weight increase and LAI from 8 to 16 months after planting over all sites and varieties (Fig. 6). A marked optimum LAI of 2.5-3.5 exists for the maximum root bulking rate. Cock et al (1979) and CIAT (1976) reported a similar optimum for one temperature regime with several different clones.

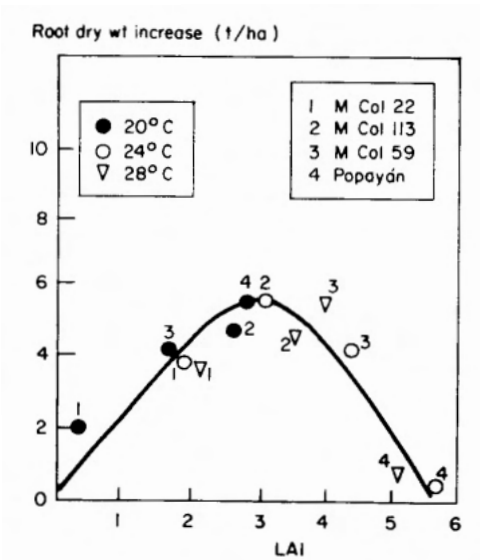
LAI increased at the intermediate and higher temperatures. At higher temperatures, leaf formation rate per apex and total number of apices (branches) increased. Individual leaf size was slightly less at lower temperatures and maximum size was reached somewhat later. Leaf life, however, markedly increased, up to 200 days at the lowest temperature. But such increase in leaf life did not offset the greater leaf production at high temperature.

Irikura et al (1979) concluded from this experiment that there is tremendous variety × temperature interaction for yield but that maximum yield will be obtained

Table 1. Fresh and dry root yield[a] of 4 contrasting cassava genotypes at different times when planted at altitudes with 3 different mean tempentures.[b]

	20°C with harvest time of			24°C with harvest time of			28°C with harvest time of		
	8 mo	12 mo	16 mo	8 mo	12 mo	16 mo	8 mo	12mo	16 mo
				Fresh yield (t/ha)					
M Col 22	2.7	9.3	13.3	22.1	22.7	48.3	23.9	39.4	53.1[c]
M Mex 59	9.2	22.8	32.8	25.3	38.8	57.0	21.3	30.4	60.3
M Col 113	14.2	24.2	28.6	16.4	26.1	51.3	20.2	23.9	55.0
Popayan	10.7	28.9	39.7	6.3	15.7	13.3	4.6	9.4	13.2
				Dry yield (t/ha)					
M Col 22	0.9	3.3	5.6	8.5	11.5	18.0	8.8	14.2	18.4
MMex 59	3.0	8.2	12.9	8.2	14.2	18.1	7.5	10.1	19.7
M Col 113	4.5	8.4	15.6	5.4	10.0	19.1	6.2	7.5	17.0
Popayan	3.1	10.7	16.2	1.9	5.1	2.6	1.1	2.2	3.0

[a] For fresh and dry root yields temperature X variety interaction was significant at $P = 0.01$. [b] Source: Irikura et a1 (1979). [c] Yield wasreduced by robbery in the experimental plot.



6. Relation between root dry weight and mean leaf area index (LAI) of 4 cassava varieties at 3-16 months after planting in locations having 3 mean temperatures (Isikura et a1 1979).

at different temperatures by phenotypically similar plants, even though they may have to be genotypically different. This phenotype must be such that a LAI of about 3 is maintained throughout the bulking period.

The data of Irikura et a1 (1979) are only for constant temperature and do not take seasonal effects into account. Cours (1951) followed the growth of cassava over a seasonally changing temperature regime. However, his plots were not irrigated, and the cool and dry periods occurred at about the same time. Nevertheless, his data suggested that at lower temperature leaf life was greater, but leaf area development was slower because the leaf expansion rate was greatly reduced.

Day length

Various greenhouse studies have shown that long days decreased root production (Bolhuis 1966, Mogilner et a1 1967, Nair and Sinha 1968). No differences in top

growth were observed. In a field experiment with supplementary light that provided insignificant amounts of extra total radiation, Cock and Row (1975) found a lower HI at 15-hour days than at 12-hour days, and Lowe (quoted by Hunt et al 1977) found the same effect in a growth cabinet study. My more recent data show reduced root weight in plants of one variety grown at 18-hour days for the first 3 months. These data suggest that cassava is photoperiod sensitive; however, photoperiod-insensitive lines may exist.

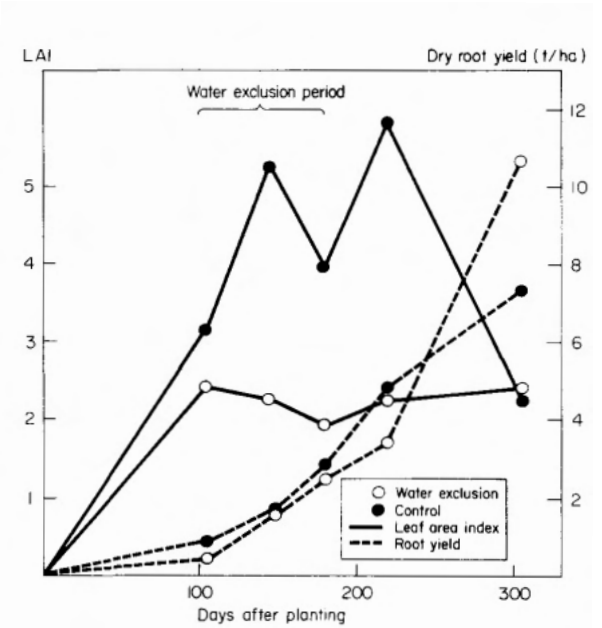
Solar radiation

There is little direct information on the effects of solar radiation on cassava. Over short periods (2 months), reduced radiation by shading has little effect on top growth but markedly reduces root growth (Cock et al 1979). In most crops increased radiation leads to increased CGR; simulation using the model of Cock et al (1979) indicates that for every 10% increase in CGR, root yield should increase by about 20%. This suggests that cassava yields will be rather sensitive to changes in radiation receipt.

Water relations

Cassava is highly drought tolerant (Jones 1959, Montaldo 1977, Onwueme 1978, Da Conceicao 1979). However, until recently, little research effort had been done on cassava-water relations.

Connor et al (1981), Connor and Cock (1980), and Connor and Palta (1980) subjected a vigorous clone M Mex 59 and a low-vigor clone M Col 22 to drought stress for 76 days, covering the ground with plastic to exclude rainfall. They compared the growth of the plants during the stress period and monitored their recovery. Under drought stress, rate of leaf formation per apex, apex number (branching), and leaf size were reduced. The stress treatment increased leaf life, presumably because the reduced upper leaf canopy in the stressed plots caused less shading. The net effect of the treatment, however, was a marked decrease in LAI (Fig. 7). The CGR was decreased by the treatment, and to an even greater extent than would have been expected from the reduction in LAI. Decrease in root growth rate was much less and, in M Mex 59 particularly, the portion of the assimilate accumulated in the roots was markedly increased. In the recovery period, leaf formation rate increased to levels similar to that of the control; branching resumed but total branch number never reached the same level as in the control. Leaf size increased rapidly after stress and was somewhat greater in previously stressed than in control plants. By final harvest, 10 months after planting, the LAI of M Mex 59 in previously stressed plants was equal to that in the control, while in M Col 22 it was still lower. During the recovery period, growth rate of roots of M Col 22 was similar in treated and untreated plots; final dry root yield was 11.2 t/ha in the control and 7.6 t/ha in the previously stressed plots. In Mex 59, the previously stressed plots yielded more (10.7 t/ha) than the control (7.3 t/ha). Connor et al (1981) suggest that the restriction in branching during the stress period reduced stem and leaf growth in the recovery period, leading to a more favorable balance between top and root growth in M Mex 59, but still there was sufficient leaf area to obtain acceptable CGR. In M Col 22, LAI was so reduced that CGR values were lowered far more by



7. The growth and development of M Moc 59 during and after a period of water exclusion and in control plots.

the stress period and its subsequent effects on LAI than could be compensated for by a slightly increased distribution index.

Connor and Palta (1981) found that closure of the stomata in the stress plots resulted in extremely low stomatal conductance and that leaf water potential was maintained at levels comparable to or slightly less negative than in the well-watered plots. Leaf water potentials reached minimum levels of around -14 bars, and stomatal conductances in the stressed plots were reduced to less than 1 mm/second at midday.

Campos and Sena (1975) studied the root system of cassava and found roots concentrated in the top 30 cm, with some roots as far down as 140 cm. However, Connor et al (1981) found roots at 250-cm depth. They also observed root characteristics and found that cassava has rather thicker roots than most species (0.37-0.67 mm diam) but very short roots (less than 1 km/m^2 land surface). The low water potentials and increased hydraulic conductivity in the root zone that are expected to result from the low root densities may cause a high resistance to water flow to the roots. The sparse root system, closure of the stomata at relatively high water potentials, and the reduction in leaf area during the stress period point to a strategy of water conservation. The cassava plant, on encountering stress, immediately reduces its water uptake but conserves the carbon and nitrogen invested in leaves so that when water is again available, it can rapidly resume growth. Under more extreme drought when LAI is effectively reduced to zero, root and stem carbohydrates are used to rapidly develop a new canopy with the onset of the rains (Cours 1951).

Nutritional stress

Cassava is highly tolerant of low-fertility conditions. Edwards et al (1977) have shown that for maximal growth in solution culture, cassava's requirement for

nutrients, particularly phosphorus, is quite high. They also showed, however, that low nutrient levels reduced growth less in cassava than in several other crop species (Table 2). This result was confirmed at the University of Queensland (Spear et al 1978a, b, c). Furthermore, maximum root yield is obtained well before maximum biological yield is reached (Fig. 4). Although low fertility may markedly reduce total assimilation, the distribution to the roots is markedly increased (CIAT 1978, 1979; Cock and Parra, pers. comm.); hence cassava is able to produce well at very low nutrient levels.

Edwards et al (1977) and Cock and Howeler (1978) suggested that cassava tends to maintain the nutrient status of its leaves at low fertility levels by reducing growth and leaf area development. Thus LAI values at Quilichao, a low fertility station of CIAT, were reduced from 5.4 to 1.6 by low fertility while the nitrogen and phosphorus status of the leaves was little changed, but potassium markedly decreased (Table 3). The following hypothesis suggests that this may be an optimum strategy for obtaining good yields under low fertility, particularly where nitrogen is limiting.

Photosynthetic rate of individual leaves of most crop species is closely related to nitrogen content (see review by Natr 1972). If there is only a limited amount of nitrogen for leaves, leaf nitrogen content will decrease with increasing LAI (Fig. 8). Data from Cock and Yoshida (1973) show that in rice this does indeed occur. If we make the simple, and reasonable, assumption that below a certain nitrogen level, photosynthetic rate decreases approximately linearly with protein nitrogen content, and that this effect occurs to a similar extent at all light intensities, we can use data from Duncan's model (Duncan et al 1967) to describe CGR at different levels of nitrogen available to the leaves (Fig. 9). This clearly shows that maximal CGR

Table 2. Percent of maximum yield of cassava and other crop species at low constant solution concentrations. [a]

Crop	Percent of maximum yield at solution concn (mol/liter) of				
	K 0.5	Ca 0.5	NH_4 0.4	NO_3 0.4	P 0.05
Cassava	52	26	40	20	18
Soybean	–	2	–	–	34
Maize	36	2	7	6	21
Sorghum	–	3	5	2	–
Sunflower	43	0.2	9	3	–

[a] Edwards et al 1977.

Table 3. Effect of high, medium, and low fertility levels on leaf area index (LAI) and nutrient content of leaves + petioles of M Mex 59 six months after planting. [a]

Fertility level	LAI	Nutrient content as % dry matter			Nutrient content as mg/dm² leaf surface		
		N	P	K	N	P	K
High	5.39	3.69	0.25	2.00	18.9	1.28	10.3
Medium	3.54	3.68	0.19	1.40	20.2	1.04	7.7
Low	1.65	3.52	0.18	0.73	21.7	1.11	4.5

[a] Source: J. H. Cock and G. Parra (unpubl. data).

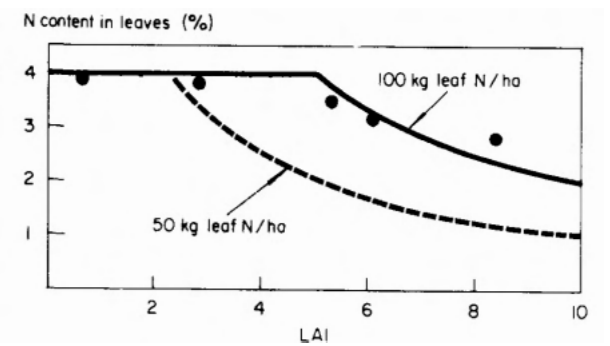
values will be obtained under nitrogen-limiting conditions by plants that reduce LAI to maintain high nitrogen concentration in the leaves. In cassava, an added advantage of this strategy is that at low LAI values the distribution index is also greater.

Recent studies have shown that cassava under low fertility conditions reduces its LAI mainly by decreasing leaf size and branching while maintaining a high unit photosynthetic rate (CIAT 1978).

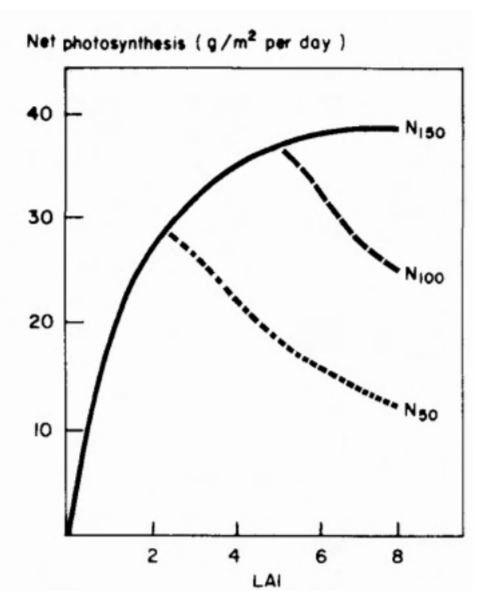
Varietal characters associated with yield

Several authors have suggested a close relation between yield and LAI (Doku 1965, Sinha and Nair 1971, Cock 1976). This relation appears to hold when LAI is small but not when LAI is higher (Irikura et al 1979, Cock et al 1979) or optimum.

Cock et al (1979) studied and reviewed a large number of morphological and development characters of cassava with special emphasis on their genetic variability and their possible interactions. From these data they concluded that root sink was not normally limiting unless roots number less than 7 or 8/m^2, and that yield was



8. Calculated leaf nitrogen contents at different leaf area index (LAI) values and 2 levels of available leaf nitrogen. Points represent data for rice with 150 kg applied N/ha, reported by Cock and Yoshida (1973).



9. Estimated net photosynthesis at different leaf area index (LAI) values at 3 levels of available leaf nitrogen (Duncan et al 1967).

largely determined by the excess of carbohydrates over those needed for top growth. This conclusion is supported by Tan and Cock (1979).

As shown earlier, CGR is largely determined by LAI. The development of LAI is controlled by leaf formation rate per apex, apex or branch number per unit land area, leaf size, and leaf longevity. Little varietal difference in rate of leaf formation per apex was found. However, leaf formation rate per apex declines with time after planting. Branching, which determines apex number per plant, is a varietal character, there being early and late branching types. Branching interval also differs between varieties, but for any one variety, in the absence of stress under given conditions, branching interval is constant. Leaf size increases to a maximum about 4 months after planting 2nd then declines. The decline in leaf size, although modulated by the branching habit (CIAT 1977), occurs in all clones tested. The maximum leaf size is, however, a varietal character. In spaced plants leaf life of leaves formed from 2 months after planting was nearly constant and varied from 60 to 120 days for different clones. Under competition, leaves that received less than 5% of incoming solar radiation fell within 10 days after being shaded. All the parameters of leaf area development were studied with different levels of root sink activity effect. The root sink effect was altered either by root clipping or by ring barking. Root sink changes in no case altered the overall trends observed in normal plants.

These data enabled Cock et a1 (1979) to construct a model for leaf area development. Furthermore, it was possible to determine top growth rate from node weights, specific leaf weights, node production per branch, and branching. In addition, the CGR could be predicted from the LAI, the top growth rate subtracted from CGR, and root growth rate estimated for a number of different genetic combinations. For a full description of the model, the reader is referred to the original text (Cock et a1 1979).

The model predicted that under good conditions with solar radiation about 450 cal/cm^2 per day, maximum yield could be obtained from a variety that at 4 months had a leaf size maximum of about 500 cm^2; a leaf longevity, in the absence of shading, of 15-20 weeks; and 3-point branching at 30 or 45 weeks. Potential productivity of such a variety was slightly less than 30 t dry root/ ha per year under CIAT conditions. Recently under these conditions yields of more than 28 t/ha per year have been obtained (CIAT 1978).

Unfortunately the real world is somewhat different from the disease- and pest-free environment simulated by a computer. The model has, however, been used to test for the reaction of these ideal plant types to diseases and pests (Cock 1978). Complete defoliation by an insect pest will reduce yields of the ideal plant type by about 20% — a finding very comparable to that obtained in the field with local varieties (Belloti pers. comm.). However, the yield variation with diseases that reduce leaf life such as Cercospora (CIAT 1976) is much greater than that in traditional varieties. These data show that the physiologist, in his role as the designer of new plants, should also be aware of the hazards of proposing a plant type that may require much greater levels of disease and pest control than those currently acceptable.

Reaction to adverse soils. Cassava is extremely tolerant of soil acidity and associated high aluminum levels. It showed no response to lime when aluminum

saturation was less than 80% (CIAT 1978). However (pers. comm.) obtained good growth of cassava in solution culture with up to 30 ppm aluminum. In solution culture, cassava grew well at pH values as low as 5.5 and still some grew at pH 3.3 (Edwards et a1 1977). IT showed no response to lime above pH 4.7 in field trials on an acid infertile soil in Colombia (CIAT 1978).

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SUGARCANE

J. E. Irvine

Sugarcane, a perennial grass, is grown on 12 million hectares in 79 countries, from lat. 36.7°N to 31° S. The world's average annual yield of sugarcane stalks is 56 t/ ha. From the largest harvested mass of any field crop, sugarcane is reduced to sucrose and molasses for consumption and to fiber for fuel.

Acclaimed as a leading performer in the photosynthetic conversion of light to chemical energy, sugarcane has photosynthesis rates as high as 100 mg/dm^2 per hour carbon dioxide fixation. However, high rates per unit of leaf area have not been correlated with high yield. More significant is the high rate of photosynthesis per unit of land area, largely influenced by leaf area index (LAI), population density, and somewhat by crop age. While sugarcane grows more slowly than some other C-4 grasses, its high biomass production is due in part to a long growing season.

The total dry matter production rate of sugarcane is 20 g/ m^2 per day, or 75 t/ ha per year. Its theoretical maximum yield is 36 g/ m^2 per day or 129 t/ ha per year. Economic yields of sucrose average 4.7 t/ ha per year, maximum commercial yields average 15 t/ ha per year. Expressed as the ratio of economic yield to total dry matter yield, the harvest index for sugarcane can be 0.2 for sucrose only, or 0.99 for all sugars including fiber for fuel.

BOTANICAL AND ECOLOGICAL CHARACTERISTICS

A monocot, sugarcane belongs to the family Gramineae and the subfamily Panicoidea. The ancestral form is generally accepted as *Saccharum spontaneum,* a species with chromosome numbers ranging upward from 32 (n), and one which probably evolved from *Ripidium (Erianthus)* and *Miscanthus. S. spontaneum* is highly variable in form; usually it is low in sugars and high in fiber. It is found wild from central Africa to central Asia. *S. spontaneum* was probably the ancestor of the north India canes, formerly classified as *S. barberi* and now included in *S. sinense.* These canes were the first to be cultivated for the manufacture of sugar, an industry

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developed in the Indus valley before 200 BC. The *S. officinarum* of Linnaeus, probably a sterile interspecific hybrid, has been lost from collections. What is now recognized as *S. officinarum* is a group of thick-stemmed, soft-fleshed clones with 80 chromosomes (2n). These clones originated in the gardens of New Guinea headhunters, probably as selections from *S. robustum,* another 80-chromosome species endemic to the South Pacific; they were spread through the South Pacitic by prehistoric interisland travellers. European explorers realized the potential of these new clones, and Bligh, of the Bounty, brought *S. officinarum* to the Americas, where it replaced the older Indian variety (Creole) introduced by Columbus. Rapid expansion of the cane sugar industry spurred the development of slavery and subsequent social changes throughout the tropics.

The new *noble* varieties gave higher yields but, after a period of cultivation, succumbed to a complex of diseases. The introduction of new noble clones gave no lasting resistance. In 1888, Soltwedel, in Java, discovered that *S. officinarum* produced fertile seed, a discovery that launched breeding programs around the world. He also made interspecific crosses and a successor, Jeswiet, in 1921 produced the interspecific hybrid POJ 2878 that began sugarcane's green revolution. POJ 2878 rapidly replaced the noble varieties, is still grown commercially, and is involved in the pedigrees of varieties in all the world's sugarcane breeding programs. Modern commercial clones are trispecific and quadrispecific hybrids and occupy more than 90% of the world's sugarcane fields. The interspecific hybrids have a highly variable chromosome number, usually exceeding 100, and form an aneuploid series.

Sugarcane is a perennial grass that can reproduce from true seed, from nodal buds, or, in certain species and a few interspecific hybrids, from rhizomes. A young stalk, whether seedling or vegetative in origin, branches readily at the lower, belowground internodes, forming a compact stool. Once the young stalks provide mutual shading, tillering ceases and terminal growth accelerates and height rapidly increases. Growth continues until water or temperature becomes limiting, or until the terminal bud develops into an inflorescence. After flowering, unharvested stalks begin to regrow from a young lateral bud. If flowering does not occur, terminal growth may continue indefinitely with successive phases of upright growth, lodging, adventitious rooting, and renewed upright growth. Flowering is undesirable in commercial fields.

The number of culms per stool is determined by varietal characteristics and by population; crowding reduces stalk number and diameter. Culm diameter varies from a few milimeters in some clones of *S. spontaneum* to nearly 10 cm in *S. officinarum* and some hybrids; commercial clones range from 2 to 5 cm in diameter. Height, also a variety character, is governed by environmental and cultural conditions, and by flowering. Leaf width and canopy architecture are highly variable. Widths may vary as much as stalk diameter, and commercial hybrids have leaves from 3 to 8 cm wide. Leaf length varies with age and season. Canopy architecture is a distinctive varietal character unrelated to yield. Wide spacing enhances the expression of canopy characters between varieties; crowding erases them.

The widely divergent members of *Saccharum* succeed in a range of habitats extending from the deserts of India and Pakistan to the high-rainfall areas of Assam and New Guinea. Wherever they are found, the wild *Saccharum* spp. show a

preference for watercourses; they are grouped near intermittent desert streams or areas inundated by rivers. Stream-bank habitats provide light as well as water. *Saccharum* thrives in full sun and is intolerant of shade.

Sugarcane is produced commercially from lat. 36.7°N (Spain) to 31°S (South Africa), and from slightly below sea level to above 1,000 m. It is grown on 12 million hectares in 79 countries. India has the largest area, about 3 million ha, in cane followed by Brazil and Cuba with over 1 million ha each. In Asia, individual fields are small (1 or 2 ha), and sugarcane grown as a cash crop is frequently interplanted with subsistence crops. On the other continents, sugarcane is usually produced under monocrop management with individual units as large as 100 ha (same variety and planting, irrigation, and harvesting dates). Efficient family farms in mechanized regions have 20-200 ha; corporation and state farms usually are larger.

Sugarcane has a long growing season, a high water requirement, some salt and drought tolerance, but little cold tolerance. It responds well to high fertility, irrigation, drainage, and abundant sunlight.

LEAF PHOTOSYNTHETIC RATE

Expressed as net carbon exchange, the rate of photosynthesis (p_n) of sugarcane leaves is among the highest found in crop plants. Sugarcane also produces more biomass than any other field crop and it is easy to link the two phenomena. A simple model, with photosynthesis as a valve regulating the flow of carbon into the biomass-generating system, would emphasize the importance of p_n as a regulator of ultimate yield. The genetic or physiologic manipulation of p_n should have a pronounced effect.

Varietal differences in p_n of excised sugarcane leaves held at moderate light intensities were obtained by Hartt and Burr (1967) who separated 4 varieties into 2 groups with a difference in p_n of about 25%. In a field experiment, using a ^{14}C technique on intact leaves, Irvine (1967) found an overall average value of 54 mg/dm^2 per hour for 10 varieties. The highest varietal rate was 2.5 times the lowest. Bull (1969) reported a rate of 100 mg/dm^2 per hour for Australian cane. Rosario and Musgrave (1974) used an infrared analyzer in a field test to compare 14 varieties and found an overall average p_n of 47 mg/dm^2 per hour. The highest varietal rate was 1.9 times the lowest. In a laboratory study using intact leaves and an infrared analyzer, Irvine (1975) compared p_n in 30 varieties represented equally by *S. spontaneum*, *S. officinarum*, and interspecific hybrids. The overall average was 39 mg/dm^2 per hour. The highest varietal average was 3 times the lowest. The p_n of the three groups were clearly different, *S. spontaneum* averaged 51.4, *S. officinarum* averaged 29.7, and the interspecific hybrids were intermediate with an average of 36.0 mg/dm^2 per hour.

Several studies (Rosario and Musgrave 1974, Irvine 1967,1975) have shown that specific varietal characters are related to p_n. There is a strong negative correlation between p_n and leaf width. Foil leaf models with the same dimensions as sugarcane leaves had boundary layers that deepened with increasing width (Irvine 1975), indicating increased resistance to carbon dioxide diffusion at low airflow rates. Specific leaf weight (mg/dm^2) is highly correlated with p_n, as is leaf thickness. Leaf

porosity is positively correlated with p_n, but the number of stomata on the abaxial side is not correlated at all (Irvine 1975). Nor is there any correlation between the chlorophyll content of the normal leaves of different varieties or mesophyll thickness and p. (Rosario and Musgrave 1974).

Factors affecting p_n are the accumulation of metabolites, stomatal behavior, plant health, and angle and age of the leaf. Ham (1963) suggests that accumulation of sucrose in the leaf could inhibit photosynthesis and might slow p_n on days when other factors might favor high p_n. Work by Waldron et al (1967) with excised leaves showed no depression of p_n attributable to sucrose accumulation. They (Waldron et al l967) and others (Alexander 1973, Irvine 1967) indicate that there is no tendency of p_n to drop even under high light intensity unless moisture is limiting. Limitation of p_n by the accumulation of sugar is also unlikely because leaf starch accumulates rapidly during the day, peaking by evening, and disappearing during the night.

Stomatal behavior is governed largely by light intensity, airflow rates, and their interaction (Irvine 1971 b). High light intensity and low airflow enhance stomatal opening and decrease leaf resistance. At high light iritensities, p_n increases as airflow rates increase, even though stomata begin to close and leaf resistance rises. These observations suggest that, unless it is very high, leaf resistance due to stomatal behavior has little effect on p_n.

Four virus strains that caused sugarcane mosaic reduced the chlorophyll content and increased light transmissivity of the leaves of several sugarcane varieties, but only two of the strains significantly lowered p_n (Irvine 1971a). In addition to mosaic, leaf variegation, red-freckling, and frost damage reduced p_n. Chlorotic streak and ratoon stunting diseases had no significant effect on p_n (Irvine 1972).

The photosynthetic rate is highest when the leaf is oriented perpendicular to the incident light source. Burr (1969) and Irvine (1975) attached importance to the leaf angle in the canopy, both favoring (for different reasons) a conformation consisting mostly of upright leaves. Irvine and Benda (1979) found no difference between the photosynthetic efficiency of five varieties with upright leaves and that of five varieties with horizontal or droopy leaves. They observed that varieties that had horizontal or droopy leaves at wide spacings had upright leaves at narrow spacings (Table I).

Hartt and Burr (1967) reported p_n gradients within a blade and between blades on a plant. Very young and old leaves had a lower p_n and the younger, fully expanded leaves had a higher p_n. Waldron et a1 (1967) confirmed that by positioning the leaves in the field so they would not be shaded by younger leaves, and determined that age as well as position affected p_n. Kortschak and Forbes (1968) used leaves of constant age and found that plants at 5 months (grand growth period) had the highest p_n. The rate declined 30% to a plateau at 15 months. Bull and Tovey (1974) verified this and noted a winter rate far below the summer maximum.

Environmental limitations of p_n in sugarcane include light spectral quality and intensity, availability of carbon dioxide, temperature, moisture, and nutrition.

Alexander and Biddulph (1974) state that the photosynthetic-action spectra of sugarcane species differ from those of other plants because rates are higher in the blue (480 nm) spectrum than in the red (620 to 695 nm). The average blue-red ratio for 9 clones of *Saccharum* was 1.57 compared to a previously published mean of 0.7 for 22 other crop plants. The authors found spectral variation among *Saccharum*

Table 1. Photosynthetic efficiency of sugarcane varieties with upright or horizontal leaves.[a]

Variety	Photosynthetic efficiency[b]	
	Narrow spacing	Wide spacing
	Upright leaves	
L 62-96	1.41	0.55
L 60-25	1.36	0.56
Co 281	1.22	0.52
CP 36-13	1.03	0.50
CP 44-101	1.61	0.56
Av	1.33	0.54
	Horizontal leaves	
CP 65-357	1.86	0.63
F 36-819	1.71	0.50
NCo 310	1.05	0.52
Co 290	1.07	0.46
CP 61-37	0.99	0.53
Av	1.34	0.53

[a]Plants were grown in a wheel design with 10 varieties/wheel, 3 radii/variety, and 3 replications (Irvine and Benda 1980). [b]Biomass calories harvested ÷ incident calories × 100.

species. They suggested that breeding might consolidate and reinforce scattered maxima and thus enhance overall p_n for the crop.

The interdependence of light intensity and p_n has been shown in several ways. Kortschak and Forbes (1968) found summer p_n lower than winter p_n even though temperatures were 5° C higher in summer than in winter. They related the lower p_n to less solar radiation due to increased cloud cover and confirmed their observation with artificial shading experiments. Others (Bull and Tovey 1974, Irvine 1967, Hartt and Burr 1967, Waldron et a1 1967) showed a close correlation between p_n and diurnal light variation. P_n declined during midday if clouds obscured the sun or if moisture stress became limiting (Ashton 1956). Waldron et al (1967) found a linear rise in p_n when light intensity was increased from 0.2 to 0.6 cal/cm^2 per minute but no further rise up to 0.9 cal/cm^2 per minute. They found that the youngest, fully expanded leaves in the canopy received 0.6 cal/cm^2 per minute, an intensity reduced to 20% at the level of the lowest, oldest green leaves.

The effect of the availability of carbon dioxide on p_n in sugarcane has been demonstrated by Hartt and Burr (1967), who showed a fourfold increase in p_n when carbon dioxide in air was increased from 0.01 to 0.06%, while saturation occurred at levels about 0.06%. Hartt and Burr, who monitored carbon dioxide levels in a sugarcane field exposed to strong tradewinds and found no change in concentration, concluded that Hawaiian sugarcane leaves had ample carbon dioxide for photosynthesis at all times. Similar work in Louisiana (Irvine, unpubl.) showed that carbon dioxide levels in canopy air were higher at night than during the day and markedly depressed at midday. Unlike fields in Hawaii, those in Louisiana frequently have a uniform canopy, with only light air movement above the canopy and still air beneath. Turbulent mixing is minimal and air movement over the leaf surface is very

slow. Moss (1963) showed that p_n increased with turbulence within a leaf chamber. Irvine (1971b) showed that p_n increased with increased wind speeds. These observations suggest that boundary-layer thickness may be a limiting factor in photosynthesis at low airflow rates.

Working with temperature-equilibrated plants, Waldron found that the photosynthetic process in sugarcane had a Q10 value of 1.1. Others (Alexander 1973) indicate a maximum rate of 34° C with a decline at higher temperatures. Hartt and Burr (1967) reported that when air temperature was lowered from 23.1° to 13.6°C, p_n decreased 84%; a similar decrease occurred when the root temperature was lowered from 22.2° to 16.7° C.

Soil moisture availability has a pronounced effect on photosynthesis. Ashton (1956), using potted plants of a Hawaiian variety, followed the rate from field capacity to permanent wilting. His results indicate a threshold effect, with p_n unaffected, until moisture stress becomes pronounced. As permanent wilting approaches, p_n nears zero and does not recover for several days after the moisture stress is removed.

Hartt and Burr (1967) and others (Alexander 1973) showed that deficiencies of nitrogen, phosphorus, and potassium depress p_n in sugarcane leaves. It would also seem logical that any mineral deficiency resulting in chlorosis would affect p_n, but the data for sugarcane are not available.

It is difficult to verify the model that would have p_n as a controlling factor for yield. Irvine (1975) found no correlation between p_n and yield or any yield component. Rosario and Musgrave (1974) found no significant correlation between p_n and yield of cane or sugar/ ha, although they reported a significant correlation ($p = 0.05$) between p_n and sugar content of cane and between p_n and stalk number.

The interpretation of p_n as a valve for regulating yield ignores the many other factors involved in both yield and the variability of p_n. A complete carbon budget for sugarcane has not been developed, although significant effort has been expended on the metabolic pathways.

Kortschak et al (1965) published the first clue that the C-3 pathway of Calvin and Bassham is not universally applicable. Kortschak showed that sugarcane leaves accumulate usually high amounts of malate as an early product. Hatch and Slack (1966) quickly showed that in addition to malate and aspartate, oxaloacetic acid is an early product of photosynthesis in sugarcane. They established a new pathway which Black (1970) proposed as a major new system for a variety of plants. The full significance of the C-4 pathway has not been determined. Its association with the highly productive tropical grasses, and with dicots capable of growth under unusual conditions, encourages the assumption that it is a more efficient or productive pathway.

Less thoroughly explored than carbon fixation is carbon loss. A major factor in carbon emission by sugarcane is dark respiration. Bull and Tovey (1974) report whole cane respiration rates varying from 0.3 to 0.8 mg/g per hour and dark respiration rates of leaves varying from 0.4 to over 1.6 mg/g per hour, with dark respiration related to prevailing daily solar radiation. Glover (1972) found respiration rates of leaves to be three times that of stalks. A crop of 163 t/ha of millable cane

would have a cumulative respiratory loss of 42 t incurred in production. In the dark the rate of carbon dioxide loss from leaves of sugarcane, maize, and sorghum is approximately 10% of the rate of photosynthesis in full sun (Irvine 1970). It may be significant that *Zea* and *Sorghum,* both of which have higher dark respiration rates than sugarcane, also have a faster growth rate.

Plants having the C-3 pathway respire relatively large quantities of carbon dioxide in the light as well as in the dark. Photorespiration was thought to be absent in C-4 grasses and, in the narrow sense of the glycolate system, it may be. However, Bull (1969) demonstrated photorespiration in a water-stressed sugarcane plant, and Irvine (1970) demonstrated its presence in normal sugarcane, maize, and sorghum plants. A combination of ^{14}C and infrared analyzer techniques showed that sugarcane leaves emit carbon dioxide in the light, but that this emission decreases with increasing light intensity as p_n increases. The respiration curve is almost the reciprocal of the curve of p_n. This suggests that C-4 grasses are able to reincorporate photosynthetically the respired CO_2 before it escapes the leaf.

While less is known about carbon dioxide emission than about its fixation in sugarcane, still less is known about the loss of organic compounds. Sugars and amino acids are leached from sugarcane leaves, but nothing is known of the magnitude of loss or the conditions regulating it. Preliminary evidence (Irvine, unpubl.) suggests the emission of volatile organic compounds from sugarcane. It can be calculated (Coffey and Westberg 1977) that the emission of volatile organic compounds (terpenes, etc) by the earth's terrestrial plants is 0.5 t/ha per year. Because much of the earth's surface is barren or marginally productive, it is probable that a highly productive crop such as sugarcane would emit a larger than average amount of volatile compounds.

CROP GROWTH RATE

Because the stalk is the portion of the sugarcane crop that is harvested, the crop's growth rate has been determined largely as a function of stalk elongation. After the lateral buds on the planted seed piece germinate and emerge, stalk elongation remains minimal from 1 to 3 months while tillering occurs. As the population increases and mutual shading occurs, tillering slows and may even be absent under low light intensity.

Stem elongation in crops of 12 months or less follows the classic pattern; accumulated growth is represented by a sigmoid curve, and incremental growth, by a normal or skewed bell-shaped curve. When the crop length is 24 months or more (Hawaii, Peru), the incremental growth curve is bimodal with higher summer and lower winter growth rates.

Average maximum growth rates in Java, with nearly uniform day lengths and temperatures, have been reported (van Dillewijn 1952) as 2.33 cm/day. Maximum growth rates in Hawaii (Clements and Kubota 1942) with a 2-year crop were 2.3 and 1.9 cm/day for the first and second summers. Winter minimum rates were 0.3 and 0.1 cm/day. In the more extreme climate of Louisiana where there is no aboveground winter crop, a 10-year average maximum growth rate of 2.45 cm/day was

reported (Irvine et al 1968). The absolute maximum growth rate was 3.74 cm/day and the minimum was zero. In Australia, Bull (pers. comm., Davy Agro, Bundaberg, Queensland 4670, Australia) obtained sustained field growth rates of 2.9 cm/day and maximum rates of 3.2 cm/day under optimum conditions.

Factors affecting stalk elongation are temperature, moisture, age, and variety. Temperature and elongation are most closely related. Because stalk elongation occurs primarily at night (van Dillewijn 1952), the daily minimum temperature is a limiting factor in growth, especially in temperate areas. Buds germinate at temperatures as low as 6° C, but leaves grow and tillers usually form above 12° C and stalks usually elongate above 21° C. In Louisiana, mean air temperature and stalk elongation are closely correlated ($r = 0.93$) (Irvine et al 1968). In phytotron trials, Bull (pers. comm.) obtained stalk elongation rates of 2.9 cm/day at a constant temperature of 29° C, 1.2 at 23° C, and 0.8 cm/day at 17° C.

Moisture obviously limits growth under extreme conditions. Unirrigated cane is grown for 2 years in some low-rainfall areas of South Africa with seasonal rainfalls of 60 cm/yr. During the intervening dry season, sugarcane leaves fire completely, but at the advent of the next rainy season the terminal bud regrows. The crop produced in 2 years is equal to that made in 1 year in more fortunate areas. There is a controversy regarding how close the relation is between moisture availability and growth. Quoting an r value of 0.756 for the correlation between the water content of a cane plant and its rate of elongation, van Dillewijn (1952) reports that a sugarcane stem grows at a uniform rate as long as the soil moisture is above the wilting point. In Louisiana (Irvine et al 1968), a correlation between rainfall and growth was spurious and became nonsignificant when temperature variables were eliminated. Soil moisture was not related to growth rate either, but Louisiana has high rainfall and soil moisture may have been adequate at most times.

Plant age and growth rate are intimately related. Even in the tropics, there is little stem elongation during the first several months; the grand growth phase normally occurs from age 3 to 6 months. This period may be delayed until the crop is 5 or 6 months old by fall planting in temperate areas. Borden (1945) found that the highest production of fresh weight in Hawaii occurred when the crop was 3 to 6 months old. At the same season the following year the rate of the unharvested crop growth fell to a quarter of that in the previous year.

Varieties differ in rate of stem elongation and the difference, even in closely related clones, may be striking. However, stalk length is not as important as stalk number in determining yield. Some harvest systems may eliminate any height advantage.

Sugarcane leaves grow in a basipetal direction; the tip expands first and elongation proceeds down the blade and the sheath to the internode. Trimming a leaf will shorten the internode. Small leaves produced under adverse conditions produce short internodes. New leaves are produced at intervals of about one a week under favorable conditions, or one every 2 or 3 weeks under less favorable conditions. Sugarcane leaves vary in longevity; the leaves on young plants may last only a month and those on older plants may live 5 months. The average life expectancy of sugarcane leaves is from 60 to 75 days in Hawaii (van Delliwijn 1952) and Louisiana (Irvine, unpubl.).

LEAF AREA INDEX

The leaf area index (LAI), a function of the leaf expansion rate in sugarcane, is closely related to age and growth rate. The leaf expansion rate of sugarcane is noticeably slower than that of Zea or Sorghum (T. Bull, pers. comm.). The area of individual blades increases from the base to the top of the stalk, reaching a maximum at about 9 months and decreasing if conditions are less than favorable. The total leaf area per stalk is a varietal character that may be affected by location, population, and time of planting. Plants in the period of maximum growth rate do not have maximum leaf area.

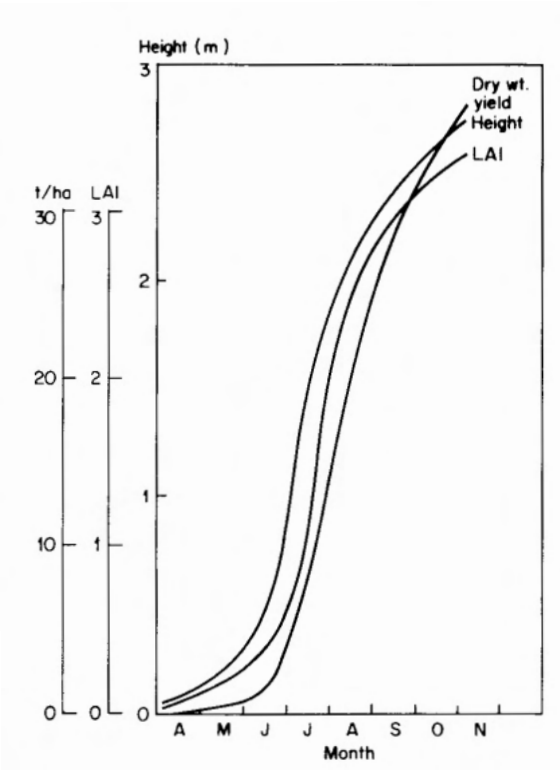
In Taiwan the leaf area of shoots entering the grand period of growth was 1,000 cm^2; that of plants completing this period was 3,000 cm^2. The maximum per shoot was 6,750 cm^2 at 8 months (van Dillewijn 1952). Figure 1 shows that for Louisiana sugarcane, stalk height, biomass, and LAI increase at parallel rates, and the period of maximum growth rate precedes the maximum LAI. In this study, the LAI during the period of maximum crop growth rate was approximately 2 and ranged from 0.6 to 2.6. Bull (pers. comm.) obtained for the maximum growth period LAI values of 5.8 for the plant crop and 3.0 for the ratoon.

Maximum LAI values for plant cane were 7.7 for Zimbabwe, Rhodesia and 7.9 for Australia (K. Cackett, Zimbabwe Rhodesia Sugar Assn. Experiment Station, Zimbabwe, Rhodesia, and T. Bull, pers. comm.). The Rhodesian figure was for 10-month-old NCo 376. As the tillers and older leaves died, the LAI gradually fell to 3.0. In Australia, a cane plant's LAI of 7.9 was followed by a ratoon LAI of 2.5. These values compare with the average Australian LAI values of 4 to 5. Bull and Tovey (1974) reported a maximum LAI of 7.5 at 224 days, which gradually decreased to 6.0 at 336 days. Glover (1972) in South Africa reported a maximum LAI of 5.0 which 5 months later declined to 3.5.

In sugarcane, the LAI is largely a function of population which, at least in short-duration crops, is a function of spacing. In an interrow spacing trial in Louisiana, plants on rows spaced 60, 91, and 182 cm apart had maximum LAI values of 5.7,4.8, and 2.8, respectively. The same variety in equidistant spacings of 15,30,60, and 120 cm produced maximum LAI values of 8.2,6.6,4.8, and 3.3 (Irvine and Benda 1980). The leaf area, stalk number, and yield of the individual plant, which are highest in isolated sugarcane plants, are drastically reduced by very close spacing. However, the effect of increased population is so great that yield per unit area increases exponentially with decreased spacing (Irvine et a1 1980).

TOTAL DRY MATTER PRODUCTION

Glover (1972) estimated that if sugarcane in South Africa used all of 8% of the incident light, the crop should produce 232 t dry matter/ha. Corrections for observed p_n and dark respiration lowered the estimate to 119 t/ ha per year at an accumulation rate of 32.6 g/m^2 per day. Bull and Glaziou's model(1975) predicted a maximum sugarcane yield of 280 net cane ha per year. Adjusting the fresh weight of the stalks to dry matter weight (30%) gives a maximum dry matter yield of 84 t/ha



1. Increase in height, dry matter yield, and leaf area index (LAI) in sugarcane variety CP 65357, plant cane, 5 replications, 1.8 m rows in Louisiana.

per year (23 g/ m^2 per day). Again, adjusting Bull and Glaziou's figure to get biomass by adding the average trash value (35%) gives a maximum total dry matter production of 130 t/ ha per year (35.6 g/m^2 per day). Differences between the two estimates can be reconciled because one is a specific estimate and the other general.

Total dry matter production is not routinely determined in sugarcane trials because leaves and immature stalk material are not desirable in sugarcane processing. Therefore, the dry matter production data in Table 2 are limited, but the table shows that measured yields are a fraction of the predicted maxima. Higher figures have been obtained; Bull (pers. comm.) reports 27.5 g/m^2 per day for field production of aboveground dry matter, and 32.4 g/ m^2 per day in a phytotron experiment where roots were included. Thompson (1978) shows an individual rate for a field of South African sugarcane of 20.1 g/m^2 per day and a rate for a Hawaiian field of 22.3 g/ m^2 per day. The highest short-term (2-mo) production rate was 40.6 g/ m^2 per day in South Africa and 44.0 g/m^2 per day in Hawaii. Thompson's data for South Africa are averaged in Table 2.

A different approach to estimating total dry matter production is presented in Table 3, where yields of cane from commercial or experimental fields are converted to dry biomass. The average yields for the different countries or areas are well below the commercial, experimental, or predicted maxima, and the average calculated yields in Table 3 are close to the observed yields in Table 2. Three of the calculated values in Table 3 (28.2, 30.9, and 31.9 g/m^2 per day) approach the theoretical

Table 2. Dry matter production for the aboveground portion of sugarcane.

Location	Harvests (no.)	Dry matter production Av (g/m^2 per day)	Total (t/ha per yr)	Remarks	Source
Australia	1	16.8	61		Bull and Tovey (1974)
Florida	1	11.0	40	0.5-m rows	Lipinsky et al (1979)
		10.1	37	1.5-m rows	
Hawaii	3	20.5	75		Borden (1942,1945,1948)
Louisiana	1	18.3	46	0.6-m rows	Irvine (unpubl.)
		17.1	43	0.9-m rows	
		14.3	36	1.8-m rows	
South Africa	16	12.4	49	Irrigated, non-irrigated	Thompson (1978)

[a]Dry matter yields adjusted to yearly basis except for the 252-day crop at Louisina, because that area cannot grow 12-mo cane.

maximum accumulation rates of Glover (32.6 g/m^2 per day) and Bull and Glaziou (35.6 g/m^2 per day). These theoretical rates are for an entire crop and are exceeded by maximum short-term rates in South Africa and Hawaii, which in turn are exceeded by the maximum short-term rates of Monteith (1978) for other C-4 crops. However, some of the calculated dry weight yields for commercial and experimental crops (Table 3) exceed the crop yield maximum of Monteith, indicating the advantages of rapid leaf expansion for short-term yield and of a long growing season for long-term yield.

ECONOMIC YIELD

Sugarcane is harvested for chewing, and for the manufacture of alcohol, syrup, molasses, gur (panela), and raw or refined sugar. In much of the sugarcane world, the farmer is paid for the weight of sugarcane delivered free of leaves or soil. Net cane yield forms one basis for determining economic yield and, for the farmer it is the common form. The yield of cane has increased (Fig. 2) with advances in technology. The world average is 53 t/ha. Yields are frequently low in labor-intensive systems, higher in technologically intensive, irrigated areas.

The most valued component of sugarcane is sucrose. Sucrose content, rather than cane weight, is the preferred basis of payment in some areas, and more frequently farmers refer to their harvest in terms of sugar/ha. Sucrose recovered in processing ranges from 7 to 13% of the net weight of cane delivered. Reducing sugars are also present. In processing they are combined with uncrystallized sucrose to form molasses, a salable product in some places and a road surfacing material in others. The clean cane delivered to the mill contains 11-16% fiber (Meade and Chen 1977) and when leafy trash is included, the fiber content is much higher. Farmers are not paid for fiber, but many mills use it as a fuel to replace diesel or natural gas.

Table 3. Average and maximum sugarcane yields and the equivalent total dry matter production.

Location and type	Cane Yield (t/ha per Yr)	Biomass[a] (t/ha per yr)	Biomass[a] (g/m^2 per day)	Source
Australia				
Av	81	38	10.3	Irvine (1 980)
Commercial max	100	47	12.7	Bull (pers. comm.)
Experimental max	193	90	24.6	Bull (pers. cornm.)
	220	102	28.0	Hogarth (pers. comm.)
	250	116	31.9	Ham (1970)
Colombia				
Av	78	36	9.9	lrvine (1980)
Commercial max	202	94	25.7	C. Cassalett, CENICANA, Colombia (pers. comm.)
Experimental mx	219	102	27.9	C. Cassalett. CENICANA, Colombia (pers. comm.)
Iran				
Av	100	47	12.7	Sund and Clements (1974)
Commercial max	167	78	21.3	Sund (pers. comm.)
Experimental max	221	103	28.2	Sund (pers. comm.)
Louisiana				
Av	53	25	6.8	Irvine (1980)
Commercial max	129	60	16.4	Anonymous (1964)
Experimental max	242	113	30.9	Matherne and Irvine (1978)
South Africa				
Av	94	44	12.0	Irvine (1980)
Commercial max	141	66	18.0	Thompson (pers. comm.)
Experimental max	166	77	21.2	Thompson (pers. comm.)
Zimbabwe Rhodesia				
Av	115	53	14.6	Cackett (pers. comm.)
Commercial max	180	84	22.9	Cackett (pers. comm.)
Experimental max	200	93	25.5	Cackett (pers comm.)

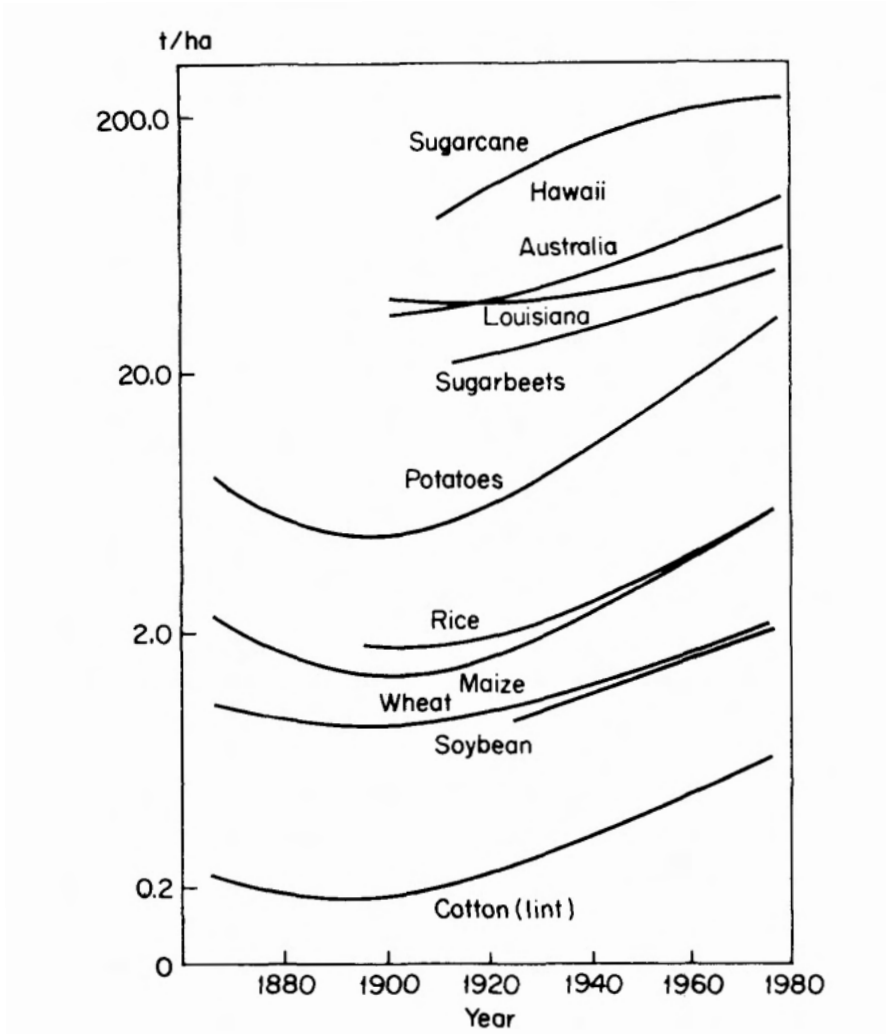
[a]Cane yield was converted to biomass dry matter first by calculating stalk dry wt, then by including the proportion of trash dry wt, as calculated from Thompson (1978). Stalk dry matter = t cane/ha per yr x 0.30. Biomass dry matter = (stalk dry wt x .30) + .65 (stalk dry wt x .30).

The yield of sugar (sucrose) averages 4.7 t/ ha per year worldwide and is higher in areas with intensive technology (Table 4). Yields of 15 t/ ha per year in the irrigated Burdekin District of Australia are outstanding, as are yields of more than 10 t/ ha per year in Iran despite the short growing season. Yields of fiber (in clean cane) approximate the yield of sucrose.

Representative production costs are available for some areas. In 1975, India's average production cost was US$644/ ha (Anonymous 1978), with cane yield of 56 t/ ha or a cost of $11.50 / t. Louisiana's 1979 yield was 47 t/ ha (9-month crop) and costs were estimated at $1,729 /ha (J. Campbell, Louisiana State University, Baton Rouge, LA, unpubl.). Hawaii's 1978 yield of 112 t/ ha per year cost $4,628/ ha to produce.

HARVEST INDEX

Donald's (1962) harvest index relates economic yield to total dry matter. Its application to sugarcane gives highly varying results. With sugar assumed the product of



2. Quadratic regressions of yields, on a logarithmic scale, of the harvested portion of 8 major crops (U.S. data) and sugarcane from 3 areas. Calculated from USDA Agric. Stat. (1936-1978), Hogarth (1972 and personal communication). King (1954), and HSPA Hawaiian Sugar Manual (1979).

most interest, the harvest index for the world's average sugarcane yield would be 0.19 (4.77 t sucrose ha, and 24.65 t dry matter ha). If syrup, gur, or molasses is manufactured instead of, or in addition to, sucrose, then the harvest index is based on all sugars present (10.86%) and the index becomes 0.23 (5.76 t sucrose/ha and 24.65 t dry matter/ ha). Because the fiber in the sugarcane stalk is used as fuel in many mills and is valued at fuel replacement cost, it is permissible to add stalk fiber (less ash) to the economic yield, giving a harvest index of 0.63. Hawaiian producers practice biomass harvesting. They deliver to the mill the aboveground crop and part of the underground crop. When the crop is used for sugar and fuel, with surplus fiber

Table 4. Incident radiation and its conversion into sugar and biomass in several sugarcane areas.

Location	Av daily radiation (kcal/cm^2 per day)	Av sugar yield[a] (t/ha per yr)	Incident calories recovered (%) as		Source
			Sugar[b]	Biomass[c]	
Iran	0.446	10.6	0.10	–	Sund and Clements (1974)
Hawaii	0.425	11.8	0.31	0.98	Gibson (1977)
Australia (Burde kin)	0.412	15.2	0.41	–	BSES (1978)
South Africa	0.404	9.6	0.26	0.8-1.1	Glover (1972), Thompson (1978)
Florida	0.390	7.2	0.20	0.78	Lipinsky et al (1979) Sund and Clements (1974)
Louisiana	0.317	4.6	0.16	0.74	Irvine (un upbl.)

[a] Production data for years when radiation data were available, according to USDA, FAS. [b] Caloric value of sucrose at 3,944 cal/g. [c] Caloric value of dry biomass averaged at 4,100 cal/g.

converted to electricity, the harvest index approaches 0.99. With ash used for fertilizer or on roads, the index nears 1.0.

CLIMATIC FACTORS AND ENVIRONMENTAL STRESSES

Of the environmental variables, temperature probably has the strongest influence on the distribution of *Saccharum* and on the production of sugarcane. Tolerant of high temperatures, intact plants of sugarcane may survive air temperatures near 60° C. Buds on stalk pieces can survive a 20-minute immersion in water at 59.5° C. The record-high temperature survival was in a commercial field in the Khuzistan Desert of Iran (32° N) where sugarcane survived an absolute maximum temperature of 52° C. In this area, the average maximum for July is 46.4°C and the average minimum is 32° C. Sugarcane in this area is skillfully irrigated, and the combination of adequate moisture and high night temperatures ensures maximum stalk elongation and high yields in a relatively short growing season. Much of the world's sugarcane experiences average temperatures of 26-30° C during the growing season. In many areas, cooler temperature (less than 21° C) slows the elongation of the stalk and increases its sucrose content.

Slightly lower temperatures (18.3° C or less) inhibit flowering if they occur during the induction period. That is an advantage in commercial fields because flowering decreases yields. It is a disadvantage for breeders because they may need heated greenhouses to ensure successful crossing programs. Temperatures of 17° C may induce pollen sterility, and supplemental heat may be needed for seed set.

Crop damage from cold seldom occurs at temperatures above 0°C. After exposure to 0° C, cold chlorosis in fields of cane may be seen as occasional white stripes on the leaf blade. Although there are significant varietal differences in field response to cold, a general rule is that a temperature of -2.8° C browns the leaves of young plants, -3.5° C kills the terminal bud of standing mill cane. -5.5° C kills the whole stalk above the ground, and -11°C kills the underground portion of less tolerant varieties.

Solar radiation data for six disparate areas are in Table 4. At 32° N, southern Iran has month after month of abundant sunlight and cloudless summer skies. At 30° N, southern Louisiana has solar radiation that is 70% of that of Iran and its sugar

production per hectare is 43% of that of Iran. Because Iran and Louisiana have cold winters with no appreciable growth and both grow the same varieties, Iran's abundant light and high temperatures must account for much of its higher yields. The ability of sugarcane to use high light intensities effectively is indicated in Table 4 which shows that those areas with the highest yield of sugar per hectare received the highest average amount of solar radiation. High solar radiation is inversely correlated with rainfall. As a result, areas with high solar radiation require irrigation that results in increased production costs.

Day length stimuli in sugarcane are generally negligible in commercial production. Clones of *S. spontaneum* from high latitude flower during 14-hour days and tropical clones flower during 12-hour days. Most commercial clones flower during 12-hour days and, where flowering occurs regularly, breeders select heavily against that trait. In Java, under conditions of similar temperature and moisture availability, shortened internodes were correlated with decreasing day length (van Dillewijn 1952). Similar results can be produced by clipping attached leaves. Day length responses are difficult to separate from other seasonal variables. Farmers in Spain and Morocco, who ripen Louisiana varieties during long summer days by withholding water, no longer think that sucrose storage is a response to decreasing day length.

Although *Saccharum* evolved in the high-rainfall areas from Assam to New Guinea. it has a high capacity for adaptation and survival. Its habitat varies from that of the semiaquatic riverbanks of New Guinea and Indonesia to the deserts of Central Asia. This inherent variability and interspecific fertility have helped breeders produce varieties adapted to a wide range of conditions. Research under desert conditions (Sund and Clements 1974) showed that moisture was sufficient as long as tensiometers at 45-cm depths did not record moisture tensions exceeding 0.25 atm. As is done in many irrigated areas, they used leaf sheath moisture as an irrigation index (Clements 1980) and applied an average of 1.5 cm day of irrigation water over the growing season.

Thompson (1976) compared evapotranspiration (E_t), pan evaporation (E_0), and yields of cane and sugar from different areas. Thompson found that E_t ranged from 660 to 3,840 mm/cane crop. A linear relation existed between E_t and yields of cane (r = 0.95) and sugar (r = 0.75). For each 100 mm of moisture lost, 9.7 t cane ha and 1.35 t sucrose ha were produced. The relation between E_t and E_0 is complicated by the extent of ground cover: E_t/E_0 = 0.3 to 0.4 when ground cover is less than 25%. The correlation between E_t/E_0 and ground cover had an r value of 0.81. For a full canopy E_t/E_0 is estimated at 0.8 to 0.9; however, many irrigators work on a one-to-one replacement basis. Maximum E_0 values reported for 5 countries ranged from 5.7 to 15.7 mm/day.

On the Indian subcontinent, where monsoons may be irregular and the supply of irrigation water sporadic, irrigators apply more water than is required when water is available, thus inducing waterlogging and salinity problems. The efficiency of irrigation water use (water available to the plant water applied) in sugarcane fields is estimated by Gibson (1974) as 35% for furrow irrigation, 70% for sprinkler irrigation, and 80% or more for trickle irrigation. Trickle irrigation research was begun in sugarcane in Hawaii in 1959. Trickle irrigation is now applied to more than a quarter of the irrigated fields. In addition to its efficient use of water, trickle irrigation requires far less labor and reduces weed problems.

YIELD COMPONENTS AND VARIETAL TRAITS

The entire aboveground crop is harvested in a few areas, making the standing crop a single component of yield. But in most areas, leaves, tops, and stubble are left in the fields; so the stalk becomes the significant component. Stalks may represent from 50 to 80% of the aboveground biomass. Improved yields (Fig. 2) in several countries are said to be due largely to the selection of varieties for increased stalk yield. The most significant component of yield is stalk number, and population at harvest is correlated with yield, giving an r value of 0.96 (Matherne and Irvine 1978). Harvest is coordinated with a minimum stalk height, so this component is of secondary importance. Correlations of stalk height and yield have r values of 0.66 (Legendre 1970) and 0.48 and 0.53 (R. Breaux, U. S. Sugarcane Field Laboratory, Houma, LA, unpubl.). These correlations were established with hand-cut cane where topping was varied with height. Extreme height is correlated with lodging (Breaux 1972), which reduces yield when the crop is machine harvested. Stalk diameter and density are associated with yield. Large diameter is associated with poor stubbling and small diameter with high fiber. Density is increased by sucrose content and decreased by pithiness or lacunae.

The sucrose content of the stalk is a major yield component, and within the genus sucrose ranges from 3-18% of the stalk weight (Alexander 1973). In most countries, harvest is begun when sucrose levels rise naturally to acceptable levels of 7 to 9% and purity (sucrose divided by soluble solids) is near 70%. Harvest is a year-long process in Hawaii, Peru, and Colombia, and sucrose level and purity are regulated by withdrawing water, or by applying ripeners to inhibit growth and increase sucrose. Sugar recovery has fallen in some countries and risen in others. Where it has fallen, the decrease has been attributed to high tonnage varieties, mechanized harvesting, and extended milling seasons. Where it has risen, the increase has been credited to plant breeders and improved varieties.

Fiber is also a yield component although its desirability depends on the availability of cheap petroleum. Fiber is used primarily as a fuel, although paper of acceptable quality is made in several countries and furfural is produced in others. Pilot studies have shown that the rind of the sugarcane stalk is a promising raw material for synthetic lumber. Fiber accounts for 5-50% of the stalk weight in *Saccharum* and for 9-18% in commercial varieties. Breeders have selected against high fiber because millers complain of losing sugar in the stalk residue (bagasse) as it leaves the mill. Surplus fiber not sold for paper etc. is used to generate steam for producing electricity that in some areas is fed into the national grid. Fuel shortages make the generation of electricity from fiber an attractive prospect. Renewed interest in fiber may change selection criteria and even lead to the selection of varieties with greater photosynthetic efficiency.

Except in a few Asian countries where the entire plant is dug out and processed. sugarcane is grown for several years from one planting and stubbling contributes greatly to accumulated yield. Clones of *S. officinarum* collected from New Guinea gardens will stubble only if one stalk at a time is harvested. Complete harvest results in the death of the stool (J. Skinner, Queensland Bureau Sugar Experiment Station, pers. comm.). Other varieties, selected for hand harvesting, may survive complete

harvesting for 15 to 20 cycles, but when they are machine harvested the potential number of harvests is reduced. Because the biggest single expense in producing the crop is planting, good stubbling ability is prized. Other factors affecting stubbling ability are weed competition and overwintering. In temperate areas, the ability to overwinter is affected by low temperatures, high water tables, and weak pathogens.

YIELD POTENTIAL

Yield potential in any crop is the expression of environmental, managerial. and technological potentials. After agriculture became established, yield potential was largely a function of environment, because as a class, farmers were conservative and made few, managerial or technological changes. From the early development of seeding, tillage, and irrigation practices to the modern development of mechanization and chemical protectants. the 9,000-year history of crop production was saved from tedium only by the introduction of new crops and the development of the concept of plant nutrition.

Long-term yield records are fragmentary, and continuous records for the United States are available for fee crops and these only since 1866. Yields of cotton, maize. and wheat did not change appreciably from the beginning of record keeping in the 19th century to the end of the first quarter of the 20th century. In about 1930 yields of these crops began to increase at a remarkable rate. Rice yields were increasing by 1890, and potato yields had stabilized and began to increase by 1910 (USDA Agricultural Statistics) through 1978. Figure 2 shows the regression curves for yields of 7 major crops and for sugarcane in 3 areas; all regressions were highly significant.

The immediate reaction may be to question why the increase occurred. Environmental changes can be dismissed because the data are from the entire U.S. mainland. Hawaii, and Australia. The primary cause must be managerial and technological improvements. A discussion of managerial changes is best left to others except for the observation that managerial improvement depends on incentive, and incentive depends on gain.

Technological improvement began with the adoption of mineral fertilizers, a gradual process that began in the 19th century. Plant protection took a large step forward with the discovery of Bordeaux mixture in 1882, and the use of herbicides began with the development of sodium chlorate in 1935. The U. S. production data show dramatic yield increases for cotton, maize, rice, and potato beginning about 1940, and for wheat about 1950. Just before and during this period, American agriculture was undergoing a revolution. Tractors had virtually replaced animal power; mechanization was becoming sophisticated. And the 1940s saw the development and rapid use of a wide range of agricultural chemicals: DDT, 1940; 2,4-D. 1942; MCPA. 1945; parathion, 1945; TCA. 1947; dieldrin, 1948; and folpet, 1949 (Geissbuhler 1979). The subsequent development of crop protectants has increased steadily. Not to be overlooked is the contribution of plant breeders to yield increases and the adaptation of crops to changing practices.

Ronner (1962) expressed the opinion that crop yields were approaching their limits. He felt that further increases might follow the breeding of plants with more efficient chloroplasts (perhaps anticipating C-4 photosynthesis). However, U.S.

yields continue to rise, setting new records every year. The regression curves of Figure 2, and those of six out of eight sugarcane-producing areas, indicate that Bonner was too pessimistic. The optimistic view for sugarcane is that yields can continue to increase. This opinion is reinforced by other considerations. Glover (1972) stated that the observed yield for South Africa was 70% of his theoretical. maximum yield. However, the average yield for South Africa (Table 9) is 47% of his theoretical maximum and 34% of that of Bull and Glaziou (1975). Models for maximum yields are based on the limitations as we understand them, not necessarily as they might really be. Ham (1970) obtained the closest yield (89%) to Bull and Glaziou's maximum, and Bull (pers. comm.) feels that there may well have been cases where fields have achieved or exceeded his theoretical maximum.

Aside from the differences between theoretical and achieved yields, higher yield potential can be predicted from improved breeding. Higher yields of cane in Australia and Hawaii (Fig. 2) are said to result from improved varieties. Part of the increase could be attributed to disease resistance and part to varieties that are inherently high-tonnage producers. Breeders in Louisiana and Argentina have made significant improvements in sucrose content, bringing sugar recoveries from 70 to 100 kg/ t of cane milled. The trend to higher tonnage and sucrose content continues and could accelerate if breeders disregard characters such as low fiber and high purity — selection criteria that tend to decrease the frequency of high-yielding varieties. Breeding for total carbon may be more productive.

Previously I said that the rate of photosynthesis per unit of leaf area was not positively related to yield, but that the rate per unit of land area was. Increased photosynthesis per hectare is achieved by increasing the LAI, which rises with increased population. The most practical means of increasing population in temperate areas is to place the rows closer together or to widen the band of cane planted in a row. Louisiana, whose cane-growing season is the world's shortest and yields, among the lowest, has the widest row spacing. Experiments on population increase (Matherne and Irvine 1978, Irvine and Benda 1980) show that Louisiana has the biological and environmental potential to support cane yields three times the present average. But the technology to achieve these potentials on a large scale is not yet available.

Interrow distances in much of the sugarcane world have been fixed at 1.5 m to accommodate mechanization. A long series of experiments in Hawaii indicated that, with its 2-year crop, rows should be spaced 1.2 m apart (trickle irrigation is being done between 2 cane lines per row on rows 1.8 m apart). Because of the renewed interest in row spacing, several groups are studying possible systems based on radical changes in harvesting procedures.

The surest prediction for sugarcane is that yields will continue to rise if breeders, production agronomists, plant protection specialists, and engineers continue to contribute new information to crop production managers.

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OIL PALM AND OTHER TROPICAL TREE CROPS

R. H. V. Corley

The productivity of seven tropical perennial crops is reviewed. The most productive crops (sago palm, oil palm, rubber) have crop growth rates exceeded only by some of the C-4 grasses. The high growth rates result mainly from high leaf area indices maintained by the perennials throughout the year. Productivity on a daily basis is not outstanding.

Harvest indices for perennial crops, when considered in energy terms, are about 50%, and economic yields exceed those for annual crops.

In several of the crops, fully exposed leaves reach temperatures much higher than the optima for photosynthesis. Some crops (cocoa, tea, coffee) are usually grown under partial shade. That helps reduce leaf temperatures, but crop growth rates under shade are low.

In this paper, I review the available data on the productivity of tropical perennial crops, and briefly compare these crops with annuals. Discussion is limited to those crops for which I have data. Although only seven crops are considered, the range of harvested products involved is wide. These products include seeds (coffee, cocoa), fruit coat and seed oils (palm, coconut oil), vegetative shoots (tea), latex (rubber), and starch from stem storage tissue (sago). This diversity of products corresponds to a diversity of plant types and agricultural practices.

Purseglove's excellent works (Purseglove 1968, 1972) show that there are numerous other important tropical tree crops, but I have only been able to find productivity data for those mentioned above. I have excluded a lot of data on the productivity of tropical rain forest, timber from which is an important product in many tropical countries, and have considered only those species that are grown as agricultural crops. Cassava and sugarcane, although not tree crops, are sometimes grown as semiperennials. They are discussed by other authors in this symposium.

The scarcity of productivity data on perennial crops is easily explained. The plants are often massive and difficult to handle (a single mature oil palm may have a fresh weight of more than 2 t, and a dry weight of over 500 kg). Many crops have an

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economic life of 25 years or more and individual plants have a high value; thus the number of plants available to a research worker for destructive analysis is often severely limited for economic reasons. Most workers have developed nondestructive methods for estimating plant dry weight, leaf area, and rate of dry matter production. The data obtained by such methods may be viewed with circumspection by those more familiar with annual crops. However, the annual repetition of measurements on the same trees may give more reliable data than conventional destructive growth analysis.

ORIGINS, ECOLOGY, AND USES

Oil palm

The oil palm (*Elaeis guineensis* Jacq.) originated from West Africa, where, according to Zeven (1967), its natural habitat was in swamps and along river banks, areas too wet for true rain forests. The palm has a single stem; pinnate leaves radiate from the apex to form a hemispherical canopy, Separate male and female inflorescences are borne in the axils of the leaves; the sexes are not normally produced simultaneously, so cross-pollination is the rule. The main product is palm oil, obtained from the mesocarp of the fruit. Palm kernel oil, which has a different fatty acid composition, is produced in smaller quantities, and the kernel cake remaining after oil extraction is used as a source of protein in animal foods. Propagation is by seed, although vegetative propagation by tissue culture is being introduced (Corley et al 1977,1979).

Coconut

Harries (1979) suggests that the coconut (*Cocos nucifera* L.) may have originated in a now largely submerged area of the South Pacific. From there, it spread, either naturally or through man's influence, throughout the tropics. Like the oil palm, the coconut has a single unbranched stem and a crown of pinnate leaves, with inflorescences borne in the leaf axils. Each inflorescence has both male and female flowers. The coconut has numerous uses, but in plantations the primary product is copra, the solid part of the endosperm. It may be consumed directly, either fresh or as desiccated coconut. Usually, however, coconut oil is extracted and the residue is used as animal food. Other products include coir (fiber from the mesocarp) and timber. Propagation is by seed. Because an individual tree produces only 50-100 nuts/year, breeding progress is very slow.

Sago

The sago palm (*Metroxylon* sagu Rottb.) originated in New Guinea and Melanesia, where it forms extensive forests in swampy areas. Sago palms are hapaxanthic, that is, once-flowering. The vegetative phase lasts for 7-15 years during which up to 200 kg dry starch/ tree accumulates in the trunk. A massive terminal inflorescence is produced after the vegetative phase. Because much of the stored starch is used during flowering and fruiting, the trees are best harvested just before flowering. The stem dies after fruiting, but lateral suckers produced during the vegetative phase

continue to grow. Most of the world's supply of sago starch is harvested from wild trees, but a system of continuous cropping has been developed in Malaysia (Flach 1976). Harvested stems are regularly replaced by suckers in such a way that annual harvesting of a portion of the stems is possible.

Rubber

Hevea brasiliensis (Willd. ex Adr. de Juss.) Muell. Arg. originated in the tropical rain forest of the Amazon Basin. The plant contains latex in all its parts. It is tapped by removing thin parings of bark from the trunk and collecting the latex that flows from the cut. The latex flows for a few hours, coagulates and plugs the latex vessels. Tapping is usually repeated every second day, although many different tapping systems are used. Rubber is normally propagated vegetatively by budding selected clones onto seedling root stocks.

Cocoa

Theobroma cacao L. is a small understory tree from the South American tropical rain forest, where it usually grows along river banks. It is cauliflorous, that is, the flowers and fruits are borne on the trunk and main branches. The seeds are fermented and dried, and the dried beans processed to yield cocoa powder and cocoa butter. Propagation is generally by seed. Vegetative propagation by cuttings or bud grafting is possible, but as almost all branches are plagiotropic, it is difficult to train rooted cuttings to produce erect bushes.

Coffee

There are three important species of coffee: *Coffea arabica* L., *Coffea canephora* Pierre ex Froehner, and *Coffea liberica* Bull ex Hierno. The first two species produce 99% of the world's coffee (Purseglove 1968). *Coffea arabica* originated in Ethiopia, 1,500-2,000 m above sea level; *Coffea canephora* occurs in lowlands throughout equatorial Africa; and *Coffea liberica* is found in West Africa. All three species are understory shrubs or small trees. They are generally grown from seed, although vegetative propagation by cuttings or grafting is possible. The pericarp is removed before or after the fruits are dried in the sun. The dried seeds are roasted before use.

Tea

Camellia sinensis (L.) O. Kuntze originated in the highlands of eastern Asia. It is widely cultivated in the subtropics and tropical highlands. Under natural conditions, the tea tree grows to about 15 m, but under cultivation it is pruned and trained as a bush about 1 m high. Young vegetative shoots are plucked, partially dried, crushed, and fermented (oxidation of polyphenols occurs during this stage), and further dried. In the production of green tea, the fermentation stage is omitted. Tea is propagated either from seed or from cuttings.

MAJOR CROP PHYSIOLOGICAL PARAMETERS

Leaf photosynthetic characteristics

The available data on photosynthesis are summarized in Table 1. The maximum observed rates of CO_2 uptake for oil palm and rubber vary with leaf age (Corley

Table 1. Leaf photosynthetic characteristics of 6 tropical perennial crops.

Crop	Max observed rate (mg CO_2/dm^2 per hour)	Light saturation (% of full sunlight)	Temp optimum (°C)	References
Oil palm	> 20	25	33	Corley et al 1973, Hong and Corley 1976
Sago	13	17	–	Flach 1976
Rubber	20	? 25		Samsuddin and Impens 1979a, b
Coffee	7	3-10	20	Tio 1962, Nunes et al 1069, Sondahl et al 1976, Yamaguchi and Friend 1979
Cocoa	6	3-20	35	Guers and Mousseau 1979, Hutcheon 1977a, Owusu 1980
Tea (shade leaves)	10	5		Barua 1970,
Tea (sun leaves)	> 20	20	c. 35	Hadfield 1968

1976, Samsuddin and Impens 1979a), and between progenies or clones (Corley et al 1973, Samsuddin and Impens 1979b), but for both crops the maximum rates are comparable to those recorded for other species with the C-3 photosynthetic pathway. For the understory shade plants coffee and cocoa, the maximum rates appear to be lower, although the results for tea suggest that the rates may largely depend on the conditions under which the leaves develop. As observed for other species, shade leaves of tea have lower maximum rates than sun leaves. Another characteristic of shade leaves is the low light intensity required for saturation of the photosynthetic response. For oil palm, sago, rubber, and sun leaves of tea, the saturating light intensity ranges from 17 to 25% of full sunlight. For coffee and shade leaves of tea, it is below 10% of full sunlight; in cocoa, it is from 3 to 20% of full sunlight, depending on whether the leaves developed in shade or in direct sunlight (Owusu 1980).

The optimal temperature for photosynthesis for these tropical species, except *Coffea arabica* (which originated some 2,000 m above sea level), is appreciably higher than for temperate species with the C-3 photosynthetic pathway.

Crop growth rates

The maximum crop growth rate (CGR) values observed are in Table 2. With one or two exceptions, it is doubtful whether they represent the maximum values attainable. First, there are considerable differences between environments. For example, in oil palms planted at commercial densities (120-150/ha), Rees and Tinker (1963) measured rates of dry matter production of 15-20 t/ha per year in a part of Nigeria that experiences a 4-month dry season every year. In Malaysia, where no such dry season normally occurs, Corley et al (1971a) found CGR values ranging from 27-33 t/ha per year. On a fertile volcanic soil in New Britain, Breure (1977) recorded a CGR of 35 t/ha per year. Again, in a spacing trial in West Cameroon (with a regular dry season), the highest total dry matter production observed was 27 t/ha per year, at a density of 235 trees/ha (Ward, 1973 personal communication). In two trials in Malaysia, the CGR at similar planting density and palm age was 34 t/ha (Corley 1973a) and 35.6 t/ha (Corley and Hew, unpubl.). Rates were higher at higher planting densities.

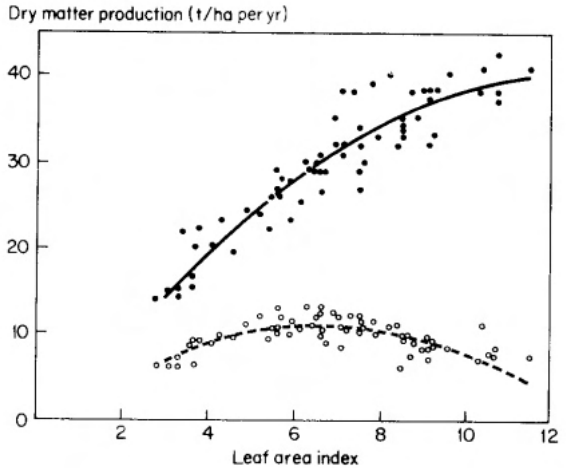
Table 2. Crop growth rate (CCR) and leaf area index (LAI) values of 7 tropical perennial crops.

Crop	Site	Max CGR (t/ha per year)	LAI at max CGR	Reference
Oil palm	Malaysia	40	10.12	Corley 1973a
Coconut	Ivory Coast	31	3	see text
Sago	Malaysia	53	6-8	Flach 1976
Rubber	Malaysia	36	6	Templeton 1968
Cocoa	Malaysia (shaded)	22	10	Thong and Ng 1980 (see text)
	Sabah (unshaded)	30	-	Lim 1980 (see text)
Coffee	Kenya	15	2.2	Cannell 1971a
Tea	Northeast India	about 15	about 5	Hadfield 1974

Another important point is that, in the case of oil palm, the CGR values listed were not from spacing trials, but from trees planted at normal commercial planting densities. For some crops, the density giving maximum economic yield may be considerably lower than that giving maximum rate of dry matter production. For example, for the oil palm (Fig. 1) the maximum economic yield was obtained at a leaf area index (LAI) of about 6, with a total dry matter production of about 30 t ha per year. At higher LAI, as competition between trees increases, vegetative growth begins to predominate, harvest index (HI) declines drastically, and, although total dry matter production may reach 40 t/ha per year, economic yields are reduced. The maximum economic yield is obtained at 150 to 160 trees/ha, whereas CGR is maximized at more than 300 trees/ ha.

Oil palm. Destructive growth analysis of oil palm has been done by Rees and Tinker (1963) in Nigeria, and by Ng et a1 (1968) and Corley et a1 (1971a) in Malaysia. Corley et a1 (1971b) also developed nondestructive methods for estimating rates of dry matter production by the oil palm, and these methods have been widely applied. Corley and Hew (unpubl.) compared destructive and nondestructive methods within a single experiment, and obtained reasonable agreement. However, the errors attached to the destructive measurements were much larger than those for the nondestructive measurements because of the small number of trees sampled destructively. The figure of 40 t dry matter/ ha per year probably represents the maximum obtainable for oil palm, at least in Malaysia. Figures obtained from two spacing trials have been very similar, and both destructive and nondestructive measurements indicate a similar maximum.

Coconut. The productivity estimate here is a composite from several sources. The mast productive cultivar now planted is the Malayan dwarf × West African tall hybrid. Vanialingam et a1 (1980) give some information on its yield, trunk growth, rate of leaf production, and leaf dry weight in Malaysia. Their figure for leaf dry weight appears very low compared with data collected in the Solomon Islands by Friend (unpubl,), and probably refers to the dry weight of only rachis + leaflets, excluding the petiole. I have therefore assumed a dry weight of 3.5 kg/leaf, based on Friend's data. Calculations based on these sources indicate a CGR of 23 t/ ha per year. Quvrier and Qehs (1980) show appreciably higher yields than Vanialingam et a1 for the same hybrid. It is unlikely that these higher yields are obtained at the expense of vegetative growth, because the coconut probably behaves just like the oil palm



1. Crop growth rate (CGK) and yield of fruit bunches (dry wt) in relation to leaf area index, for 6-year-old oil palm in Malaysia (from Corley 1973a). The points are plot means, the lines are fitted quadratic curves. • = CGR, o = yield.

(Corley 1973a) in giving vegetative growth priority over reproductive growth (next section). Thus the vegetative dry matter production of the palms studied by Ouvrier and Ochs is likely to be at least equal to that calculated from the two other sources. Combining the yield from Ouvrier and Ochs (6.7 t copra, at 6% moisture, plus 12.9 t husk and shell) with vegetative dry matter data from the other sources indicates a CGR of 31 t/ha per year for palms planted at a commercial planting density. Probably, as with the oil palm, higher productivity could be obtained at higher planting densities, although with lower economic yields.

Sago. Flach (1976) gave a rough estimate of the CGR of sago under plantation conditions in Malaysia. Trunk growth rate was estimated from starch yield data provided by sago farmers. These starch yields have been independently confirmed by Tan K. L. (personal communication). Leaf production rates were measured in a greenhouse experiment in the Netherlands. For oil palm, leaf production under greenhouse conditions in Europe is lower than in the field in the tropics. On the other hand, mature oil palms have lower leaf production rates than young seedlings. Flach's studies were conducted with sago seedlings. Because no measurements of leaf dry weight were available, Flach used dry weights of oil palm leaves, which are comparable in size to sago leaves. The source of his oil palm leaf weights is not stated, but the weights are low compared with those of mature oil palms in Malaysia. Therefore, again it is likely that the leaf weight was underestimated. The CGR of 53 t/ ha per year may therefore be an underestimate. The planting density used by the sago farmers, although determined by trial and error and not from a spacing experiment, may well be close to that giving maximum total dry matter production.

These palms are grown in tidal (but not brackish) swamps. They are probably never subjected to water stress. No fertilizers are applied, but silt is regularly

deposited during tidal flooding of the swamps. The high productivity of other swamp communities is well documented (Westlakc 1975).

Rubber. Shorrocks (1965) and Templeton (1968) both did destructive growth analysis of rubber trees. Shorrocks et al (1965) and Templeton (1968) observed a close relation between total dry weight of the shoot and stem girth, and Templeton used this relation in estimating rate of dry matter production. The maximum CGR observed by Templeton was, again, determined in a commercial planting.

Cocoa. Thong and Ng (1980) did destructive growth analysis on a small number of cocoa trees growing under overhead shade in peninsular Malaysia. The total dry weight of the trees increased by 11-15 t/ha per year; to this should be added 4.5 t/ha of leaves fallen and replaced during the year (Yegappan, personal communication). Yield of beans increases with age and the highest yield recorded by Thong and Ng was 1.3 t dry beans/ha per year. Inclusion of the dry weight of pod husks gives a total of 2.6 t ha, and a maximum CGR of 22 t/ha per year.

On deep soils with adequate moisture, yields from cocoa without overhead shade are much higher. Lim (1980) gives a maximum yield of 4.4 t/ha from cocoa grown with lateral shade (windbreaks) in Sabah. Including pod husks, this is equivalent to 8.6 t dry matter/ ha. Lim gives no dry weights of vegetative parts, but an estimate is possible from stem girth measurements, because the data of Thong and Ng show a high correlation between stem girth and total tree dry weight, as has been observed in rubber (Shorrocks et al 1965. Templeton 1968). Lim measured stem girth at 30.5 cm above ground level, and obtained values virtually identical to those measured by Thong and Ng at 10 cm above ground level on trees of the same age. Girth at 10 cm appears to be about 14% greater than that at 30.5 cm (my unpublished observations), indicating that the total dry weight of Lim's trees was perhaps 14% greater than those of Thong and Ng at the same age. The maximum rate of vegetative dry matter production in unshaded cocoa in Sabah might therefore have been 22 t/ha per year; these yield data indicate a CGR of just over 30 t ha per year.

Coffee. The figure for coffee (Cannell 1971a) refers to a crop covering only one-third of the ground area. Huerta and Alvim (1962) estimated that, with complete ground cover and a LAI of 10, coffee productivity might be about 30 t/ha per year. However, Maestri and Barros (1977) considered this unrealistic.

Tea. The productivity figure for tea is for the crop grown without overhead shade (Hadfield 1974).

Leaf area index and canopy structure

The LAI values at which the maximum recorded CGR were obtained are shown in Table 2, but because some of the CGR given are probably not the highest obtainable for the crop, not too much significance should be attached to the figures.

In contrast to many crops, leaf area per tree for the oil palm and coconut is little affected by planting density, except at very high densities. The LAI up to at least 8 is thus almost directly dependent on planting density (Fig. 1). At higher densities, senescence of the older, heavily shaded leaves is accelerated, and a ceiling LAI of about 12 is reached (Corley 1973a). Ceiling values for the other crops are not known.

The canopy of a young oil palm seedling nursery is strongly erectophile, with more than 70% of the leaves at angles exceeding 45% to the horizontal. The extinction

coefficient for light penetration may be as low as 0.3 (Hong 1979). Acock et a1 (1970) pointed out that nonrandom distribution of leaflets (such as that which occurs in an oil palm canopy with few, widely spaced, growing points) will lead to a low extinction coefficient. A coefficient of 0.44 was found in a mature oil palm stand, although in older palms the canopy is more plagiophile (Corley 1976). With such low extinction coefficients, a high optimum LAI is expected.

The cocoa canopy allows less light penetration; extinction coefficients range from 0.57 to 0.84 (Alvim 1977, Hutcheon 1977b) It seems unlikely that a LAI as high as 10 (Thong and Ng 1980) is optimal for cocoa, and Alvim (1977) and Hutcheon (1977b) indicate that values of 3-5 are normal.

Harvest index

In perennial crops, where vegetative growth and synthesis of the economic product occur simultaneously, harvest index (HI) is calculated in terms of the partition of total dry matter product over a period of one or several years. Maximum observed harvest indices are listed in Table 3. Two points should be noted:

1. The economic product of several of the crops considered has a high energy content per unit dry weight (oils, rubber). In these crops partition ratios calculated in terms of energy give a different picture compared with the ratios calculated in terms of dry matter. Table 3 gives both dry matter and energy HI values. In terms of energy, the highest HI values appear to be about 50%. Cannell (197 1 a) reported a HI up to 70% for coffee, but this figure was for only part of a year, and it is unlikely that it could be maintained for a full year.
2. At least for some of the crops, maximum HI values can be achieved only at planting densities considerably lower than those giving maximum total dry matter production. For the oil palm, for example, at a planting density giving maximum total dry matter production, HI (for dry matter) may be as low as 10% (Corley 1973a). The vegetative growing point appears to be a more powerful sink than the developing inflorescences; thus, as the level of intertree competition increases, and dry matter production per tree is reduced, vegetative growth takes priority over reproductive growth (Fig. 2). Similar results follow partial defoliation: the amount of dry matter incorporated in vegetative parts remains constant, while flowering and fruiting may stop completely (Corley 1976). During the dry season in Nigeria, complete inflorescence abortion may occur (Broekmans 1957), but the rate of leaf production is not reduced (although leaf expansion may be delayed). Observations suggest that the coconut behaves similarly: at high densities, extensive inflorescence abortion occurs, but there is no visible reduction in vegetative size. Cocoa probably shows the same kind of response. Alvim (1977) noted that cherelle wilt (loss of young pods) is greatest during periods of intensive leaf growth, indicating that the young leaves are stronger sinks than young fruits. For shaded cocoa, Mainstone (personal communication) considers that a LAI of 10 is too high and leads to excessive vegetative growth at the expense of pod production.

Coffee may behave differently. Cannell and Huxley (1969) showed that fruits were the primary sink for ^{14}C that did not move to the shoot tips or trunk when assimilate supply was restricted during the dry season. Dieback of vegetative shoots may occur

Table 3. Maximum harvest index (HI) values observed in 6 tropical perennial crops.

Crop	Product	Max HI observed (%)		Source
		Dry matter	Energy	
Oil palm	Oil	34	52	Best individual trees (Corley, unpublished)
Coconut	Copra	20	31	Estimated from Ouvrier and Ochs 1980 (see text)
Sago	Starch	41	41	Flach 1976
Rubber	Rubber	31	52	Best clone (Templeton 1969)
Cocoa (shaded)	Cocoa beans	7	11	Thong and Ng (1980), Lim (1980)
(unshaded)		15	22	
Tea	Tea	33	33	Hadfield (1974)

if a period of heavy fruiting coincides with low carbohydrate reserves (Maestri and Barros 1977).

For sago and rubber, the relative sink strengths of vegetative growth and of starch or latex production are not known, but data given by Mainstone (1970) indicate that latex yield per tree may be more markedly reduced than shoot dry weight by an increase in planting density.

Economic yields

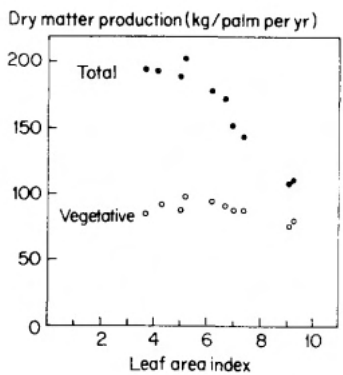
Good commercial yields for the various crops considered are listed in Table 4. The highest yields I know are also listed.

The only information on cultivated sago is that of Flach (1976). Other published data are on production of wild or semiwild sago swamps where yields may be about 10 t starch ha per year.

DISCUSSION

Leaf photosynthesis

Maximum leaf photosynthetic rates generally bear little relation to productivity under field conditions. Many of the leaves in a canopy with high LAI will be shaded



2. Effect of increasing leaf area index (by increasing planting density) on vegetative and total dry matter production per tree (oil palm). The difference between these represents yield of fruit bunches (data from Corley 1973a).

Table 4. Economic yields of 7 tropical perennial crops.

Crop	Product (dry wt)	Good yield (t/ha per yr)	Approximate max recorded yield		Reference
			t/ha per year	g/m^2 per day	
Oil palm	Palm oil	5-6	8.6	2.5	Corley et a1 1976
Coconut	Copra	34	6.3	1.8	Ouvrier and Ochs 1980
Sago	Starch	–	25.0	6.8	Flach 1976
Rubber	Rubber	2	4.5	1.2	R. Shepherd (personal communication)
Cocoa beans	Cocoa beans	2-3	4.4	1.2	Lim 1980
Coffee	Coffee beans	2	4.3	1.2	Browning and Fisher 1976
Tea	Tea	34	6.1	1.8	Purseglove 1968

below the level for light saturation of photosynthesis, while fully exposed leaves are often subject to water or temperature stress, which restricts photosynthetic rate. In particular, with high relative humidity and low wind speeds in the humid tropics, both transpirational and convectional cooling of the leaf will be limited, and leaf temperatures high. For example, fully exposed oil palm leaves may reach temperatures of more than 10° C above ambient, and well above the optimum for photosynthesis, even in plants not subject to water stress (Hong and Corley 1976). In palms subject to water stress, midday closure of stomata occurs (Rees 1961, Corley 1973b). In coffee, leaf temperature may sometime be 20° higher than ambient (Alvim 1958), and temperatures may reach 40°C (Cannell 1971b). Such temperatures are considerably above the optimum for photosynthesis (Nunes et al 1969). It appears that in coffee, midday closure of stomata occurs in fully exposed leaves during both dry and rainy seasons (Maestri and Barros 1977). In cocoa, photosynthetic rate is lower in leaves exposed to full sun than in partly shaded leaves (Alvim 1977), and leaf temperatures may reach 40° C (Hutcheon 1977a).

Coffee, tea, and cocoa are often grown under shade provided by widely spaced trees of various species. Different authors have obtained conflicting results on the effects of overhead shade on yield. In general, shade removal will be beneficial when the additional photosynthesis resulting from better light penetration into the crop canopy exceeds any reduction in photosynthesis due to stress in the upper canopy layers. This is likely to be true under good growing conditions; under poorer conditions, the stress effect may predominate and shade removal will be disadvantageous.

The effect of shade may also depend upon canopy structure. Hadfield (1968) showed two canopy types in tea: the Assam type, with large horizontal leaves, and the China type, with small semierect leaves. Leaf temperatures in full sun were lower in the erect-leaved type; in the horizontal-leaved type, the leaf temperature might considerably exceed the optimum for photosynthesis. Hadfield showed that yield of shoots (fresh weight) was greater under full sun than under 55% of full sun in the erect-leaved type, but, because of the harmful effect of high leaf temperatures, it was greater under shade in the horizontal-leaved type. The LAI in the horizontal-leaved type is normally 3-4; that in the erect-leaved type is 5-7. The China type, with its

higher LAI and ability to grow well under full sun, is much more productive than the Assam type.

Alvim and Alvim (1980) showed that shade in cocoa reduces wind damage (rupture of the pulvini). Windbreaks (lateral shade) which are just as effective, have replaced overhead shade in some cocoa-growing areas (Lim 1980). Carr (1970) studied the effect of shelter belts on tea yield. Yield in the wet season decreased with distance from the shelter. This was presumed to be a result of wild-induced stomatal closure. During the dry season. in contrast, yield increased with distance from the shelter. Measurements of soil moisture and stomatal apertures supported the argument that wind-induced stomatal closure during previous months conserved water. so that tea bushes close to the shelter belts were more subject to drought during the dry season.

Hong (personal communication) found that relative growth rate and net assimilation rate of oil palm nurser) seedlings increased under 50% shade; Rees (1963) found no reduction under 60-80% shade. In oil palm nurseries where LAI is low (normally less than 3), most leaves are fully exposed much of the time, and the increase in photosynthesis resulting from lower leaf temperature under shade offsets and loss caused by lower light intensity. In a plantation of mature oil palm with a LAI of 5-6, the effect of reduced light intensity would be greater, and the mature oil palms generally fail to produce fruit in the shade of either older palms or forest.

Crop growth rates

As might be expected, crop grown under overhead shade (coco;, tea) or with incomplete ground cover (coffee) have lower rates of dry matter production than crops grown with a complete canopy in the open.

The highest rates of dry matter production (Table 1) for sago, oil palm, and rubber exceed almost all the figures quoted lor C-3 species by Loomis and Gerakis (1975): only the C-4 grasses have higher annual CGR values. Tropical perennials achieve these high rates because they maintain a high LAI throughout the year. Daily rates of dry matter production are not particularly high. Averaged over the whole year. the daily productivities of sago (14.5 g m^2 per day) and oil palm (11 g/ m^2 per day) are comfortably exceeded by many annual crops (Cooper 1970, Loomis and Gerakis 1975), although the annuals have a growing season of less than a full year and incomplete ground cover for the first part of their growing season.

The highest daily productivities achieved by annual crops have generally been observed over periods of a few weeks. Some of the tropical perennials may achieve similar rates over short periods. We have recorded a productivity of more than 17 g/m^2 per day in an experiment with oil palm seedlings (Corley, unpubl.), but usually it is not feasible to measure productivity of tree crops over periods of less than a year. Therefore, any short periods of exceptionally high productivity are masked. However, there are some reasons for not expecting perennials to achieve daily productivities as high as those of annual species. Maintenance respiration will probably be high for perennial crops, especially some palms (Rees and Tinker 1963) whose trunks contain few, lignified fibers and consist largely of living parenchymatous tissue. Corley (1976) estimated that leaf and trunk respiration might consume 80% of total photosynthetic production in the oil palm. Hadfield (1974) estimated

that respiration might account for 80-85% of gross photosynthesis in the tea crop. High ambient temperatures in tropical crops also tend to cause higher respiratory losses than in temperate crops.

Paltridge (1973) argued that, other things being equal, short crops tend to have higher overall photosynthetic rates than tall crops because leaf water potential decreases with plant height, reducing leaf photosynthesis. We have already noted that water stress in the (upper) exposed leaves may be a limiting factor in several of the crops considered here. This effect of plant height may, to some extent, be offset by the better light penetration through a deep canopy (Teare 1972).

Harvest index and yield

When expressed in terms of energy, the HI values for rubber, sago, and oil palm approach 50%. Such figures compare well with those for annual crops and, combined with the high CGR values obtainable, lead to high economic yields. For example, oil palm outyields the highest yielding annual oil crop (sunflower) by 50 to 100%. The starch yields obtained by sago farmers in Malaysia are comparable to the record yields obtained in research trials with other starch crops.

Potential yields

In general, it appears that productivity of perennial tree crops may be maximized at LAI values of about 10. For some crops, considerable increases in planting density would be needed to achieve such LAI values. An estimate of potential yield can be obtained by combining the maximum observed CGR with the maximum HI (Table 5) although, as noted above, for some crops a high HI can be obtained only at a planting density considerably lower than that giving maximum CGR. In such crops, one breeding objective should be to produce varieties capable of giving high HI at planting densities closer to those maximizing CGR.

For oil palm, if an HI of 34% (Table 3) could be combined with a CGR of 35 t/ha per year, 12 t oil ha per year would be produced. Individual trees, which appear capable of such yields, are currently being propagated vegetatively by tissue culture (Corley et a1 1977, 1979) to produce high-yielding clones. If we could identify trees capable of maintaining high HI at LAI values giving maximum dry matter production, yields of 14 t oil ha might be achieved.

For coconut, higher LAI values should certainly give increased productivity, and it seems possible that a CGR of 40 t/ha per year might be achieved, comparable to the maximum observed in oil palm. Coconuts appear particularly sensitive to high-density planting. Nut production drops abruptly above a certain point, but if an HI of 20% could be maintained with a CGR of 40 t/ha per year, a copra yield of 8 t, equivalent to more than 5 t oil and 0.5 t protein, might be achieved. Propagation of the best individual trees by tissue culture could give even higher yields; attempts are presently being made to develop a propagation technique. Friend (personal communication) suggests that dwarf cultivars may have higher HI values than talls or the dwarf × tall hybrids described by Ouvrier and Ochs (1980). High-density planting of such dwarf cultivars might be worth investigating.

Table 5. Potential yields of tropical perennial crops.

Crop	Product (dry wt)	Max CGR x max HI (t/ha per year)	Yield potential (t/ha per year)	Reference
oil palm	Palm oil	13.6	12	Corley et al 1976
Coconut	Copra	6.2	8	see text
Sago	Starch	25.0	34	Flach 1976
Rubber	Rubber	11.2	7	Templeton 1969
Coffee	Coffee beans	-	6.6	Browning and Fisher 1976

Flach (1976) estimated the potential dry matter production of the sago palm at 73 t/ha per year, based on total radiation figures. At an HI of 47%, that would be equivalent to 34 t starch/ ha per year.

Combining the maximum CGR with the maximum HI for rubber indicates a potential rubber yield of nearly 11 t/ha per year. However, Templeton (1969) considered 7 t more realistic, as the clones with the highest HI values were highly susceptible to wind damage (trunk breakage), presumably because an insufficient portion of assimilates is used for trunk growth.

For coffee, Browning and Fisher (1976) estimated a yield of 6.6 t/ha at one site by extrapolation from spacing trial data. I have found no estimate of potential yields for the other crops.

These crops have high yield potentials, but maximizing biological productivity must not be our sole objective. We should aim, rather, at the most efficient or most profitable system. Two examples will suffice.

If oil palms are planted at the densities that maximize productivity, the ground-cover plants beneath them cannot survive the dense shade and are eliminated. The ground-cover plants are of some value, however. They help prevent soil erosion. Some are food plants for the parasitic wasps that control insect pests, and others provide fodder for the draft animals commonly used for transporting fruit within the plantation. Eliminating ground-cover plants has a cost that must be set against the value of increased productivity.

Coconuts have traditionally been grown at planting densities somewhat below those required for optimum yield. The historical reasons for this are unclear, but the large amount of light penetrating the canopy has allowed underplanting with cocoa, which tolerates a certain amount of overhead shade. This combination has proved highly profitable in the last decade, but under coconuts planted at higher densities, cocoa yields would be negligible.

CONCLUSION

Watson (1952) first drew attention to the importance of obtaining complete ground cover, hence, high light interception, early in the growing season. In the tropics, with a 365-day growing season, this can be achieved best with perennial crops. The limited data reviewed here indicate that such crops can give high CGR values and high economic yields. In addition, perennial cropping is probably less damaging to the long-term fertility of tropical soils than the repeated cultivation of annual crops.

Therefore, perennial crops should be considered in agricultural planning for the tropics whenever possible. Similarly, emphasis should be given to perennials in the search for new crop species for the tropics (NAS 1975).

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CROP PRODUCTIVITY UNDER DIFFERENT ENVIRONMENTS

COMPARISON OF CROP PRODUCTIVITY IN THE TROPICS AND TEMPERATE ZONE

L. D. Haws, H. Inoue, A. Tanaka, and S. Yoshida

Yield per unit field area per crop tends to be lower, growth duration shorter, and yield per day in the field slightly higher in the tropics than in temperate areas. The reason for these tendencies is that leaf area expansion and phasal development are faster in the tropics because of higher temperatures during vegetative growth.

Equivalent yield (amount of primary photosynthates which can be used for production of harvesting organs) per day in the field is within a range of 70-90 kg/ ha per day in almost all crops studied.

Assuming that the season available for crop production in a year is the duration of the frost-free period in the temperate and subtropical zones, the estimated potential productivity (dry weight of cereals) using the land at a maximum efficiency is 21.6, 13.6, and 9.5 t/ha per year at places with frost-free periods of 365, 230, and 160 days per year. These estimates coincide reasonably well with recorded yields. In tropical areas with dry seasons without irrigation facilities, such an estimation may be possible through considering the duration of the dry season. With irrigation, potential productivity would be higher than the estimate because of increased solar radiation in the dry season.

Because yields of field crop species are generally lower per unit field area in the tropics than in temperate zones, it is believed that tropical lands capability to produce foods is lower because of inferior climatic, edaphic, and biological conditions.

Soils in the humid tropics are highly weathered because of the leaching of nutrient elements from the soil. In tropical dry areas, salts accumulate and water shortage is a serious problem. Weeds, pests, and diseases are more abundant in areas of high temperature and humidity.

Nevertheless, high temperatures and abundant solar radiation in the tropics are favorable for crop production. Current yield differences are at least partly due to differences in the technology farmers use. It may be possible to produce more food per unit field area in the tropics than in the temperate zones when varieties are

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improved, soils are ameliorated, water is controlled by irrigation and drainage, fertilizers are applied. and pests and diseases are controlled.

This paper compares the productivity of crops grown with intensive management in the tropics and in the temperate zones by analyzing the nature of crop species in relation to climatic factors.

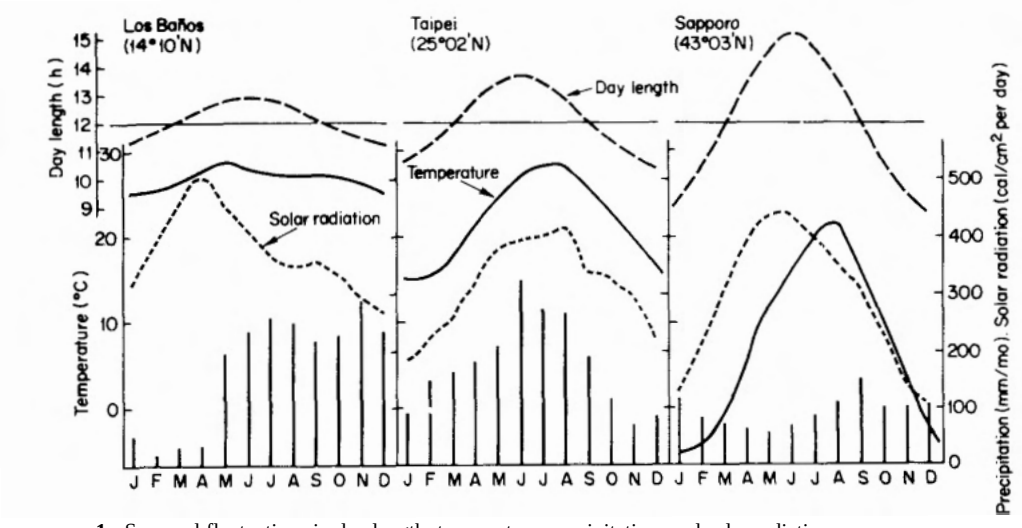
CHARACTERISTICS OF CLIMATIC ZONES

Climatic groups can be defined on the basis of temperature and precipitation. A dry climate is one in which potential evaporation exceeds precipitation. Temperature classifications are:

- Tropical No killing frost in continental areas: 18° C coolest month average in marine areas.
- Subtropical 10°C or above for 8 months.
- Temperate 10°C or above for 4-7 months,
- Boreal 10°C or above for 1-3 months,
- Polar below 10°C all months.

Major agricultural areas can be divided into tropical, subtropical, and temperate zones distributed between the Tropic of Cancer (23.5-31°) and the Tropic of Capricorn (37-50°; 60° in Europe). Seasonal fluctuation of climatic factors at 3 sample locations (Los Baños — tropical, Taipei — subtropical, and Sapporo — temperate) are shown in Figure 1.

Day length controls the phasal development of photoperiod-sensitive crop species (or varieties). It is 12, hours at the equinoxes, shortest at the winter solstice, and longest at the summer solstice. The seasonal day length fluctuation is zero at the equator, becomes larger from lower to higher latitudes, and is more than 6 hours at Sapporo.



1. Seasonal fluctuations in day length, temperature, precipitation, and solar radiation.

In the tropics, where the temperature is high throughout the year, low temperature causes no serious problem to crops, although it may cause a slight decrease in growth rate. The season available for crop growth is 365 days a year. Three or more crops of ordinary growth duration can be grown in a year. High temperatures may cause low yields in crop species adapted to low temperatures, and extremely high seasonal temperatures in some dry areas can be a serious problem.

In subtropical and temperate zones the summer temperature is high enough for the growth of almost all crops, but the winter temperature is too low for some. The period with temperatures above critical varies, depending upon the location and the nature of crops to be grown. For example, the frost-free duration at Sapporo is about 160 days in a year and even within this period the temperature is below 15° C in spring and autumn. Low-temperature-tolerant crops such as sugarbeet can have a growth duration of 160 days or longer, but low-temperature-susceptible crops such as rice can be grown only by transplanting seedlings raised in protected seedbeds. The frost-free duration available for crop growth in the subtropical zone is longer and more than one crop can be grown in a year.

Total annual precipitation and its seasonal distribution vary remarkably from place to place. The variation is not associated with latitude. In areas with limited annual precipitation, no crop can be grown without irrigation. In areas where there is a prominent dry season, no crop can be grown without irrigation during the dry season even if annual precipitation is high. The time within a year available for crop growth is determined by the duration of the dry season and the drought resistance of the crop to be grown. In the tropics, for example, cassava, with a growth duration of more than 1 year and drought resistance, can be grown in areas with a prominent dry season. But rice, with a high water requirement, can be grown only in a rainy season if no irrigation is available. In temperate zone areas where winter is humid and summer is dry, wheat is grown.

Solar radiation is the key factor in photosynthesis. The amount of solar radiation is controlled by the angle of the sun, day length, and cloudiness. In the temperate zone, where solar radiation is less in winter and more in summer, the abundant solar radiation in early summer when the temperature is not yet high is not fully utilized by crops that are adapted to high temperature. In the tropics, where solar radiation is a function of cloudiness, the abundant solar radiation during the dry season is wasted for crop production if there is no irrigation.

CROP SPECIES NATURE, DISTRIBUTION, AND YIELD

Crop species have short-day and long-day varieties (Table 1). In rice, a short-day plant, the panicle-primordia is initiated when day length becomes shorter than critical. But photoperiod sensitivity varies remarkably — some varieties are very sensitive and others are practically neutral. The potato is considered a short-day crop because the tubers start to grow when day length becomes shorter than the critical. Potato varieties also differ in photoperiod sensitivity. Generally, photoperiod sensitivity can be changed considerably through breeding. Thus, day length is not a key factor limiting the distribution and planting season of a crop species.

Table 1. Characteristics of field crops.

crop	Photoperiod response[a]	Temperature adaptation[b]	Growth duration (mo)
Rice	S	H	3.5-5
Wheat	L	L (FR)	3-11 (winter wheat)
Maize	S	H	4-6
Sorghum	S	H	4-8
Soybean	S	H-M	3-6
Field bean	S	H-M	2-5
Groundnut	N	H	3-5
Potato	S	L	3-5
Sweet potato	N	H	3-8
Cassava	S	H	9-24
Sugarbeet	N	L (FR)	5-8
Sugarcane	N	H	9-24

[a]N = neutral, Sand L = short-day and long-day plants. Because of large varietal differences, some varieties are neutral. [b]H, M, L = adapted to high, medium, and low temperatures. (FR) = frost resistant, at least at some growth stages.

Adaptability to low or high temperatures often determines the distribution and planting season of a crop species. The critical temperature varies among crop species and some can tolerate frost. A decrease in temperature generally causes a decrease in growth rate and a delay in phasal development. The degree of the decrease or the delay differs among crop species. On the other hand, some crops are adversely affected when the temperature is above a critical level at which other crops can grow normally.

Drought resistance differs among crop species. Cassava and sorghum are more resistant to drought, and rice and field beans are more susceptible. Distribution and planting seasons frequently are controlled by drought resistance.

The growth duration of a crop is determined by the interaction between plant characteristics (basal vegetative period and sensitivity to day length and temperature) and climatic conditions (day length and temperature). Growth duration varies considerably among varieties of a crop species. The range in rice is 90-180 days in the tropics, depending upon photoperiod sensitivity and growing season. In Hokkaido, the range is very narrow, 130-150 days. Hokkaido varieties planted in the tropics mature less than 90 days after sowing because of their short basic vegetative period and temperature sensitivity.

The growth duration of a crop species under commercial production has a relatively narrow range. For example, it is about 120-140 days for medium duration rice varieties in any location. In this sense, there are differences in growth duration among crop species. The growth duration may be very short in field beans, considerably longer in sorghum, sweet potato, and sugarbeet, and generally very long in cassava and sugarcane.

By the combination of these characteristics, crop species planted for commercial production differ by location and by seasons. Cassava and sugarcane are grown almost solely in the tropical zone and occupy the field for 1 year or longer. In areas with prominent dry seasons, cassava is grown without irrigation and sugarcane with irrigation. Sorghum, groundnut, and sweet potato are grown in the tropical and the

subtropical zones in relatively dry seasons. Rice is grown mainly in the tropical and subtropical zones, and also in the temperate zone by using low-temperature-protected seedbeds. It is grown either in rainy seasons or in dry seasons with irrigation. Maize and field beans are planted in the tropical, subtropical, and temperate zones, preferably in seasons with a reasonable amount of rain. Wheat, soybean, and potato are planted in the subtropical and temperate zones and in the tropics at high altitudes. Sugarbeet is planted in the temperate zone.

The distribution of crop species reflects their places of origin. Rice was domesticated in the humid tropical area of Asia and was grown during the rainy season. Its cultivation expanded to dry areas and dry seasons by improving irrigation facilities and modifying photoperiod sensitivity, and to the subtropical and temperate zones by increasing low temperature tolerance, eliminating photoperiod sensitivity, and improving cultural technology. Potato was domesticated on the Andean mountains in low-latitude areas, was taken to high-latitude areas, and became a very important crop with the selection of varieties with photoperiod sensitivity adapted to the new environment.

One might expect that yields would be higher in areas where a crop was domesticated than at the periphery of its distribution. The average crop yields for tropical and temperate area countries (in this case the subtropical and temperate zones are considered as the temperate area) were computed from FAO statistics (countries in the dry zone were excluded, countries whose major portion of territory is located between 23.5° N and S are considered tropical, and others are temperate). In all crops, yields were higher in the temperate area than in the tropics (Table 2).

High yield records of crops in various locations are listed in Table 3. The data are far from complete, nevertheless, they indicate that present world record yields are mostly from the temperate areas.

GROWTH AND YIELD AT IRRI AND SAPPORO

A set of observation trials was established in 1978 to compare thegrowth and yield of crops under ordinary cultural conditions in the tropical and temperate areas. Field crops that are being grown commercially or could be grown commercially in each

Table 2. Average yields in the temperate areas and in the tropics.

Crop	Temperate area yield (kg/ha)	Yield in tropics	
		kg/ha	%[a]
Rice	4,109	1,958	48
Wheat	2,984	1,363	46
Maize	3,993	1,351	34
Sorghum	2,270	1,249	55
Soybean	1,620	1,038	64
Beans (dry)	1,079	640	59
Groundnut	1,667	1,036	62
Potato	18,056	8,704	48
Sweet potato	13,594	6,881	51
Cassava	11,844	9,103	77
Sugarcane	61,190	53,328	87

[a]Percent of temperate area yield.

Table 3. High yield records of field crops in various locations.

Location	Yield (t/ha)							
	Rice	Wheat	Maize	Sorghum	soybean	Peanut	Potato	Sweet potato
Temperate areas								
USA	–	14.1	22.2	14.6	6.0	8.6	126	65
Japan	10.5	10.1	14.3	9.1	7.3	6.3	69	47
Holland	–	10.4	–	–	–	–	70	–
Australia	–	10.5	14.3	–	5.0	5.0	–	–
Tropics								
Asia[a]	7.4	10.3	8.1	10.3	3.6	4.7	52	–
Rhodesia	–	10.3	12.9	–	4.8	9.6	–	–
South America[b]	–	10.3	10.3	7.0	3.5	3.0	60	–

[a] Philippines, Thailand, and India. [b] Colombia and Mexico.

Table 4. Variety, plant density, and nitrogen applied to crops grown at IRRI (Los Baños) and Sapporo (University of Hokkaido). [a]

Rice	Location	Variety	Plant density (plants/m^2)	Nitrogen applied (kg N/ha)	
				Basal	Top-dressing
Rice	IRRI	IR36	25	90	60
	IRRI (dryland)	IR36	180 (25-cm row)	60	90
	Sapporo	Ishikari	44.4	100	0
	Hokkaido Agric. Expt. Stn.	Yukara	44.4	180	60
Wheat	IRRI	Acc. No. 4073	160 (25-cm row)	60	30
	Sapporo (winter)	(Muka-Komugi)	340 (30-cm row)	80	40
Maize	IRRI	WCA var. 1	5.3	60	30
	Sapporo	Wisconsin Hyb. 110	6.7	100	50
Sorghum	IRRI	B8417	17	60	30
Soybean	IRRl	Clark 63	67	45	0
	Sapporo	Kitanusume	33	20	0
Groundnut	IRRI	Moket	20	45	0
Potato	Sapporo	Danshaku	5.6	100	0
Sweet potato	IRRl	Georgia Ked	7.7	60	30
Sugarbeet	Sapporo	Solorabe	6.1	100	50

[a] Sowing date at IRRI: 24 January 1978: wetland rice was transplanted 7 February. Sowing dates at Sapporo: Potato, maize, and soybean in early, middle, and late May 1978, respectively; sugarbeet and rice transplanted in early and late May, respectively; winter wheat in mid-September 1977.

area were planted at IRRl (Los Baños) and Hokkaido University (Sapporo) under the cultural conditions listed in Table 4.

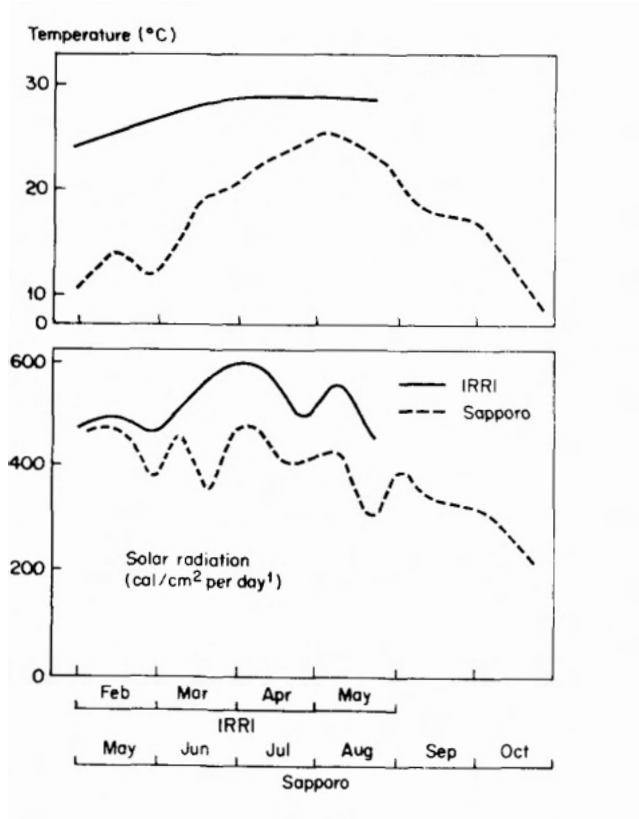
At IRRI rice (wetland and dryland), wheat, maize, sorghum, soybean, groundnut, and sweet potato were planted on 24 January, when they could be expected to grow better, if properly irrigated, because of day length and the limited number of rainy days in that season. Varieties of all crops were selected for similar growth durations.

Plant density and fertilizers were those recommended by the Rice Production Training and Research Group of IRRI.

At Hokkaido University, recommended varieties of rice, winter wheat, maize, soybean, potato, and sugarbeet were planted using standard farmer practices. An additional observation plot of rice at Hokkaido National Agricultural Experiment Station received a very large amount of nitrogen to obtain a high yield.

At IRRI, the temperature was about 25°C at the beginning of February when germination started and increased slightly to 29° C in May. These temperatures were high enough to enable all crops to grow rapidly (Fig. 2). At Sapporo, the temperature was below 15° C till early June and seedlings of rice and sugarbeet were raised in low-temperature-protected seedbeds to extend the total growth period. Potato, maize, and soybean were planted in early, middle, and late June in consideration of their tolerance for low temperatures. The temperature increased progressively from June and reached 25°C in the middle of August, then decreased rapidly to below 10° C by late October. Low temperature slowed the ripening of many crops.

At IRRI the day length increased from 11.5 hours to 13 hours during the cropping season. At Sapporo, it was 14 hours in May, increased to 15.5 hours in June, then decreased to 10 hours by the end of October. These differences in day length between the two locations was not a critical factor because varieties used were selected tor the differences in day length.



2. Temperature and solar radiation during growth at IRRI and Sapporo. 1978

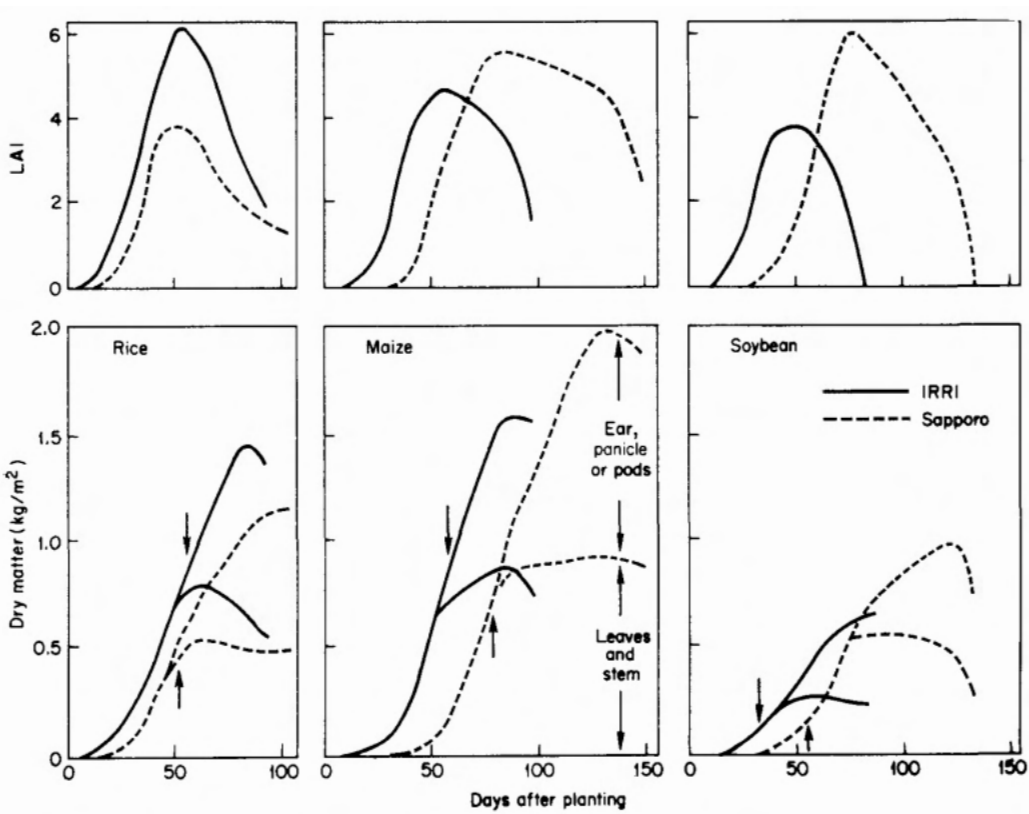
Precipitation at IRRI was very low from February to April and the crops were irrigated to maintain active growth. Precipitation was abundant in May. At Sapporo, precipitation was evenly distributed throughout the season. There was no serious water stress at either location.

The time from sowing to germination (or from sowing to transplanting) was shorter at IRRI than at Sapporo. The time from germination to flowering was almost the same at both locations, but shorter in maize and soybean at IRRI. The time from flowering to harvest was shorter at IRRI in three crops (Fig. 3). Total growth duration for all crops was shorter at IRRI (Table 5).

The leaf area index (LAI) at IRRI started to increase earlier, reached a maximum earlier (maize and soybean) or at the same time, and decreased more rapidly than at Sapporo (Fig. 3, top). The maximum LAI was larger in rice, but smaller in maize and soybean at IRRI.

Because of the faster decrease of LAI and shorter ripening period, the leaf area duration (LAD) during ripening was larger at Sapporo except for rice, for which it was almost the same at both locations (Table 6).

The crop growth rate from germination to flowering was higher at IRRI except for soybean (Fig. 3, bottom; Table 6). After flowering, the increase in total dry



3. Leaf area index (LAI) and dry matter weight of rice, maize, and soybean at IRRI and Sapporo, 1978.

Table 5. Growth duration and yield of crops at IRRI and Sapporo.

Crop	Location	Growth duration[a] (days)	Dry matter yield (t/ha)	Harvest index	Yield per day[b] (kg/ha)		
					Dry matter	Equivalent yield'	Protein[c]
Rice	IRRI	107[93]	6.02	0.43	64.8	87.5	5.7
	IRRI (dryland)	118	4.65	0.33	39.4	53.2	3.4
	Sapporo	141 [105]	5.04	0.44	48.0	64.8	4.2
	Hokkaido Agric. Expt. Stn.	145 [109]	7.14	0.45	65.5	88.4	5.8
Wheat	IRRI	84	1.67	0.31	31.8	42.9	3.8
	Sapporo (winter)	320[d]	5.28	0.32	39.1	54.4	4.7
Maize	IRRI	98	6.03	0.39	61.5	87.4	5.8
	Sapporo	150	7.68	0.41	51.2	72.7	4.9
Sorghum	IRRI	90	7.04	0.48	78.2	105.6	6.5
Soybean	IRRI	84	3.03	0.47	36.1	75.4	14.1
	Sapporo	133	3.71	0.48	27.9	58.3	10.9
Groundnut	IRRI	112	2.95	0.36	26.3	68.2	7.3
Potato	Sapporo	139	11.27	0.88	81.1	104.6	7.5
Sweet potato	IRRI	126	6.26	0.60	49.7	61.6	2.1
Sugarbeet	Sapporo	218[172]	11.91	0.53	69.2	85.8	3.9

[a]Figures in brackets mean days in main field. [b]Day in main field [c]Values are calculated on the basis of Table 8 in A. Tanaka (this volume). [d]For 135 days, mean temperature was above 7°C.

Table 6. Crop growth rate (CGR) and leaf area duration (LAD) during ripening of rice, maize, and soybean at IRRI and Sapporo.

Crop	Location	Mean CGR[a] (g/m^2 per day)	LAD[b] (LAI/day)	Equivalent yield/LAD (g/m^2 per leaf per day)	Solar radiation ($kcal/cm^2$)	Conversion efficiency[c]
Rice	IRRI	13.0	153	5.31	19.4	1.57
	Sapporo	9.9	148	4.59	18.4	1.38
Maize	IRRI	15.4	158	5.42	22.2	1.44
	Sapporo	11.3	336	3.24	23.9	1.71
Soybean	IRRI	3.9	137	4.62	28.8	0.82
	Sapporo	4.3	311	2.49	27.6	1.05

[a]From germination to start of flowering [b]From flowering to harvest LAI = leaf area index. [c]Energy efficiency to convert solar radiation to primary photosynthates: (equivalent > yield y 3.74 kcal/g) ÷ solar radiation.

matter was due mostly to the increase of grain weight, although a considerable decrease in leaf-and-stem weight took place in rice at IRRI and in soybean at Sapporo (Fig. 3). Ripening of grains could be considered to depend mostly on the photosynthates available during ripening.

Wetland rice yield was higher at IRRI (Table 5). However, the rice which received a larger amount of nitrogen at Hokkaido Agricultural Experiment Station outyielded that at IRRI. The yields of wheat, maize, and soybean were higher at Sapporo than at IRRI. At Sapporo, too, the yields of potato and sugarbeet were far higher than those of other crops.

The harvest indexes of a given crop were almost the same at both locations. However, there was considerable difference between crops. For example, the harvest index was high in potato and low in wheat.

At Sapporo, the higher yields of wheat and maize and the higher yield of sugarbeet compared with yields of other crops may indicate that the longer the growth duration, the higher the yield per crop. Yield per day in the field was computed (Table 5). In rice, the yield per day was higher at IRRI but was equivalent to that at the Hokkaido Agricultural Experiment Station. In wheat, the yield per crop was much higher at Sapporo (winter wheat); however, the difference in yield per day was small. In maize and soybean, the yield per day was higher at IRRI.

Yield per day apparently was lower in wheat, soybean, and groundnut and higher in sorghum and potato. The lower values for soybean and groundnut may be associated with the high protein and lipid contents of these crops. To compare productivity per day among crops with different chemical compositions, yield per day was converted to equivalent yield per day following the concept described by Tanaka (this volume). The equivalent yields per day of soybean and groundnut are almost comparable to those of wheat or rice.

The amount of protein produced per day in the field is also shown in Table 5. It is far higher in soybean and higher in potato and groundnut than in other crops.

Because most grain constituents are considered the photosynthetic products of ripening, the equivalent yield/LAD during ripening was calculated (Table 6). This value indicates that leaf efficiency was higher at IRRI. However, there was no clear difference in efficiency of solar energy utilization during ripening. The higher efficiency of photosynthesis during ripening at IRRI probably was due to higher solar radiation.

This comparative study indicates that

a) yield per crop tends to be higher in temperate areas than in the tropics;
b) growth duration tends to be longer in the temperate areas than in the tropics:
c) yield per day frequently is higher in the tropics than in the temperate area;
d) the LAI in the tropics increases more rapidly during vegetative growth because of higher temperatures:
e) although the leaves die sooner, the efficiency to produce grain during ripening is higher in the tropics because of more abundant solar radiation especially during the dry season; and
f) the productivity per day is higher in the tropics than in temperate areas.

ANNUAL PRODUCTIVITY

In terms of equivalent yield per day, potato productivity appears to be higher and wheat productivity appears to be lower than that of other crops. These differences seem to be associated with differences in the harvest index. Nevertheless, it can be generalized that the productivity of a crop is similar in the tropics and in the temperate areas and that the differences in productivity among crops are smaller than are commonly considered when differences in yield are evaluated.

Although rice productivity between the tropics and temperate areas is similar, far more effort is necessary in the temperate areas to counteract low temperatures and in

the tropics to counteract weeds, pests, and, in the dry season, water stress. Thus, it is difficult to compare productivity per unit of inputs. Only potential productivity, free from various stresses, is discussed here.

In a temperate area such as Sapporo, it is almost impossible to grow more than one crop on a field in a year because of the limited duration of the season with temperatures above critical. Although there is no serious issue of cropping systems to secure maximum production per year from a unit land area, the issue of rotation exists, in relation to maintenance of soil fertility. Thus, productivity of land is equal to productivity of a crop. The yield per crop is higher in sugarbeet or potato — these crops can have a longer growth duration because of their tolerance for low temperatures. The yield is reasonably high in maize and rice, although a large amount of input is necessary for rice. Yield of field bean is low because this crop is susceptible to low temperatures. Yields of more than 20 t ha have been recorded in maize and potato at favorable places in temperate areas.

In the tropics, such as at Los Baños, it is possible to grow more than one crop on a field in a year, especially when irrigation is available. The issue of cropping systems is important in efficient land utilization. In a year, one crop of cassava or sugarcane and three crops of rice may produce more than 20 t/ha if irrigation is available. However, pests and diseases can be serious problems when rice is planted throughout the year. It is possible to grow two or three crops a year, but comparison of the numerous crop species combinations in cropping systems is beyond the scope of this paper.

To compare productivity with ordinary cultural techniques, it was assumed that the season available for crop production is the frost-free period. If the equivalent yield is 80 kg ha per day, the conversion factor from equivalent yield to dry weight of harvested material (cereals) is 0.74. The expected yield in dry matter per year at places with frost-free periods of 365, 230. 180. 160, and 130 days (for example, at Okinawa. Tokyo, Sendai, Sapporo, and Obihiro) would be 21.6, 13.6, 10.7, 9.5, and 7.7 t ha, respectively.

Using the same approach, if production of protein is assumed to be 6 kg ha per day, protein production per year would be 2.19, 1.38, 1.08, 0.96, and 0.78 kg ha. respectively. These values could be higher if leguminous grain crops such as soybean or groundnut are included in the cropping system.

These values have very limited theoretical meaning but correspond well to high production in places in the temperate and subtropical zones. In the tropics, similar estimations may be possible by considering that the season available for crop production without irrigation is determined by the duration of dry season. If irrigation is possible, it becomes more difficult to estimate productivity because solar radiation is apparently higher in the dry season and equivalent yield per day would be higher.

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CROP PLANNING FOR DIFFERENT ENVIRONMENTS

A. R. Pereira

Agriculture is highly dependent on environmental conditions and climate is likely the most important factor in determining the agricultural potentialities of a region. The macroclimate determines the adequacy of a region for a crop while weather conditions determine the yield. The crop requirements with respect to temperature and moisture should be adequately assessed. If possible the probability of extremes of temperature and moisture should also be used.

Crop zoning should include 9 teams of specialists in many areas. Field trips should be made to observe the physical and social characteristics of the region. Climatologically, the region should be classified as suitable, marginal, or unsuitable for a crop. Agronomic techniques to overcome some of the climatic limitations to the crop should also be considered.

The food and energy problem has emerged as one of the most critical contemporary issues. With the increasing demand for food, fiber, and energy, planners are becoming more and more aware of the need for efficient use of natural resources. The full realization of this need is seen in the efforts of the United Nations Food and Agriculture Organization, the World Health Organization, the Commission on Agricultural Meteorology of the World Meteorological Organization, and many regional scientific associations to bring scientists and policy makers together.

Agriculture is the most important of all the primary economic activities and the most dependent on environmental conditions. The environment — climate and soil —controls the growth and development of plants. Consequently the environmental conditions should be adequately assessed in any regional development plan. The first and most decisive step in any development planning should be the identification of areas capable of high agricultural output, that is, areas where the soil and climate are adequate for a given crop. Crop zoning is the art of choosing the right crop for the right environment. But even for the adequate areas the success or failure of a crop depends on the economic and social factors of the society that grows the crop. The

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combination of environmental, economic, and social factors dictates the agricultural system most suitable for a region and it has to be identified locally (Landsberg 1968).

Climate is likely to be the most important factor in determining the agricultural potentialities of a region. This paper concerns the climatological aspect of crop zoning. Obviously the main soil characteristics likely to affect the agricultural potential must also receive due consideration.

The agroclimatic potentialities of many regions of the world have already been assessed, at least on a first-approximation basis. Examples of such studies are listed by Burgos (1968). The work by Williams (1969,1971) in Canada and the agricultural zoning atlas of Sao Paulo State in Brazil (Sao Paulo Secretaria de Agricultura 1974) could also be added. The latter work includes the environmental zoning of 24 crops. The atlas took a team of agronomists, soil scientists, economists. and agroclimatologists 5 years of concentrated efforts to produce. It dictates the agricultural priorities of the region.

CLIMATIC REQUIREMENTS OF CROPS

In climatological zoning one is concerned with the macroclimate, i.e., the climate of a weather station where measurements are taken at conventional exposures and times. That permits comparisons of the climates of different regions. Obviously the crop creates its own microclimate, which is the result of the interaction of the crop and the macroclimate.

The macroclimate cannot be changed to suit the crop. However, within the regional climate, the farmer might use the topographic features (topoclimate) that best fit the crop requirements. That involves a different level of planning — farm planning — and should be taken care of locally by a crop specialist.

The climatic elements to be considered depend on the climatic requirements of the crop being zoned. That involves the survey of the climatological conditions of as many areas as possible where the crop is successfully grown or where its introduction has failed (Burgos 1968). The Techniques Agricoles et Productions Tropicales collection, the Longmans' Tropical Agriculture Series, and Barrett (1928), de Camargo (1963, 1966b), de Camargo and Ortolani (1964), Ortolani and Silva (1965). Papadakis (1966), Wilsie (1966), Williams and Joseph (1970). de Camargo et al (1971), Alvim and Kozlowski (1977), and others give reasonable accounts of the climatic requirements of most crops.

The crop requirements are not constant throughout the growing season. Consequently seasonal variation of the climate is important. Annual crops take, in general, 3-6 months to complete their life cycle. Thus, their planning can be made to fit the most adequate climatic conditions. Perennial crops, on the other hand, do not permit such adjustments and have to be grown where climatic stresses are least.

In general, the most-used climatic elements are temperature and rainfall. If the crop is sensitive to photoperiod, this factor also has to be considered.

WATER REGIME

Rainfall is only one component of the water balance of the soil, or rather that corresponding to soil moistening. Evapotranspiration, which corresponds to the soil's drying out, is another equally important component in the soil water balance.

If there is no water deficiency in the soil, evapotranspiration is considered potential and may be regarded as a climatological element (Thornthwaite 1948, de Camargo 1965, Hudson 1968) characteristic of the region and depending solely on the region's meteorological conditions. In spite of the difficulty of measuring evapotranspiration, potential evapotranspiration can be evaluated through some equations that use standard, easily measured meteorological elements. The pertinent literature contains many evapotranspiration models.

The annual distribution of the water budget depicts the moisture situation of the region. In many annual crops moisture stress at germination, flowering, and fruiting (grain filling) greatly affects the yield. In some cases, where the economic importance of the crop permits, irrigation might solve the water deficit situation. On the other hand, the problem of excess water is not so easily handled.

TEMPERATURE REGIME

Crops vary in their sensitivity to temperature but, in general, there are lower and upper threshold temperatures beyond which crop growth and development is affected. The lower threshold is called base temperature. The temperature regime of large areas is still beyond effective modification. Tropical crops generally are frost sensitive and the best protection available is to grow them in frost-free regions. Sometimes, for economic reasons, it is desirable to extend to subtropical climates the cultivation of tropical crops. In such situations the probability of frost occurrence should be carefully assessed. Once again, the economic factor determines the acceptable probability level.

In some circumstances, even tropical crops suffer some damage with the occurrence of high temperatures. High temperature causes flower abortion with consequent loss of production in coffee arabica even though the plant grows normally (Ortolani et al 1970, de Camargo 1977).

ENVIRONMENTAL ZONING CRITERIA

The adequate climatic elements are mapped on a cartographic chart to give an overall view of the agroclimatic resources of a region. The *adequare climatic, elements* during the period refers to those most likely to affect the growth and development of a crop. Obviously the phenology of the crop dictates the periods to be considered.

The chart scale used in the Sao Paulo State zoning is 1:1,000,000. In Canada, Williams et al (1980) used a scale of 1:2,000,000. By taking into account the topography of the region, isolines for the climatic elements can be drawn:

- by interpolation through the charted data points;
- with the aid of a regression equation that relates the climatic element and the topographic as well as the geographic characteristics of the region (Hopkins 1968, Pereira et al 1973); or
- by computer mapping (Williams and Sharp 1972, Pinto and Alfonsi 1976, Williams et al 1980) when adequate computer facilities and spatial distribution of data points are available.

By overlapping the different climatic maps and considering the climatic requirements of a crop, the region can be considered climatologically suitable, marginal, or unsuitable for the crop. A region is considered suitable when the macroclimate does not impose any restriction upon crop growth and development. In such a region the crop can be grown successfully. The region is unsuitable when there are serious climatic restrictions to the economic exploitation of the crop, Most of the time such climatic restrictions do not prevent the crop from being grown as a backyard crop for the farmer's own subsistence. The region where the climatic restrictions are not too serious is marginal. Such a region might even be considered suitable if 1) deeper soils are available, 2) irrigation is economically feasible, or 3) resistant crop varieties are used.

The resulting climatic map for the crop is then overlapped on the soil-use-capacity map of the region to obtain the final environmental (climate and soil) map.

Alternatively crop phenology-climate equations can be used as proposed by Williams et al (1980). However, such equations are available for very few crops and they have to be determined locally. Such an approach demands considerable time and research before the equations can be of any value. Consequently such a refinement should be a second approximation, perhaps on a mesoscale basis.

CONCLUSIONS

Plant growth and yield are directly dependent upon weather and climate. While climatic and edaphic factors limit the areas of the world where any specified crop can be grown successfully, the weather determines the yield. On a first approximation, the agroclimatic potentialities of a region should be assessed on a macroscale basis, i.e., through standard macroclimatic information. The climatic elements most used are temperature, precipitation, evapotranspiration, and their seasonal variations. Whenever possible the probability of extremes should also be considered with the value of the crop dictating the acceptable probability level.

Obviously a great deal of knowledge of the region to be planned and of the crop and its requirements is needed before any zoning can be done. Crop zoning is a team effort that should include specialists in agronomy, agroclimatology, soils, photo-interpretation, economics. etc. Visits to the region are indispensable for there is no substitute for the local inspection of the region’s physical and social characteristics.

As stated by de Camargo (1965), one *uses* the macroclimate existing in the regon, *selects* the proper topoclimate of the farm, and *conditions* the microclimate desired for the crop.

Crop zoning has to be fairly simple and straightforward to be of any value to the layman, i.e., the region should beconsidered as suitable, marginal, or unsuitable for the crop. Where possible the marginal and unsuitable classes should be further subdivided according to the limiting factor.

The use of varietal resistance, irrigation, double-cropping, pest management, crop rotation, and many other agronomic techniques should be considered to overcome some of the limitations to the crop.

Even though the approach here described is rather subjective, it has been used successfully in the tropical areas of Brazil.

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PRODUCTIVITY OF LOWLAND SOILS

K. Kyuma

Lowland soils may be defined as those having an aquic moisture regime. Most are derived from recent sediments and have weakly developed profile morphology. For crop production, they have relative advantages over upland soils in ease of fertility maintenance and soil conservation.

Hydrography, as determined by climate and physiography, is the most fundamental constraint to the agricultural use of the lowland. During the rainy season, rice is the only important food crop; during the dry season, lack of water and poor physical soil properties restrict upland crop cultivation.

Lowland soil materials range from almost fresh volcanic ejecta, with high inherent potentiality, to those resembling oxic horizon materials with low potentiality.

Lowland soils in the tropics generally have poor organic nitrogen reserve and available phosphorus. Those with low inherent potentiality tend to show multiple nutrient deficiencies. Thus, for rice, iron toxicity and *akiochi* are feared even with nitrogen and phosphorus fertilization. Calcareous and saline lowland soils in regions with drier climates would suffer from zinc and other micronutrient deficiencies.

Acid sulfate soils, peat soils, and saline and sodic soils are the major problem soils in the lowland.

Lowland has been the center of activity of man. In the past, it was the area where he could secure water, easy land and water transportation, and above all, fertile soils for growing crops. It is not accidental that the places of origin of civilization were almost all situated in lowlands, such as the Nile Delta and the Mesopotamian Plain in the Near and Middle East, the Indo-Gangetic Plain in South Asia, and the Yangtze and Hwang Basins in the Far East. Even today, cities, industrial areas, and productive farmlands are concentrated in the big river basins, deltas, and coastal lowlands.

A look into some statistics of tropical Asia, shown in Table 1, shows the importance of lowlands in agriculture. The Asian tropics extend to the east of the Indus

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Table 1. Basic statistics for tropical Asia.[a]

Population, land, and crop	Tropical Asia	Percentage of world total
Population (X 10^3)	1,165,082	28.4
Land area (X 10^3 ha)	897,060	6.1
Arable land area (X 10^3 ha)	253,356	18.1
Ratio of arable to total land area (%)	28.2	
Rice land area (X 10^3 ha)	86,553	60.6
Rice production (X 10^3 t)	171,101	46.7
Cereals other than rice		
Land area (X 10^3 ha)	81,602	13.5
Production (X 10^3 t)	79,614	7.3

[a]Sourcc FAO Production Yearbook (1977).

and to south of China and include insular Southeast Asia. The population of the region is a little more than 1 billion. Its cereal crop production consists of about 80 million t of upland cereals and 170 million t of rice, coming from 82 million ha and 87 million ha of arable land, respectively. It is clear that the output from lowlands is nearly twice that from uplands. In fact, the majority of the extremely dense population in tropical Asia is supported by the products of lowlands.

In this paper, characteristics of lowlands with respect to climate, physiography, hydrography, and, particularly, soil will be considered first; then probable constraints of lowland soils in relation to crop productivity will be examined.

GENERAL CHARACTERISTICS OF LOWLANDS

Definition

The term lowland is not easy to define. Land that is low in terms of elevation no doubt is a lowland, but land that is high in elevation but occupies a relatively lower terrain position is also referred to as lowland for this discussion. Thus, lowland in this paper includes land referred to by such conventional terms as alluvial plains, deltaic plains, coastal plains, floodplains, valley plains, tidal flats, marshes, swampy lands, boggy lands, and peat lands.

It may be convenient to use the definition of aquic moisture regime of U.S. Soil *taxonomy* (USDA 1975) to define lowland for the present discussion. It reads: "The aquic moisture regime implies a reducing regime that is virtually free of dissolved oxygen because the soil is saturated by ground water or by water of the capillary fringe . . . The duration of the period that the soil must be saturated to have an aquic regime . . . must be at least a few days."

If we define lowland as having aquic moisture regime for a few days in the year. then most of the lands referred to by the conventional terms above qualify. Climate, however, may condition the entry of a land into the lowland. Under an arid climatic condition, even a flat, lowlying land may not have aquic moisture regime and thus would be excluded from lowlands. Therefore, the discussions in this paper are confined to potentially productive lowlands that are under nonarid climatic conditions.

Hydrography

In the previously stated definition of lowland. hydrography, as determined by climate and physiography, is the most important factor. We therefore look into the hydrography of lowland in relation to climate and physiography.

Climate. Kyuma (1972) proposed a climatic regional division of tropical Asia based on a numerical taxonomic processing of climatic data of more than 300 stations throughout the region. Kyuma (1973) also studied soil water regimes for paddy lands in the climatic regions, considering the balance between rainfall and evapotranspiration and water retention in and on the soil. Typical patterns of soil moisture regimes for the nine climatic regions are illustrated in Figure 1, which shows that, in some climatic regions, the land is naturally inundated a sufficiently long time to allow rainfed rice cultivation. In some others, for example the climatic regions I, V, VII, and IX, land is inundated only for a short period or not at all. Except for region IX, which is the lower Indus Basin with arid climate, even the regions that are naturally inundated have abundant paddy lands. This apparent contradiction can be resolved if we consider the physiography of the land.

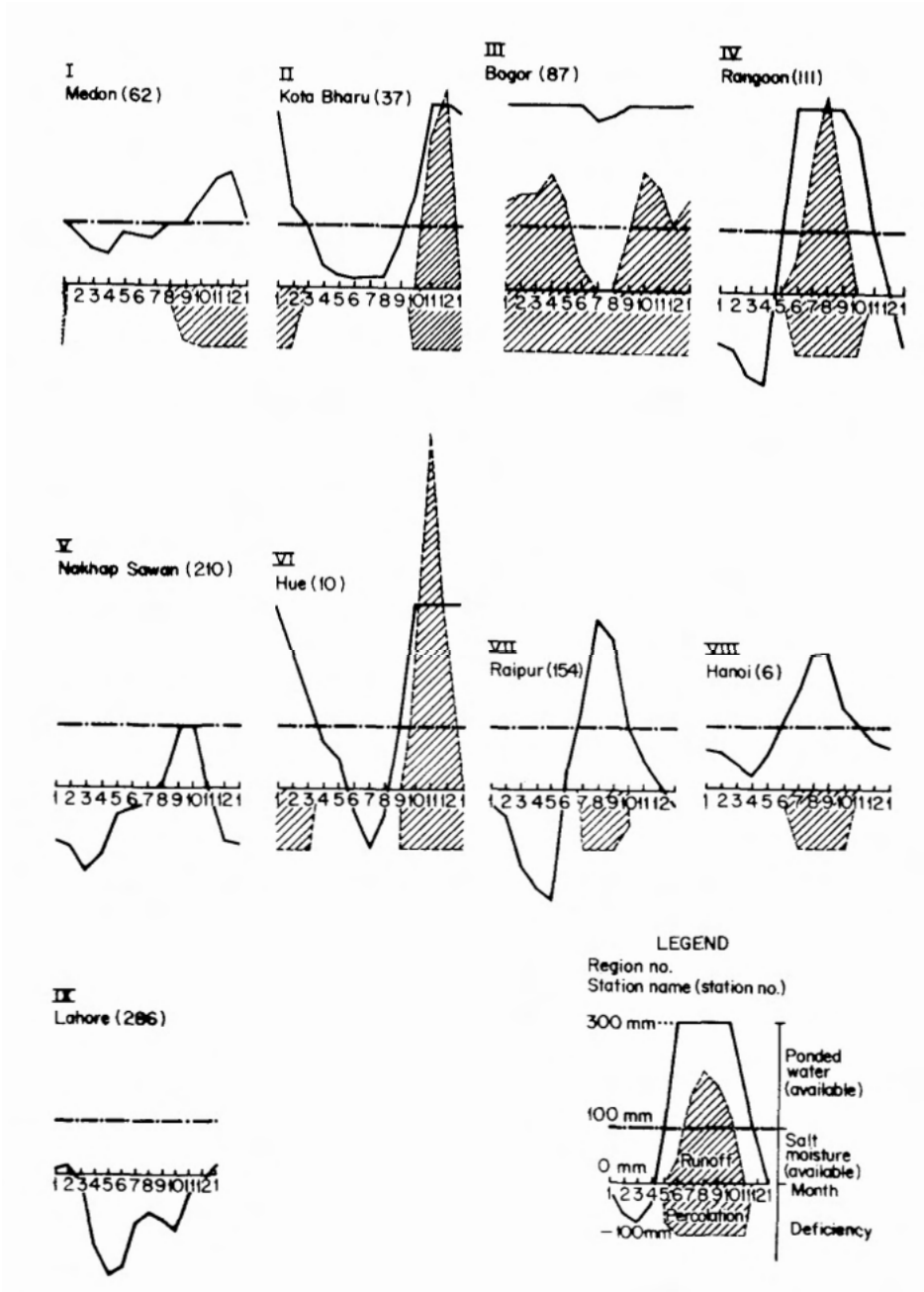
Physiography. Most lowland, as defined in this paper, is situated on recent floodplains and deltas and, to a lesser extent, on lower terrace surfaces. In the terms newly proposed by Moormann and van Breemen (1978), lowlands comprise both phreatic and fluxial lands. If the catchment area is sufficiently large, such lowlands can be supplied with water from their surroundings and inundated for some time, as can the lowlands in climatic regions I, V, and VII. If the catchment area is small relative to that of lowland, inundation does not last long and water conditions, especially for lowland rice, become unfavorable.

In the climatic regions with year-round heavy rainfall and natural inundation, a *peraquic,* condition may prevail in the broad depressions of floodplains and deltas. On such lowlands deep and continuous flooding could be a constraint to agriculture. Much of the swampy land with unripened clays and peat has remained idle because of this constraint.

Another hydrographic factor important for the agricultural use of lowlands is the extent of tidal fluctuation along the coastal areas. Salt water inundation at the time of high tides and its intrusion into the upstream part during the low-water season are a serious constraint locally. Thus the hydrographic conditions, as determined by combined climatic and physiographic conditions, set the fundamental constraints to the agricultural use of lowlands.

Crops adaptable to lowlands

Crops suitable for lowlands are restricted because of the hydrographic condition. Rice is the first and only choice for lowlands with prolonged aquic water regime. Taro and sago palm are also starchy crops that can tolerate aquic water regime but the area under them is not large. In areas with distinct dry seasons such as those in climatic regions IV, V, VI, and VII, the possibilities of growing upland crops in a rice-based multiple cropping system vary, depending on the availability of irrigation water. In areas with more well-distributed rainfall and better drainage, upland crops can be cultivated throughout the year.



1. Typical patterns of soil water regime for different climatic regions in tropical Asia.

However, rice is the most stable and productive crop for lowlands almost everywhere, as long as sufficient water can be supplied. Therefore, unless otherwise specified in the discussions that follow, rice is assumed as the crop to be grown on the

lowland. Furthermore, the discussions will center on tropical lowlands, for they have the greatest potential for crop production in the future.

CHARACTERISTICS OF LOWLAND SOILS

Lowland soils are almost exclusively on sediments of relatively recent geological origins. Most are on the Holocene alluvial and deltaic sediments and some are on the late Pleistocene alluvia constituting fan and terrace surfaces, implying that lowland soils are undeveloped in their profile morphology and richer in mineral nutrients than soils in the areas where the parent sediments originated. In the catchment areas, soils undergo continuous erosion and leaching; thus rich surface soils and more mobile mineral elements tend to be washed down to be deposited on the lowland.

Classification of lowland soils

Soils in lowlands, in US *Soil taxonomy* (USDA 1975) terms, are mostly aquic suborders of Entisols and Inceptisols, e.g., Aquents and Aquepts, and Histosols. Some Fluvents are also distributed on the natural levee parts of the lowland. The absence of well-defined diagnostic horizons produced by a long-term pedogenetic process characterizes them. They may have only ochric or histic epipedon and cambic subsurface horizon. In other words, they have only weak or immature profile characteristics.

Other soils of some importance that occur in lowlands include Aqualfs and Aquults on terrace surfaces. Generally, Aqualfs occur more frequently in the areas where ustic moisture regime prevails, whereas Aquults occur under a more humid climate. Although an aquic feature is not clearly visible in lowlands, Vertisols also occur, but are confined to fine clayey, montmorillonite-rich sediments under the climate with distinct dry seasons.

Soil material characteristics

Lowland soils have undergone little or no pedogenetic modifications. That implies that the nature of the parent sediments directly determines the soil's characteristics. It follows further that lowland soils vary widely because either the geology and the degree of weathering in the catchment area or the millieu of sedimentation, or both sets of factors, condition the nature of the parent materials. At one extreme, fresh volcanic ejecta are laid down in the lowland. as on the island of Java. At the other extreme, there are such cases as those mentioned in the Seventh Approximation (USDA 1960), in which "Chemically and mineralogically the materials in an oxic horizon may be indistinguishable from materials at comparable depths in Entisols." The range of variability is wider in the tropics than in the temperate and cold regions.

Recognizing the importance of parent sediments in soil fertility and their wide variability, Kawaguchi and Kyuma (1977) attempted a classification of soil materials for 410 paddy soil samples from tropical Asian countries and set up 10 soil material classes on the basis of textural composition and total chemical composition (Table 2).

Although the samples the authors used originated in tropical Asia, the proposed soil material classes could be regarded as exhaustive for the lowland soils occurring

Table 2. Mean mechanical and total chemical composition and some other related properties of lowland soil samples in each soil material class.

		Soil class[a]										All classes
		I (61)	II (68)	III (66)	N (29)	V (42)	VI (31)	VII (25)	VIII (44)	IX (25)	X[b] (19)	(410)
Sand	%	12.40	34.45	8.64	21.83	58.12	20.33	18.82	73.78	68.38	54.63	33.81
silt	%	22.73	34.05	35.21	33.93	19.84	25.92	49.76	15.54	10.05	25.70	27.60
Clay	%	64.87	31.52	56.15	44.20	21.43	53.76	31.43	10.68	21.56	19.68	38.59
SiO_2	%	62.85	80.45	67.40	66.55	73.81	59.00	66.65	94.62	77.55	62.70	72.12
Fe_2O_3	%	9.90	3.07	5.71	1.69	4.51	11.95	6.71	0.82	5.41	6.89	5.96
Al_2O_3	%	22.12	12.78	21.53	19.25	14.58	20.98	18.31	3.45	11.87	18.41	16.38
CaO	%	1.31	0.39	0.46	1.95	2.03	3.22	1.58	0.22	0.98	6.89	1.42
MgO	%	0.90	0.38	0.94	1.23	0.95	1.57	1.98	0.05	0.68	2.28	0.92
MnO_2	%	0.22	0.06	0.06	0.18	0.11	0.31	0.10	0.02	0.14	0.16	0.12
TiO_2	%	1.54	0.99	1.11	1.04	0.86	1.59	0.96	0.64	1.98	0.94	1.14
K_2O	%	1.04	1.85	2.67	1.96	2 99	1.16	3.59	0.40	1.31	1.49	1.83
P_2O_5	%	0.12	0.09	0.13	0.15	0.15	0.22	0.13	0.06	0.12	0.24	0.13
pH		6.1	5.3	5.2	6.5	6.8	7.0	6.6	5.3	6.0	6.9	6.0
PBS	%	94.2	59.1	81.5	100.0	103.2	106.2	98.9	65.0	83.0	105.8	85.6
CEC	meq/100 g	31.1	12.3	20.4	26.7	13.9	34.4	15.4	4.2	10.3	15.5	18.6
7A	%	43.1	57.4	46.1	32.6	36.8	37.3	32.4	70.1	63.0	29.3*	46.4*
10A	%	5.0	19.2	20.9	12.4	20.2	3.9	28.2	5.1	8.2	12.3*	13.9*
14A	%	51.9	28.5	32.4	55.0	43.0	58.9	39.4	24.8	28.8	58.4*	39.7*

[a]Figure in parentheses after class number is number of samples. [b]Because 4 samples in group X have no crystalline minerals, the means for the other samples were taken.

in nonarid regions. Such a classification allows good inference on soil fertility. For example, soils with class VI material are base-saturated and contain a large amount of better quality clay. Their mineral-nutrient reserves are moderate to high, and their nutrient-holding capacity is also high. In contrast, the poorest soils are those with class VIII material, in which only silica is abundant.

Soil fertility characteristics

What then are the fertility characteristics of lowland soils? Kawaguchi and Kyuma (1977) elucidated in their study of paddy soils in tropical Asia that soil fertility is made up of at least three independent components, which they numerically evaluated for each sample soil. The ratings for several discrete geographic regions in South and Southeast Asia are in Table 3. The three fertility components have the following characteristics:

- Inherent potentiality (IP) — the soil character determined by the nature and amount of clay and base status,
- Organic matter and nitrogen status (OM) — the soil character related to the organic matter and nitrogen reserve, and
- Available phosphorus status (AP) — the soil character related to available phosphorus-supplying power.

As the numerical rating was done to make the overall mean for the 410 samples hero and the variance 1, the positive numbers indicate an above-average rating and the negative numbers below-average.

Table 3. Means and standard deviations of the numerical ratings of 3 fertility components tor selected regions.[a]

Regions	Samples (no.)	IP		OM		AP	
		Mean	SD	Mean	SD	Mean	SD
India: Godavari-Krishna delta	10	1.38	0.29	- 0.73	0.47	1.11	0.95
Bangladesh.							
Ganges	15	0.33	0.35	0.04	0.82	0.90	0.50
Madhumur-Barind	9	- 0.75	0.60	0.35	0.64	- 0.14	0.40
Marginal	16	- 0.87	0.62	0.36	0.66	- 0.06	0.77
Brahmaputra	13	- 0.57	0.48	- 0.01	0.64	1.01	0.66
Sri Lanka:							
Wet and intermediate zones	14	- 1.07	0.64	0.84	1.10	- 0.10	0.64
Dry zone	19	- 0.10	0.76	- 0.36	0.70	- 0.12	0.67
Thailand:							
NE Plateau	32	- 1.18	1.27	- 1.14	0.77	- 0.94	0.70
Upper Central Plain	14	- 0.04	0.76	- 0.05	0.49	- 0.31	0.69
Bangkok Plain	24	0.53	0.64	0.24	0.66	- 0.51	0.86
South	6	- 0.40	0.74	0.58	0.48	- 0.29	0.39
Cambodia:							
Central Plateau	8	- 0.91	0.76	- 0.60	0.94	- 1.19	0.69
Peninsular Malaysia:							
Kedah-Perlis	10	0.25	0.44	1.21	0.56	0.02	0.54
East Coast	10	- 1.23	0.20	0.78	0.59	- 0.54	0.57
Indonesia:							
Central and East Java	28	0.91	0.59	- 0.29	0.53	0.10	0.81
Philippines:							
Central Luzon	25	0.91	0.54	- 0.10	0.41	- 0.36	0.97

[a] IP = inherent potentiality, OM = organic matter and nitrogen status, AP = available phosphorus.

It is generalized from the foregoing results that IP is rated highly in the regions where active volcanism can continuously rejuvenate the soil materials (Central and East Java, Central Luzon). In the deltaic areas where sediments from soils with more or less ustic moisture regime are deposited (Godavari-Knshna Delta, Bangkok Plain, Gangetic sediment area in Bangladesh, Kedah-Perlis Plain in Peninsular Malaysia), IP ratings are also high. On the contrary, they are low for the soils on sandy, old alluvia (northeast plateau of Thailand, Central Cambodia, Madhupur-Barind Tract of Bangladesh, marginal plain of Bangladesh) and on the sediments derived from acidic rocks (wet and intermediate zones of Sri Lanka, east coast of Peninsular Malaysia). High OM ratings are correlated with the more humid climatic condition and fine-textured sediments in the lower terrain position (Peninsular Malaysia, south Thailand, wet and intermediate zones of Sri Lanka). But most lowland soils, which are dominant in subhumid to semiarid climatic regions, have low OM ratings. In the areas with either acidic rocks or sandy sedimentary rocks as the parent rock of the soil (northeast plateau of Thailand. Central Cambodia, east coast of Peninsular Malaysia), AP ratings are low. They are high for the soils in the Ganges and in Bhramaputra sediment areas of Bangladesh and the Godavari-Krishna Delta.

Fertility characteristics common to lowland soils

Aside from the regional variations previously discussed, lowland soils have a common favorable fertility feature that is associated with aquic moisture regime. This may explain why reasonably high, if not very high, rice yields have been maintained in hundreds of years of continuous cropping and accordingly why tropical Asia has been supporting an exceptionally high population density.

First, rice cultivated under naturally or artificially flooded condition can avoid soil sickness, often a serious constraint to upland farming. The alternation of moisture regime from flooded or aquic to dry exposes pathogenic microbes and fauna to conditions so severe that no soil sickness can be carried over, making continuous cropping possible for lowland rice.

Second, lowland soils receive substances lost from the catchment uplands through erosion and leaching. In this way, they maintain fertility. Instead of losing fertility by erosion, they are enriched by silting in the long-term rejuvenation of soil materials. Nutrients dissolved in the flood or irrigation water are readily available to the crops growing on lowlands. In one instance, Yoshida (1961) showed that the amount of calcium and magnesium supplied by irrigation water exceeds the requirement for rice by 2-6 times, while the supply of silicon satisfies 30% of the crop need, potassium 17%, phosphorus 1%, and nitrogen 8%. Thus flood or irrigation water is a significant source of nutrients, except phosphorus and nitrogen.

Third, phosphorus and nitrogen status is also favorable in lowland soils. Nitrogen fixation by lower plants and microbes is said to be much higher under waterlogged condition than under upland condition, except in upland carrying leguminous crops. Less of the nitrogen applied or released by mineralization of soil organic matter is lost through leaching in lowlands than in uplands because the ammoniacal nitrogen can stay adsorbed in the exchange complex. However, losses due to

ammonia volatilization and denitrification are considerably more in lowland soils than in upland soils. Deep placement of fertilizers could reduce denitrification losses.

The availability of phosphorus is rendered more favorable in lowland soils with aquic moisture regime than in upland soils because of the release of occluded phosphorus during iron reduction, release of a part of the phosphorus in iron phosphate reduction, and higher solubility of phosphorus from iron and aluminum phosphates under reduced, high pH condition. In short, phosphate availability is higher in lowlands than in uplands for the same total content of phosphorus.

To summarize, the soil fertility advantages of waterlogged or aquic lowland soils over upland soils came about through:

- ease of soil conservation, and
- ease of maintenance of soil fertility.

These two are more important in the tropics than elsewhere.

Physical properties of lowland soils

Because the greater part of lowland soils are derived from fine clayey sediments on the alluvial and deltaic plains, they generally have poor physical properties. Some 40% of all the paddy soils studied by Kamaguchi and Kyuma (1977) contain more than 45% clay.

Under monsoonal climatic condition, soils in lowlands are too wet during the rainy season and too dry during the dry. During the wet season, soil workability is poor, while during the dry season, soils tend to cohere to form very hard, big blocks. Because puddling for rice destroys existing soil structure, cultivation of upland crops becomes particularly difficult, causing problems in germination and seedling establishment. Thus, physical properties of clayey lowland soils often pose severe constraints, particularly to upland crop cultivation in rice-based multiple cropping. Lighter textured soils are preferred in such cropping systems.

For rice cultivation, however, soil physical properties are relatively unimportant as long as sufficient water is available. Probably a yield up to 4-5 t/ha would not require particular physical properties on rice-growing soils. That is another reason, besides those stated in relation to soil fertility. why rice is preferred to upland crops on lowlands. In Japan, however, elaborate water control and management, which require good soil physical properties, are said to be necessary to attain much higher yields, say 10 t paddy/ha. But the investment needed to provide good physical properties to lowland soils is prohibitive in most areas.

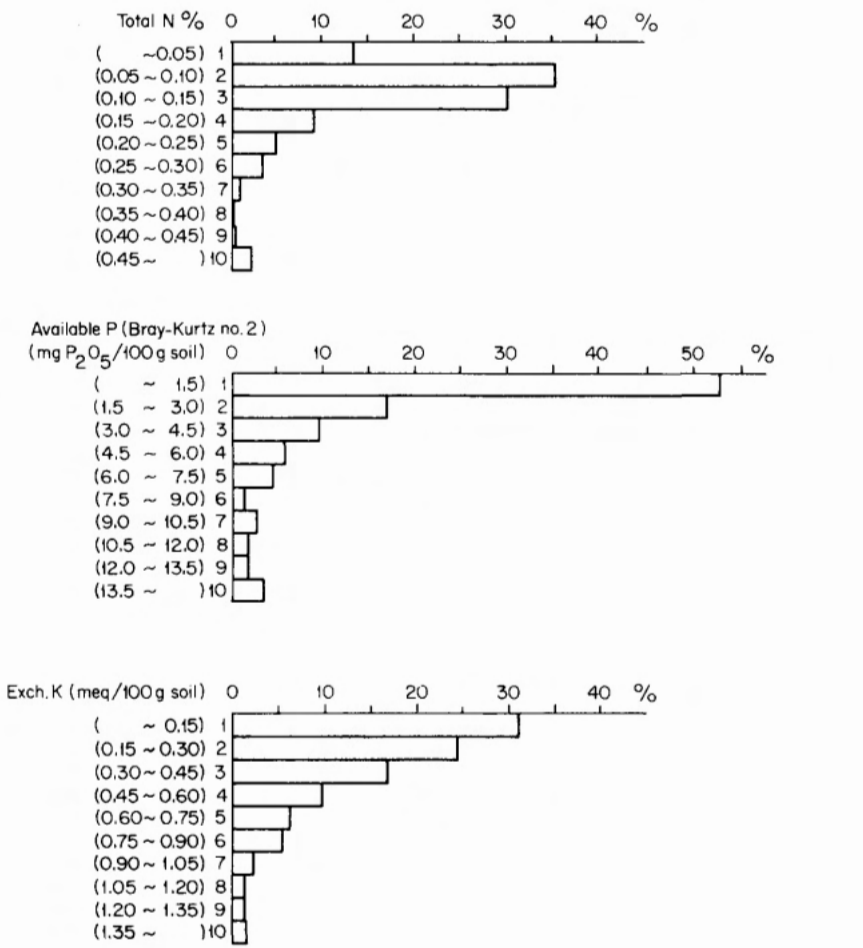
PROBABLE FERTILITY CONSTRAINTS OF LOWLAND SOILS

Nitrogen

It is generally believed that ammoniacal nitrogen released from decomposing soil organic matter contributes significantly to the nitrogen taken up by the rice plant. Many studies in Japan have shown that even in a field that has received sufficient fertilizer, the nitrogen supply from mineralization of organic matter is greater by a ratio of about 2:1 than that from fertilizers. In the tropics, Koyama et a1 (1973) confirmed that for a Bangkok plain soil.

Figure 2 shows a histogram of the total nitrogen content of tropical Asia paddy soils studied by Kawaguchi and Kyuma (1977). About 78% of the samples contain total nitrogen of less than 0.15% of air dry soil; the overall mean for tropical Asian paddy soils was as low as 0.l3%, compared with 0.29% tor Japanese paddy soils studied by the same authors. Obviously the potentially mineralizable nitrogen in most tropical Asian lowland soils is much too low.

Not only the total quantity but also the pattern of nitrogen mineralization should receive attention. Using ^{15}N Koyama et a1 (1973) clarified that in a tropical paddy soil the plants absorbed 60% of the mineralized soil nitrogen until the end of tillering, 36% during the panicle formation stage, and 4% during the ripening stage, compared with 45, 27, and 28% for the same periods in a Japanese soil Koyama et al concluded that a high temperature in the tropics is relevant to the pattern of mineralization of soil organic nitrogen and, accordingly, a topdressing of nitrogen fertilizer at a later growth stage would be effective.



2. Histograms of the major nutrient contents for 410 paddy soils in tropical Asia.

Phosphorus

A histogram of available phosphorus content of paddy soils in tropical Asia as determined by Bray-Kurtz No. 2 method is shown in Figure 2. More than half of all the test samples contain less than 15 ppm available P_2O_5, which is obviously far below the sufficiency level. According to Komoto (1971), the soil requires at least 60 ppm of Bray No. P_2O_5 to attain normal rice yields in the warmer region of Japan. As outlined previously, phosphorus-deficient soils occur in the areas with siliceous parent materials, such as Cambodia, Thailand, and the east coast of Peninsular Malaysia, Tanaka and Yoshida (1970) also noted widespread phosphorus deficiency in tropical Asian lowlands.

High phosphorus-absorption capacity and low absolute content of phosphorus cause content of available phosphorus in a soil. The phosphorus absorption coefficient, measured by a method routinely used in Japan, was usually moderate to low and did nor seem to be a serious problem. Only the soil containing free lime and ando soils (Andepts) showed high phosphorus absorption coefficients. Even soils rich in active iron oxides did not show particularly high coefficients. Moreover, if iron were the absorbent, phosphorus availability would not be seriously lowered in paddy soil condition. Therefore, it seems that the main cause of a soil's low available phosphorus status is its low absolute phosphorus content. In fact, nearly 25% of the samples studied by Kawaguchi and Kyuma (1977) contained less than 400 ppm total P_2O_5, which is thought to be critically low for normal rice growth even at the present low rice yield.

Farmers in tropical Asia are aware of such low phosphorus content and try to apply locally available phosphatic materials such as bat guano obtained from limestone caves. But the amount thus applied is far less than that required in intensified rice cultivation, and the use of chemical fertilizers is compulsory.

Potassium

Figure 2 shows a histogram of exchangeable potassium for 410 tropical Asian paddy soils. Exchangeable potassium level below 0.15 meq/ 100 g soil is low according to Kemmler (1980), and about 30% of the samples are in that class. But the mean content of exchangeable potassium for tropical Asian paddy soils, 0.4 meq/ 100 g, is not lower than that for Japanese soils. Furthermore, for elements with abundant reserves in the soil such as potassium, not only the static analytical value but also the rate of release should be considered. If its rate of release by weathering is higher under tropical conditions, potassium could be more available in tropical than in Japanese paddy soils. In addition, some supply from irrigation water can be expected. Thus, generally no serious deficiency problems would be expected. Some of the tropical soils are, however, so strongly depleted, as indicated by very low IP ratings (Table 3), that they need fertilization.

What has been stated here also applies to other basic cations, calcium, and magnesium. There is an antagonism among the basic cations and a high concentration of one in the soil solution suppresses the plant's uptake of another. Potassium deficiency from this cause may be seen in some high-pH soils.

Other probable constraints

Akiochi. In strongly depleted soils such as those found in northeast Thailand, a problem called *akiochi* may occur. It is a Japanese word meaning autumnal decline in plant vigor. In Japan, with heavy doses of fertilizers, rice plants grow vigorously until mid-summer, but toward the end of summer, growth declines and yield is very unsatisfactory. The type of soil that shows this phenomenon is normally a whitish sandy soil. A process called *ferrolysis,* operating in seasonally submerged soils, may lead to the formation of akiochi-inclined soil (cf. Brinkman 1979).

Akiochi is linked most directly to a low, free iron oxide content of the soil. High summer temperature accelerates organic matter decomposition, causing a strong reduction in the plow layer. Of the anaerobic decomposition products, butyric acid and hydrogen sulfide are particularly toxic to the rice plant. If the content of free iron oxides is kept sufficiently high, the root surface is coated with iron oxides and the plant becomes more resistant to the noxious effect of the toxic substances. Therefore, the first remedy for akiochi soil is to incorporate iron-rich, red soil materials into the plow layer (soil dressing).

Usually, however, soil dressing alone does not sufficiently improve akiochi-affected soil. The low content of free iron oxides may indicate general paucity of nutrient elements and poor quality of clay minerals. Thus, akiochi soils also tend to be poor in potassium, calcium, magnesium, manganese, silica, and even micronutrients. The word *degraded paddy soil,* denoting akiochi-affected soil is, therefore, a proper choice. Rice grown on degraded paddy soils frequently shows helminthosporium spots and the application of potassium, manganese, magnesium, and silica often effectively improves rice growth and prevents akiochi. Soil dressing supplies not only iron but also other nutrients and better-quality clay minerals.

Physiological iron deficiency is not a problem in degraded soils although they are poor in active iron oxides. It is sometimes reported, however, in high-pH soils such as saline and sodic soils.

Iron toxicity. Another fertility problem related to iron is iron toxicity. As the soil is reduced, ferrous iron concentration increases in the soil solution, at times reaching 500 ppm or higher. But this high level of ferrous iron does not by itself necessarily cause iron toxicity (Takagi 1958). According to Tanaka and Yoshida (1970), the symptoms of iron toxicity are not directly connected with a high iron content in the medium nor with that in the plant. They regard the toxicity as a result of interaction between a high iron content in the soil solution and deficiency of one or more essential nutrients such as potassium and phosphorus. According to Tadano (1979, rice plants that are nutritionally healthy, especially with respect to potassium, magnesium, calcium, and phosphorus, have a built-in protective mechanism that enables them to exclude an excessive amount of ferrous ions.

Two kinds of soils are apt to show this trouble: 1) acid sulfate soils and 2) strongly depleted soils in lowland areas with highly weathered soils (Oxisols and Ultisols) in adjacent uplands. In the strongly depleted soils, poor nutritional status and hydrogen sulfide injury seem to be the primary cause. Moormann and van Breemen (1978) studied the interflow water from the surrounding areas as a possible cause of iron toxicity or bronzing in the wet zone of Sri Lanka. In acid sulfate soils, strong acidity and aluminum toxicity are the primary causes, and phosphorus deficiency, poor

nutritional status, and at times, high salinity, are the secondary causes that weaken the protective mechanism against excessive uptake of ferrous iron.

Silica deficiency. It has not yet been proved that silica is an essential element for rice. However, a proper content of silica in the leaves and stalks of rice gives the plant resistance to blast and lodging, thus making a higher nitrogen dose and, accordingly, a higher yield possible.

Imaizumi and Yoshida (1958) developed a pH-4 N-acetic acid extraction method of assessing available silica in the soil and correlated this available soil silica level with the plant silica content and yield responsiveness. Based on this result, they proposed the following threshold values of soil silica content for judging the effectiveness of silica application for rice cultivation in Japan.

Response	*Available SiO_2 (mg/100 g soil)*
Always negative	> 13.0
Positive or negative	10.5-13.0
Always positive	< 10.5

The same criteria, however, may not be applicable to soils in tropical Asia, where the rate of silica release from soil minerals seems higher.

Silicate slags from iron foundries are most commonly used for amending available silica in the soil. They contain either calcium-metasilicate ($CaO\text{-}SiO_2$) or calcium-orthosilicate ($2CaO \cdot SiO_2$) as the main constituent and accompany minor amounts of magnesium, iron, manganese, and boron. Straw and farmyard manure can also be used as amendments.

Two more factors affect the availability of silica status in paddy soils. One is the supply of silica by irrigation water. As stated earlier, a substantial amount of silica is supplied by irrigation or floodwater. The other factor is reduction of paddy soils during the cropping season. Because a part of soluble silica is stabilized in the soil as amorphous iron silicates, it is released for plant uptake in the reduction process.

Silica deficiency would also be a problem for the strongly depleted soils with low IP ratings.

Manganese deficiency. The solubility of manganese in upland soils is determined mainly by the soil reaction; in the alkaline reaction above pH 8.5, its solubility is critically low, while in the acid reaction below pH 4.5, it is sufficiently high. In the pH range in between, redox condition affects the solubility of manganese more significantly. As the redox potential at which Mn (IV) compounds become unstable is about 300 mV (Patrick and Reddy 1978), they are relatively easily reduced to a more soluble manganous form. Thus, manganese is almost as mobile as other basic cations in paddy soils. That implies that there may be many paddy soils from which manganese has been leached out.

In Japan, the threshold value for manganese deficiency for paddy soil is set empirically at 2.5 mg MnO/ 100 g air dry soil, which is extractable with neutral N-ammonium acetate solution containing 0.2% hydroquinone (readily reducible manganese). The soils containing manganese below this level are expected to respond positively to manganese application, which is usually 20 kg MnO/ ha, as manganese sulfate or manganese-containing silicate slag. But as manganese defi-

ciency is often a part of the general akiochi phenomenon of rice that is grown on degraded soils, manganese application alone is rarely sufficient.

Sulfur deficiency. Sulfur deficiency has rarely been a problem in rice cultivation. In the past, sulfur-containing fertilizers were commonly used, and the adverse effect of sulfur as hydrogen sulfide in the reduced condition was feared in relation to akiochi.

In recent years, however, as the use of high-analysis fertilizers has become popular, incidences of sulfur deficiency have increased. Recently Ismunadji et al (1975) reported sulfur deficiency in Grumusol and Planosol areas in Java.

Zinc deficiency. Zinc deficiency in rice was also rare in the past. Since the 1960s, however, many incidences of zinc deficiency have been reported from various regions throughout the Asian rice zone. About 2 million ha of paddy soils are suffering from zinc deficiency (Randhawa et al 1978). This is related to conversion of more and more lands previously unused for rice in the drier climatic regions to paddy fields as irrigation systems have developed.

Soils that show zinc deficiency are mostly calcareous, saline or sodic with alkaline pH, because the solubility of zinc compounds is low in the alkaline reaction range. Because zinc carbonate ($ZnCO_3$) and hydrozincite ($Zn_5(OH)_6(CO_3)_2$) are among the probable forms of zinc compounds that determine the solubility of zinc in the pH range of reduced paddy soils, carbonate concentration of the soil solution is also relevant, e.g., the higher the total carbonate, the lower the zinc solubility. According to Tadano and Yoshida (1978), a high concentration of bicarbonate in reduced soil would also inhibit the translocation of zinc from root to the top and, thus, aggravate zinc deficiency.

The critical zinc content of the plant is about 15 ppm on dry weight basis (Tadano and Yoshida 1978). Zinc deficiency can be overcome by dipping seedlings in a 2% suspension of zinc oxide in water. Such a simple treatment can increase the rice yield remarkably.

Copper deficiency. A few papers from India report a substantial increase in rice yields resulting from soil and spray application of copper. In organic or peat soils. copper deficiency is sometimes suspected of being responsible for poor performance of rice, although this has not yet been verified in the literature. Based on his research in the peat lands in Kalimantan and Sumatra, Driessen (1978) recently suggested that the sterility of rice on deep peat could be attributed to the uncoupling of oxidative phosphorylation in a copper-deficient environment. The copper deficiency in peat soils is ascribed to chelate formation by organic compounds.

PROBLEM SOILS IN LOWLANDS

Acid sulfate soils

Acid sulfate soils or cat clays are formed as a result of oxidation of sulfide-containing sediments that are exposed to the atmosphere during natural or reclamation processes. Most of the oxidizable sulfide compounds are present in the form of pyrite, FeS_2. Upon exposure to air, pyrite undergoes oxidation as follows:

$$FeS_2 + \frac{15}{4} O_2 + \frac{7}{2} H_2O \rightarrow Fe(OH)_3 + 2SO_4^{2-} + 4H^+.$$

This reaction produces 4 equivalents of acid from oxidation of 1 mol of pyrite. Oxidation of ferrous iron as a part of this overall reaction is mediated by iron bacteria. Another important reaction is the oxidation of pyrite by the Fe^{3-} formed:

$$FeS_2 + 14Fe^{3+} + 8H_2O \Rightarrow 15Fe^{2-} + 16H^+ + 2SO_4^{2-}.$$

Thus, more acidity is produced. As Fe^{3+} can be replenished via microbially mediated ferrous iron oxidation, once the process has started pyrite can be oxidized even with limited oxygen supply as long as the medium remains acid.

Rice is often the first crop to be considered in acid sulfate soils which usually occur in swampy lowland. It is known to tolerate relatively high acidity; in solution culture only pH below 4 affects it adversely. Under such a low pH, aluminum toxicity may be more important than the direct effect of hydronium ion concentration. A high ferrous iron concentration produced in the oxidation process of pyrite can cause a physiological disorder in rice. Iron toxicity, the rice disorder frequently found in acid sulfate soils, results from complex nutrient imbalance, but the high ferrous ion concentration, coupled with high acidity and high salinity, is still an important factor.

Among the nutrient elements, phosphorus is probably the most critical in acid sulfate soils. In addition to the inherent paucity of phosphorus, the high activity of aluminum lowers the availability of phosphorus to rice. Phosphorus deficiency is so acute in some soils that no response, even to lime and nitrogen, can be expected unless phosphorus is supplied.

Three measures can alleviate the harmful concentrations of toxic substances:

1. Do not allow oxidation of pyrites contained in the potentially acid sulfate sediments, i.e., mud clays.
2. Leach the harmful substances out of the rooting zone after allowing oxidation to occur.
3. Inactivate aluminum by raising the pH of the medium with lime, which also reduces ferrous iron concentration in the soil solution.

All these measures have been recommended by researchers who have dealt with acid sulfate soil problems in rice cultivation.

The first measure is not a positive solution for acid sulfate soil problems. It suppresses the natural ripening process of the so-called mud clays. Because of strongly reductive conditions and very unfavorable working conditions, rice yield remains very low and no positive measures to improve it can be taken. In addition, this apparently easy solution is actually not so easy because of unpredictable climatic fluctuation. When dry spells are unusually long, the soil surface is oxidized and strongly acidified, which leads to total rice crop failure.

In the second measure, open drainage ditches are dug. Often tidal gates have to be installed in coastal areas to prevent saltwater intrusion. This investment certainly reinforces the washing effect of fresh rainwater during the rainy season, but it is not effective at all during the dry season unless the supply of freshwater is ample — a condition difficult to obtain in a monsoonal climate region. Upward capillary movement of water may cancel the washing effect, bringing the toxic substances back to the surface. Mulching should lessen this effect if adequate materials are available.

In areas with year-round heavy rainfall, as in Sarawak, East Malaysia, leaching, first with sea or brackish water, then with plenty of rainwater, could be effective provided major drainage is provided. Ridging or a dense network of shallow ditches should also prove effective in such areas.

The third measure, liming, is effective in raising soil pH and thus inactivating toxic aluminum. But if this measure alone is taken, the amount of lime required would easily amount to 10 t/ha or more, which is hardly economical. And, it is extremely difficult to transport huge quantities of lime to the originally swampy land. Another point to consider is that oxidation of pyrites is retarded in a neutral reaction range. Therefore, if lime is applied at the beginning of reclamation, the time required to leach out the toxic oxidation products is prolonged. Thus, liming should be carried out after the effect of oxidation and leaching becomes apparent.

When oxidation and leaching, with or without liming, are practiced, the loss of soil mineral nutrients and the attendant lowering of soil fertility due to acid leaching are worrisome. Although fertility was not lowered significantly in the experiment conducted by Murakami (1965) in Japan, further studies should be carried out to determine fertility deterioration in the reclamation of acid sulfate soils.

Actual and potential acid sulfate soils occur extensively in tropical Asia, especially in the deltas and coastal lowlands of Southeast Asia. More than 1 million ha occur in the Mekong Delta of Vietnam. About 800,000 ha are found in Thailand, including those areas having cat clays in the subsoil (Van der Kevie 1972). Peninsular Malaysia has about I 10,000 ha, of which 25,000 ha are already under rice (Kanapathy 1973). Driessen and Soepraptohardjo (1974) reported that about 2 million ha are present along the coast of Sumatra and Kalimantan. Most of these acid sulfate soil areas will become important agricultural lands for food production in the future.

Peat soils

About 32 million ha of peat land occur in the tropics. The share of Southeast Asia is large, between 14 million ha (Andriesse 1974) and 18 million ha (Driessen 1978) around the Sunda shelf.

According to Driessen (1978), the tropical peat may be classified into topogenous peat and ombrogenous peat. Topogenous peat formation is similar to that of low moor peat. It starts from the establishment of aquatic vegetation in the permanently waterlogged depression and ends in the complete filling of the depression with organic debris. Upon this topogenous peat the ombrogenous peat forms under continuous rainfall and excessive humidity under the closed canopy of swamp vegetation. Like the high moor peat, ombrogenous peat is poor in mineral elements because it is formed from the vegetation that supported itself on the limited supply of mineral nutrients released from the underlying peat mass. This poor nutritional status is a problem with deep peat soils.

When peat soils are reclaimed, drainage must come first, even when rice is the planned crop, because the greater volume of peat consists of water-filled pores that have almost no bearing capacity. As drainage and dehydration of peat proceed, considerable land subsidence takes place and the peat undergoes oxidative decom-

position, which enhances subsidence. Therefore, after some years the drainage must be readjusted. A subsidence as large as 1 m/year in deeply drained ombrogenous peats has been recorded. This is another problem in the reclamation of peat lands.

When a shallow peat is reclaimed, the nature of the underlying sediments should be carefully checked, because organic debris in peat will sometimes be decomposed and the underlying sediments, which are often of cat clay or acid sulfate nature, will be exposed to the surface.

Driessen (1978) reported that almost all the mineral elements contained in a peat soil are accumulated in the uppermost 25-cm layer and recycled by the vegetation. Therefore, the felling of the vegetation and the decomposition of the surface layer of the peat inevitably accelerate the loss of mineral nutrients from the soil. Thus, fertilizer application is imperative if crops are to be cultivated on reclaimed peat lands. Driessen's general recommendation is as follows: for major elements — 50-130 kg N, 30-70 kg P_2O_5, and 60-100 kg K_2O/ha per year, and for microelements – 15 kg $CuSO_4$, 15 kg $MgSO_4$, 15 kg $ZnSO_4$, 7 kg $MnSO_4$, 0.5 kg Na_2MoO_4, and 0.5 kg borax/ha.

Peat is generally very acid (pH 3 to 5), so liming is effective in almost all cases. Chew (1971) says that on acid peat soils most short-term crops will respond to 8-10 t ground magnesium limestone; ha followed annually by 1 t/ha.

Rice is considered a good crop on peat soils because it requires prolonged land submergence, which reduces subsidence and decomposition of organic matter. There have been many attempts to establish rice land on reclaimed peat, but they have not been successful in the tropics. Rice often shows sterility on deep peat. Driessen (1978) tentatively concluded that the sterility is caused by the inhibition of phosphorylation in the presence of phenolic compounds in a copper-deficient environment. Copper appears to deactivate the toxic phenolic compounds, but in the process also becomes unavailable to the rice plant. Driessen proposed two measures — draining the peat for a short period at the beginning of the reproductive stage to get rid of the inhibiting phenolic compounds and foliar and seed application of copper. Direct copper application is hardly effective because of rapid fixation.

Andriesse (1974) considers cassava and pineapple promising as upland crops in reclaimed peat lands. He also pointed out that sago palms are common under the natural conditions of peat land and, therefore, deserves more attention in the future.

There is a story of successful peat land reclamation in Japan. About one fourth of the 200,000 ha of peat lands in Hokkaido that has been reclaimed for rice since the beginning of this century is presently as productive as ordinary mineral paddy soils. The success seems attributable to a large quantity of soil dressing in addition to drainage and fertilization; mineral soil materials at about 1,000-1,500 t/ha are usually dressed on top of peat to give about a 10-cm-deep surface mineral soil. Even with the soil dressing, fertilization should be done carefully. Generally speaking, peat paddy soils are poorer in phosphorus and potassium and much poorer in silica than alluvial paddy soils. But the nitrogen supply is quite substantial, making adjustment of fertilizer application necessary. Application of magnesium sulfate often seems effective for high moor peat (cf., Nat. Hokkaido Agric. Exp. Stn. 1969).

Saline and sodic (or alkali) soils

Saline soils are soils whose electric conductivity of saturation extract (EC_e) values are higher than 4 mmho cm and exchangeable sodium percentage (ESP) values are lower than 15%. The pH of the soil is below 8.5.

Sodic soils are those with ESP values higher than 15% and EC_e values lower than 4 mmho/cm. The pH of the soil exceeds 8.5 because of frequent presence of sodium carbonate as free salt.

There are also soils with EC_e values higher than 4 mmho/cm and ESP values higher than 15%. Those are usually called saline-alkali soils.

All these soils are distributed mainly in semiarid to arid climatic regions. But they occur even under humid climate, especially in the coastal areas that are flooded by saltwater at high tides of where saltwater intrudes during the low-water season. A special type of salinity problem occurs in certain areas of northeast Thailand where salt-bearing beds intercalated in the Mesozoic sandstone formation come close to the surface and salt enters the solum by capillary movement.

Saline soils. Because the osmotic pressure of soil solution is high, saline soils are not suitable for crop growth. Because they normally occur in arid regions, desalinization with leaching is not readily practiced unless there is a source of good-quality irrigation water. In recent years, however, many salt-affected lands have come under irrigation, and numerous studies have been done on the amount and method of water application (Bhumbla and Abrol 1978).

As a method of leaching, alternate ponding and drying is often practiced to increase the efficiency of desalinization. In this practice, rice may be cropped, taking advantage of the crop's high tolerance for excessive water. Rice seems to be also tolerant of high salinity. Normally rice can endure the salinity condition up to 4 mmho/cm, but some studies show it can tolerate much higher salinity. Tolerance varies depending on variety and growth stage. During the seedling and heading stages, rice is more sensitive to salinity. Even so, Yoneda (1964) found that rice grown in the Kojima polder land could tolerate salinity up to 7 mmho/cm.

Thus, with high tolerance for both excessive water and salinity, rice appears to be the most suitable crop to grow during saline soil reclamation by irrigation.

Sodic soils. Sodic soils are characterized by two adverse conditions for crops: 1) their highly alkaline reaction and 2) their poor physical properties because of the presence of high sodium percentage in the exchange complex. Often sodium carbonate is the main soluble salt; it gives a high pH, sometimes as high as 10.5, as a result of hydrolysis. The high pH causes imbalance of nutrients and low availability of certain micronutrients.

Ready dispersion of soil clays due to high ESP causes structure deterioration which results in low available water-holding capacity and reduced permeability. These conditions are fatal for most upland crops.

For the reclamation of sodic soils, gypsum ($CaSO_4 \cdot 2H_2O$), together with irrigation water, is most commonly used to effect the exchange of sodium for calcium. Rice seems the ideal crop during the reclamation stage of sodic soils because it can stand excessive water and its requirement for soil physical properties is minimal. The highly alkaline pH is mollified by submerging the soil. An alkaline soil pH is lowered

by the carbon dioxide produced during organic matter decomposition and reduction.

The high partial pressure of carbon dioxide gas in the submerged paddy fields also facilitates mobilization of native calcium carbonate, which is almost invariably present in sodic soils, thus accelerating the exchange of sodium for calcium (Chhabra and Abrol 1977).

The fairly high pH of sodic soils seems to be tolerated by rice but it causes fertility problems, ammonia volatilization loss, zinc deficiency, and sometimes iron deficiency. But with careful management rice yields can be as high as 9 t/ha (Bhumbla and Abrol 1978).

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PRODUCTIVITY OF SOILS IN RAINFED FARMING SYSTEMS: EXAMPLES OF LONG-TERM EXPERIMENTS

P. A. Sanchez

The productivity of selected soils was estimated by average yields of long-term experiments on specific farming systems. Net primary productivity of native vegetation is more related to physical than to chemical soil properties. In pioneering farming systems, productivity is related more to soil fertility than to physical parameters, but under intensive continuous agriculture, the relationship is reversed and soil physical parameters become the main constraints.

Examples from four agroecological zones on well-characterized soils show that productivity levels obtained in long-term experiments can be related to variability in soil properties encountered within the agroecological zone. Within the humid temperate areas of the southeastern US, productivity over a 60-year span increased sixfold to tenfold as technology was adapted to farming practices. In the humid tropics productivity was assessed by comparing present agricultural yields with those obtained in long-term continuous cultivation of 3 crops/year and technological inputs in the humid part of the Amazon Basin. In acid tropical savannas, where the dry season is pronounced, pioneering agriculture with its few technological inputs was essentially nonproductive, compared with technology-based farming in the Cerrado of Brazil. The very low productivity of long-term sorghum experiments on Alfisols in Upper Volta illustrates severe soil physical property limitations and the development of secondary acidity.

Soil-productivity considerations are site- and farming system-specific. Although under optimum conditions forage dry matter production in the tropics can exceed net primary productivity values, it is more relevant to identify and correct soil constraints in a manner congruent with present socioeconomic conditions. The potential for future productivity has to be evaluated after due consideration of man's ability to reduce or eliminate some or all of these constraints.

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Soil productivity defined

Soil productivity is often viewed as a practical extension of the concept of soil fertility (the capacity of the soil to supply nutrients to plants). It can be defined as the capacity of a soil to produce plant yields within a specified environment and farming system. Factors affecting soil productivity include both soil properties and factors external to the soil such as the choice of crops or cropping systems, rainfall distribution, irrigation, level of fertilizer used, socioeconomic considerations, and many others. Obviously, soils do not have a single productivity measure.

The many ways of assessing the productivity potential of soils in large parts of the developing world have led to projections ranging from the superpessimistic to the superoptimistic. The development of policy decisions, which affect millions of people, is affected by such estimates.

Soil productivity under native vegetation or traditional agriculture can be assessed by the *constraint* approach, i.e., by analyzing soil limitations. That is a valid approach, but unfortunately certain constraints are often interpreted as insurmountable by scientists and policymakers who have limited agronomic experience. For example, assessment of the potential productivity of the US, according to the constraints of its virgin soils or under the predominant farming systems 200 years ago (shifting cultivation and nomadic grazing), would produce an outcome very different from the actual productivity under present soil management practices.

Soil productivity is not static even with the same management. It can increase or decrease with use. Farming systems developed by generations of farmers and scientists on acid infertile soils in the US and on calcareous soils in England have increased soil productivity with time. Inputs needed to improve productivity are economically and technologically time dependent. However, a point can be reached where the solutions become problems. For example, in originally acid infertile soils in the southeastern US, a current problem is to convince farmers not to apply additional phosphorus fertilizers because the soils already have more than adequate amounts. On the other hand, throughout the world, productivity of well-drained soils frequently declines because of mismanagement. The primary danger is erosion. However, I am convinced that any soil can be made productive at a price. The relevant issue is what that price is, not only in economic but in social terms.

Measuring soil productivity

The measurement of soil productivity needs to be specified beyond the obvious fact that the units should be yields either per hectare or, where space is not limiting, per unit of the more scarce input. Cooke's (1967) suggestion that single-year yields are of little use because of weather, pathogen attacks, and other seasonal variability factors is a readily accepted view of agronomists. The average yields of long-term trials are a better measure, but they have limitations. For examples of such difficulties, the reader may refer to reports by Cooke (1967, 1977) from the United Kingdom, Baldock and Musgrave (1980), Jolley and Pierre (1977) from the US, and Clarke and Russel (1977) from Australia. The main limitations are in scientists' ability to predict:

- the changes that will occur with time,
- the need to change crop species or rotation patterns when researchers find that the one they designed could be improved,
- the frequent need to increase or decrease fertilizer applications with time,
- the emergence or solution of pest and disease problems, and
- the incorporation of improved varieties in the sequence.

Nevertheless, such studies probably provide the best assessments of soil productivity. Consequently, soil productivity in this paper is measured by the average crop yields of long-term data as far as possible.

Soil productivity and soil classification

It would be most convenient to use soil classification in directly assessing soil productivity quantitatively. Broad generalizations can certainly be made, but they merely describe the main constraints that should occur in each soil class. Such generalizations have been made for the world by Dudal (1980) and for specific geographic regions by Dent (1980), Kampen and Burford (1980), Moormann and Greenland (1980), Sanchez and Cochrane (1980), and Cochrane and Sanchez (in press). Even in carefully controlled fertility experiments on soils belonging to the same family, crop yields and nutrient response curves are quite different. Quantitative soil classification systems provide a valuable guide to soil productivity, but actual productivity is so affected by transient and dynamic factors that no predictable estimates that give short-term reliability can be formulated.

Technical classification systems for soil productivity, such as the Fertility Capability Classification (FCC), however, can bridge the gap between soil classification and productivity by drawing from natural classification systems the agronomically relevant parameters that can be quantified (Buol et a1 1975). Finally, when there is a cumulus of farming experience and data at the soil phase level, productivity ratings can be given as a probability estimate for well-defined farming systems, both on agronomic and socioeconomic grounds and for a small geographical area. This is the concept of a *soil potential* now used at the county level in parts of the US.

NET PRIMARY PRODUCTIVITY AND SOIL PROPERTIES

A point of departure is to examine the net primary productivity of natural ecosystems. *Net primary productivity* is defined as the increase in dry matter per hectare per year, i.e., the difference between photosynthesis and respiration (Leith and Whittaker 1975). This measurement is compatible with the concept of soil productivity as it reflects long-term effects. Some examples in Table 1 show the higher primary productivity of tropical vs temperate ecosystems and forest vs grasslands, with the values for cultivated land corresponding more to that of grasslands. The highest recorded primary productivity value of a natural terrestrial ecosystem is 32 t/ha per year on a rain forest of Sarawak (Murphy 1975).

From a comparison of the global net primary productivity map shown in Figure 1 with soil and climatic maps of similar scale, it is evident that primary productivity is higher in the more humid regions having a udic soil moisture regime. At that scale, the dominant soils supporting the higher net primary productivities such as Ultisols,

Table 1. Worldwide estimates of net primary productivity of selected types of vegetation (from Leith and Whittaker 1975).

Vegetation unit	Annual dry matter production (t/ha)	
	Mean	Range
Tropical rain forests	20	10-35
Tropical deciduous forests	15	6-35
Temperate mixed forests	10	6-25
Tropical savannas	7	2-20
Temperate grasslands	5	1-15
Cultivated land	6	1-10
Swamps and marshes	20	8-40
Lakes and streams	5	1-15
World's continents	7	0-40

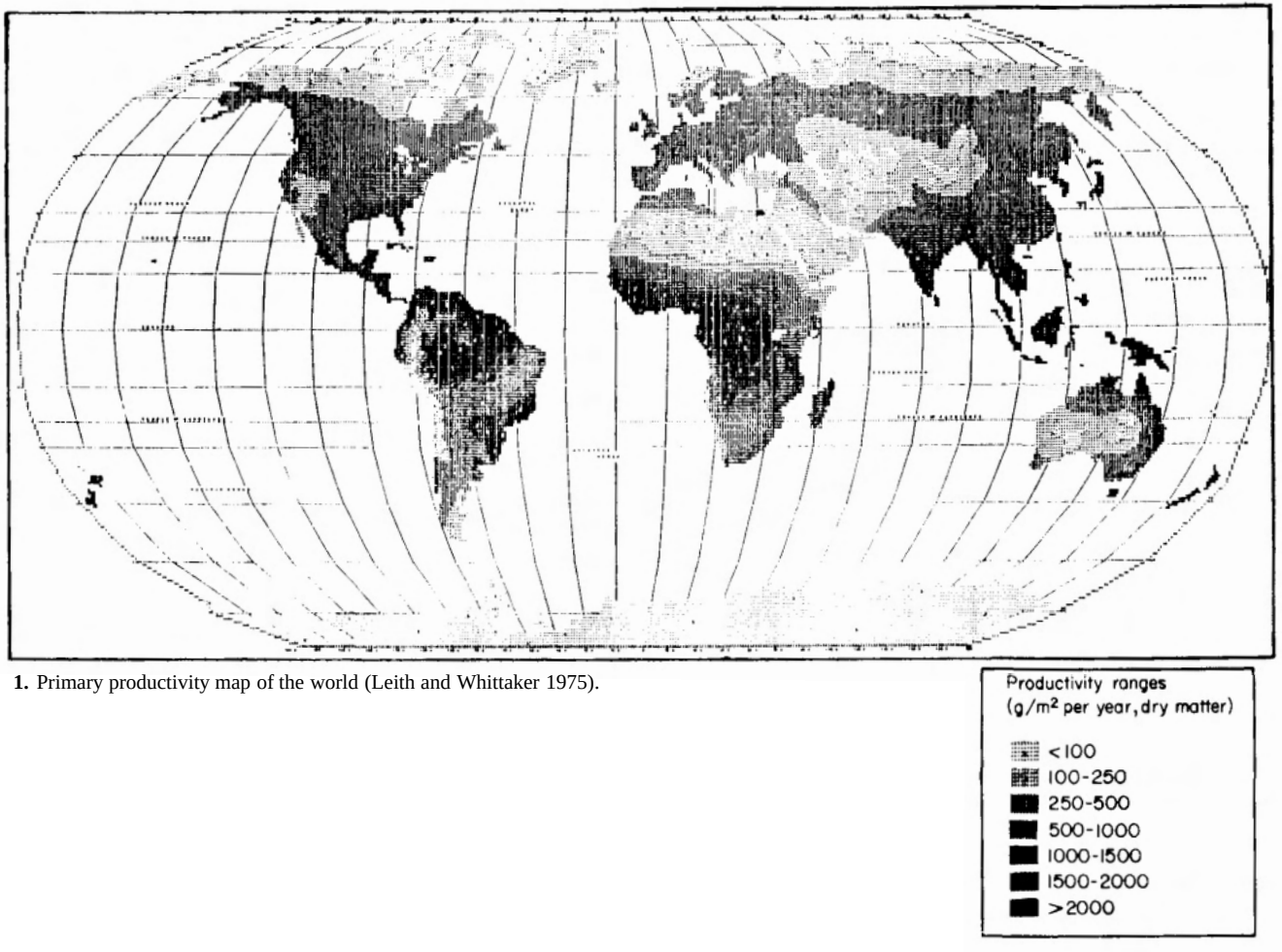
Oxisols, Alfisols with low-activity clays, and Spodosols are mainly low in native fertility. These figures suggest an inverse relation between net primary productivity and desirable soil fertility parameters, and a positive relation between net primary productivity and desirable soil physical properties that favor water availability and root development. Apparently, temperature, rainfall regime, and soil physical prop erties more markedly influence net primary productivity than do soil fertility parameters because of the efficient nutrient cycling of many natural ecosystems.

PIONEERING AGRICULTURE AND SOIL PRODUCTIVITY

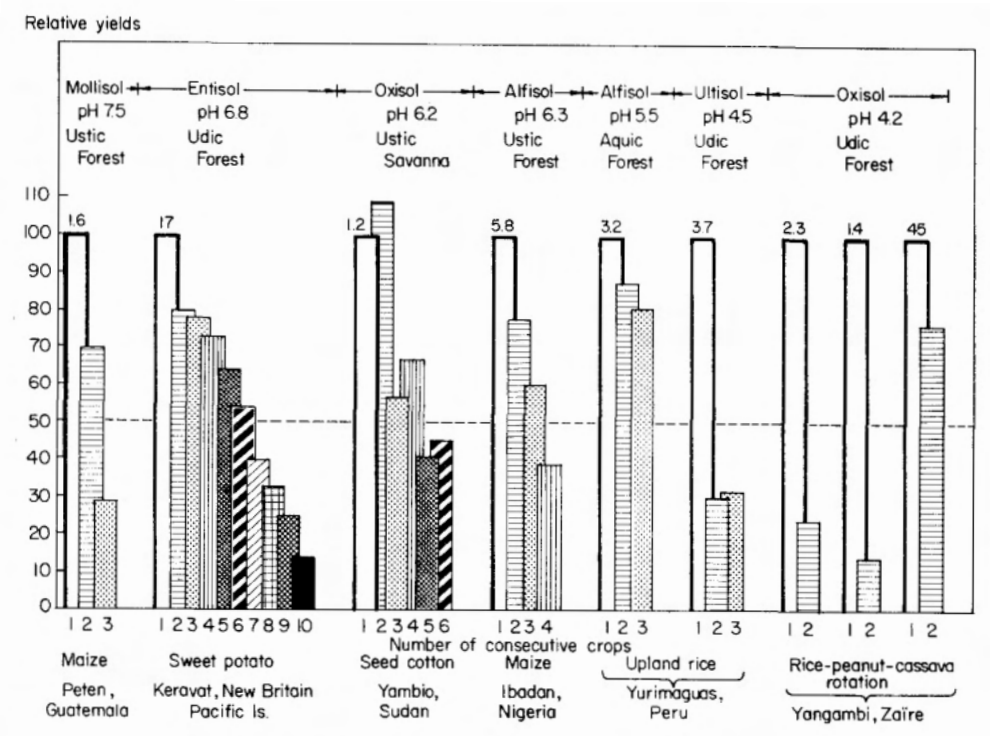
When lands are first cleared of their native vegetation and farmed without fertilizers, manures, amendments, or irrigation, the reverse relation occurs; crop yields and their stability are directly related to soil fertility parameters rather than to soil physical properties. By its very nature, cropping breaks the nutrient biocycle and results in the net removal of nutrients. Human population settles first and concentrates on areas with fertile soils, often collectively called *high-base-status* soils (Sanchez and Buol 1975), where the soil mineral components can supply nutrients, except nitrogen, and plant growth depends less on nutrient release by organic matter. The reason is evident in Figure 2, which shows the initial crop yields obtained without fertilization but with adequate weed control at seven sites with widely differing soil properties. The rate of decline in soil productivity, expressed as change in percentage of maximum yields, was slower in those soils that had pH values of 5.5 or higher before clearing than in the low-base Oxisols and Ultisols.

Although the rates of decline vary with soil properties as well as with climate and crop grown, productivity with continuous cropping declined even in the best soils, not only because of fertility limitations but because of pathogen attacks, weed problems, and many other factors.

In udic Mollisols (Udolls) in Rothamsted, England, considered one of the most naturally fertile high-base-status soils, wheat yields from the 127th through 132d year of continuous monoculture averaged 1.7 t/ha (Cooke 1977). Such yields, although high by pioneering agricultural standards, compared unfavorably with the mean yields of 5.8 t/ha obtained with the best fertility management in the same cropping system at that site.



1. Primary productivity map of the world (Leith and Whittaker 1975).

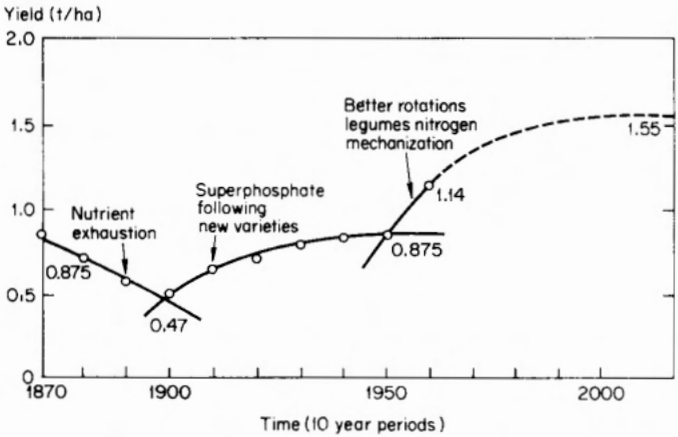


2. Yield declines under continuous cropping without fertilization in shifting cultivation areas as a function of soil, climate, and vegetation. Numbers on top of histograms are economic crop yields in t/ha (Sanchez 1976).

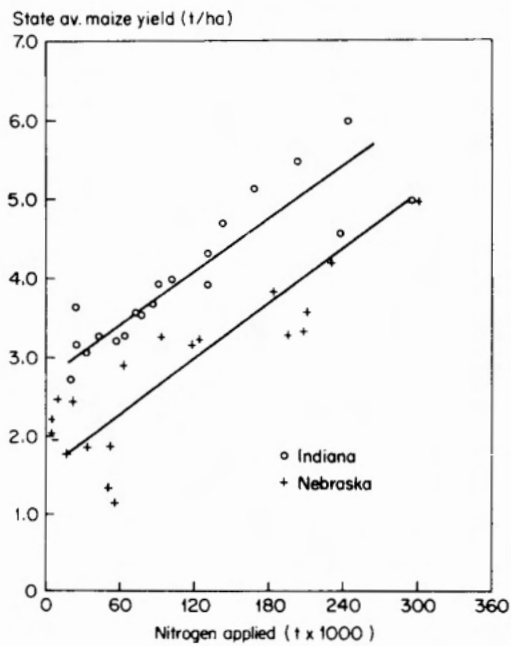
PERMANENT AGRICULTURE AND SOIL PRODUCTIVITY

The transition from pioneering to permanent agriculture is illustrated in Figure 3, which shows the trends in average wheat yields in Australia during the last century. Most of the wheat in Australia is grown on high-base-status soils with a protracted water stress period, which accounts for the lower yield levels than in the udic Mollisols of Rothamsted. According to Donald (1963), wheat yields declined during the first 30 years of continuous cultivation in Australia primarily because of soil fertility depletion. This tendency was reversed during the next 50 years with the use of ordinary superphosphate, which supplies phosphorus, calcium, and sulfur; improved fallowing techniques during the dry season; and improved varieties. Since 1950, yields have sharply increased because of improved cultural practices and better rotations with legumes to provide nitrogen.

The impact of fertilizer use on average yield levels is a major component of soil productivity. Figure 4, taken from Barber and Olson (1968), shows the close correlation between average maize yields in Indiana and Nebraska, USA, and nitrogen fertilizer consumption. This correlation is high because nitrogen is the main limiting nutrient in Mollisols and Alfisols, the dominant soils of Nebraska and Indiana. The lower yield levels in Nebraska are considered due to the drier (ustic) soil moisture regime; Indiana has a udic soil moisture regime. These differences are now probably erased because of extensive irrigation in Nebraska.



3. Trends in Australia's wheat yields (decennial means) during the past century (Donald 1963)



4. Correlation between nitrogen use and state average maize yields for Indiana and Nebraska 1948 to 1966 (after Barber and Olsen 1968).

Unfortunately, similar long-term effects, except on lowland rice production, are seldom well documented in the developing world. The remainder of this paper illustrates several examples of how soil productivity changes and how it can be improved by management in four rainfall-dependent ecosystems — one in a developed country and three in areas of current worldwide concern: the humid tropics, acid savannas, and semiarid tropics. Examples of how soil variability influences yields are also included.

Ultisols in southeastern United States

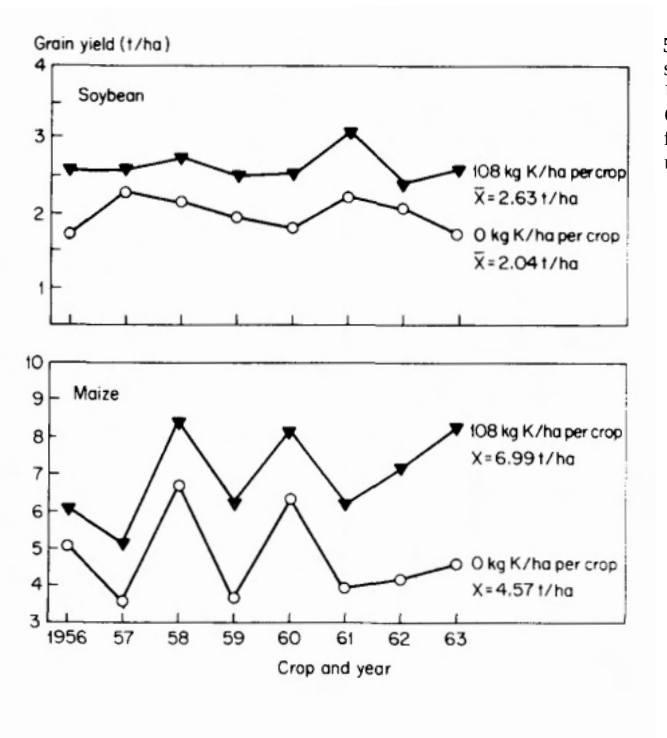
The southeastern US is dominated by low-base status, acid: infertile Ultisols. The original farming systems were forms of shifting cultivation that European settlers

adopted from the native Americans about 300 years ago, With the use of manures, fertilizers, and lime, continuous cropping systems gradually replaced shifting cultivation. In the process, much of the topsoil of the Piedmont region was eroded during attempts to intensify cotton cultivation. This area was then largely abandoned to secondary forest regrowth dominated by pine vegetation.

Permanent agriculture is largely concentrated in Ultisols of the Coastal Plain region, which was not subject to widespread topsoil erosion. Generations of farmers and agricultural scientists have increased the productivity of these Ultisols by 8-10 times during the past 70 years. For example, the average maize grain yields of Norfolk soils (a Typic Paleudult) in Edgecombe County, North Carolina, increased from 0.69 t/ha in 1908 to 6.27 t/ha in 1979 (Hearn 1908, Goodwin 1979). Therefore, estimates of soil productivity have increased by about one order of magnitude during the transition from pioneering to intensive agriculture.

Examination of long-term experimental data from this region provides a better measurement of actual productivity. The results of 8 years of continuous maize and soybean 2-year rotation on a Typic Umbraquult in the lower coastal plain of North Carolina are shown in Figure 5. Available potassium is the main limiting nutrient in this soil, which has moderate nitrogen supplying capacity and substantial phosphorus reserves built up by long-term fertilization. Under proper management, this soil annually produces about 2.6 t soybean ha and 7 t maize/ha. Year-to-year yield fluctuations were greater for maize than for soybean, which had extremely stable yields. The yield fluctuations were considered mainly a function of rainfall variability and maize is a more rainfall-dependent crop than soybean.

Local differences in available potassium levels of these soils also markedly



5. Long-term trials on maize and soybean in 2-year rotation on a Typic Umbraquult at Plymouth, North Carolina, as affected by potassium fertilization (R. E. McCollum, unpubl. data).

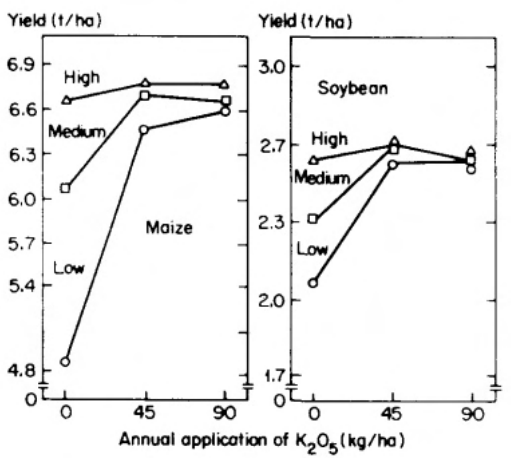
affected long-term productivity. Figure 6 shows the long-term response to potassium of both crops on sites with low, medium, and high available potassium levels before planting. There were no differences at the higher rates of potassium application but the differences were high at low intermediate levels.

One way by which the results of a long-term experiment can be understood in terms of the agroecological zone in question is through an analysis of yield records of different soils of the region. Table 2 is a summary of farmer soybean yields at 220 sites comprising 34 soil series in the coastal plain of North Carolina, which Reich (1976) collected for 2 years and correlated with soil properties at those sites. The mean yields were 2.48 t/ ha, somewhere between the high and low levels of the long-term experiment shown in Figure 5.

The effect of some individual soil constraints, defined by the FCC system of Buol et a1 (1975), is shown in Table 2. Sandy soils were definitely less productive than loamy soils. The presence of aluminum toxicity within the top 50 cm also substantially decreased yields. This parameter is probably correlated with the number of years since last lime application. Likewise, a low effective cation exchange capacity (ECEC) decreased yields, probably because of leaching losses of bases.

The presence of a g modifier, indicative of poor drainage, resulted in higher yields. This is attributed to the attenuation of drought periods by the presence of a water table at some depth within the reach of plant roots. The g soils were not so poorly drained as to impede the growth of soybean because of lack of aeration in most years. The soil on which the long-term experiment was conducted, a Typic Umbraquult, has conditions defined by theg modifier. Interestingly, the average soybean yields observed in the 76 g soils by Reich (1976) were exactly the same as the long-term yields (2.6 t/ha) illustrated in Figure 5 at the high fertility rate.

The effect of FCC parameters on 184 soybean experiments in 11 states of southeastern US from Texas to Virginia from 1968 to 1973 was studied using the same variety (Couto 1977). The sites were grouped into 26 FCC units encompassing 5 soil orders, 38 soil families, and 41 series. In spite of the intensive fertilization levels used, soybean yields were lower when the e (low ECEC) and *k* (low K reserves)



6. Maize and soybean yields as related to initial soil potash levels (high, medium, low) and annual rates of fertilization in the long-term study at Plymouth, North Carolina. Mean of 7 years (Kamprath 1964).

Table 2. Effect of soil constraints on soybean farmers' yields during 1974 and 1975 in the North Carolina Coastal Plain, according to the FCC[a] system (calculated from Reich 1976).

FCC parameter	Av yield (t/ha)	Sites (no.)
L (loamy soils)	2.77	107
S (sandy soils)	2.15	98
a (aluminum toxicity):		
Present	2.29	111
Absent	2.70	94
e (low ECEC[b]):		
Present	2.40	165
Absent	2.81	4
g (gley – poor drainage):		
Present	2.62	76
Absent	2.40	129

[a]FCC = Fertility Capability Classification. [b]Effective cation exchange capacity.

modifiers were present. Sites in which the modifiers g (poor drainage), *d* (dry season), *a* (aluminum toxic), and *h* (acid reaction) were present did not suffer yield decreases, because these constraints were alleviated by drainage, irrigation, and liming in the experimental plots. Therefore, the expression of these constraints is not marked, as in the example drawn from actual farmers' fields. The Couto study further showed that soils with the *g* modifier suffered yield decreases in years when above-average rainfall occurred during the crucial month of August, while sites without this modifier were not affected.

Long-term fertilizer experiments, therefore, provide a good assessment of soil productivity, and the FCC system provides a mechanism for relating changes in soil productivity to soil constraints. Although the productivity of southeastern US Ultisols is high because of massive use of technology designed to overcome agronomic constraints, soil properties still play a significant role in the actual yields obtained. It should be emphasized that technology is not applied equally everywhere in the region, and that the constraints are very much site specific.

Ultisols in the Amazon Basin

The following example contrasts sharply with the previous one in spite of the close similarity in soil properties between southeastern US and the Amazon Basin (Marbut and Manifold 1926, Sanchez and Buol 1975). In contrast with the stable, intensive cropping systems of southeastern US, there are no truly stable food crop production systems in the Amazon other than shifting cultivation in isolated areas. The data from field experiments are used. The two regions also contrast sharply in road and market infrastructure. Widespread migration of people from adjacent overcrowded areas of high-base-status soils is resulting in rapid settlement in parts of the Amazon Basin, where there is no sound soil management technology. This has raised worldwide concern about the ecological implications of the rapid rate of conversion of rain forests to other forms of vegetation (Myers 1980). It is also widely believed that continuous cultivation of the humid tropics' acid infertile soils, classi-

fied as Ultisols or Oxisols, is not agronomically or economically feasible (Goodland and Irwin 1975, Irion 1978). The productivity and environmental aspects must be considered together, because a significant portion of the 200 million hectares of new lands in the humid tropics of South America, Southeast Asia, and Africa is expected to be opened by 2000 (FAO 1979).

Fortunately, a reasonable body of knowledge on soil properties of the Amazon Basin and other crucial areas such as certain transmigration regions of Indonesia is available. About 75% of the Amazon Basin is dominated by Ultisols and Oxisols; 15% by Entisols and other alluvial soils; 8% by high-base-status, well-drained Alfisols and related soils; and 2% by Spodosols (Cochrane and Sanchez, in press). The approximate areal extent of the major soil constraints of the Amazon is shown in Table 3. Since 1972, a soils management research program has been operating in Yurimaguas, Peru, to develop viable annual crop production systems in Typic Paleudult soils with constraints typical of the main well-drained soils of the region: aluminum toxicity, phosphorus deficiency, low ECEC, and low reserves of potassium and other nutrients (Sanchez and Buol 1974, Tyler et al 1978). Surface soil pH values at the experimental sites ranged from 3.8 to 4.5. Annual rainfall is 2,100 mm, well distributed but with occasional drought stress. Population pressure is drastically altering the traditional shifting cultivation systems in the area.

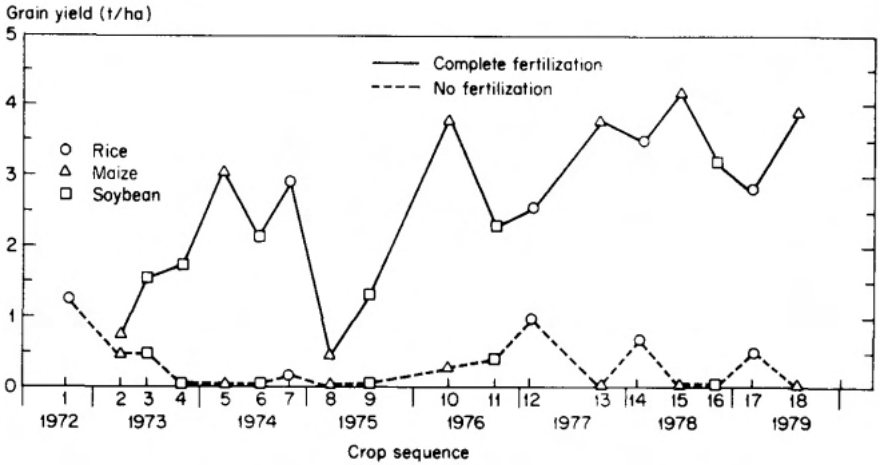
After the undesirability of bulldozer clearing compared with the traditional slash-and-burn method was identified (Seubert et al 1977), several cropping sequences were attempted on a continuous basis. Figure 7 illustrates the yields of the first 18 continuous crop harvests of a triple-cropping sequential system of upland rice, maize, and soybean. Without fertilization the yields were dismal, averaging 0.37 t/ha per crop or 1.1 t grain/ha per year. With adequate fertilization, the long-term average of the experiment was 7.4 t grain ha per year.

The term *adequate fertilization* deserves scrutiny, because it took about 5 years of research to understand soil dynamics and fertilizer needs in Yurimaguas. Figure 7 shows some low yields before 1975, and more stable and higher yield afterwards. Figure 8 shows the results of another system, continuous upland rice monoculture, which resulted in yield losses with time, even at complete fertilization levels. When fertility problems were identified and solved and the rotation was changed from

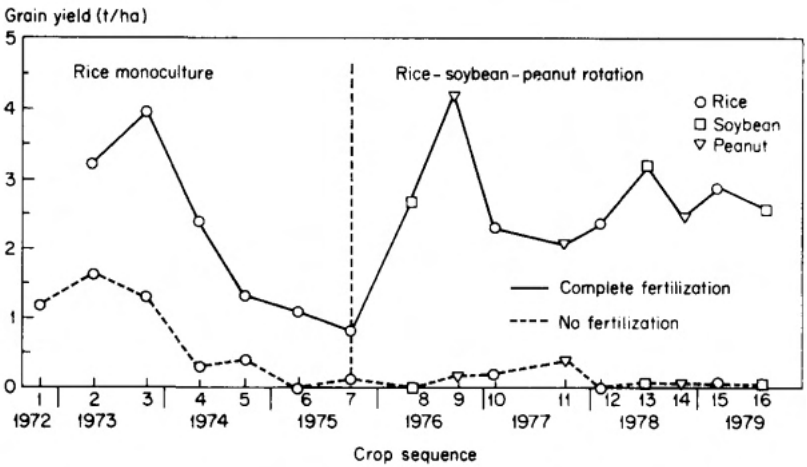
Table 3. Approximate areal extent of major constraints of soils of the Amazon, in undisturbed states (from Cochrane and Sanchez, in press).

Soil constraint[a]	Million ha	% of Amazon
P deficiency	436	90
Al toxicity	315	73
Low K reserves	242	56
Poor drainage, flood hazard	116	24
High P fixation	77	16
Low ECEC	64	15
High erodibility	39	8
So major limitations	32	7
Slopes > 30%	30	6
Plinthite hazard if topsoil is eroded	21	4

[a] N, S, Mg, and Zn deficiencies plus temporary drought stress are also widespread.
ECEC = effective cation exchange capacity.



7. Long-term yields in a rice-maize-soybean rotation with and without complete fertilization on a Typic Paleudult of Yurimaguas, Peru.

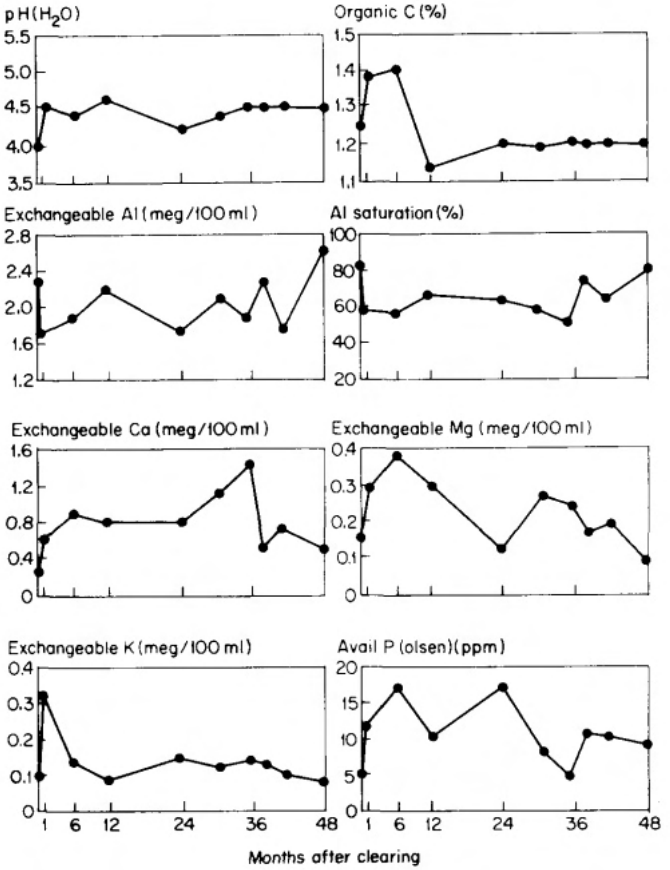


8. Long-term performance of continuous rice and rice-soybean-peanut rotation with and without fertilization on a Typic Paleudult from Yurimaguas, Peru.

upland rice monoculture to upland rice - soybean - peanut rotation, yields increased and remained reasonably stable with time. This is shown in Figures 7 and 8 for the data after 1975.

Monitoring the changes in soil chemical properties with time was crucial in developing the necessary fertilization rates for these intensive systems. Figure 9 shows some chemical changes in the unfertilized topsoil during the first 4 years after clearing. Table 4 summarizes the main changes in both fertilized and unfertilized plots, and Table 5, the suggested fertility maintenance schemes for continuous cultivation.

The implementation of such practices since 1976 has provided a very different perspective of the productivity potential of these Ultisols. The average yields obtained with these two cropping systems at three sites since 1976 are shown in Table 6. Soybean yields are very similar to those obtained in Ultisols of North Carolina, but maize yields are definitely inferior. The main constraint to high maize yields in



9. Changes in topsoil (0-10 cm) chemical properties of an Oltisol cleared by slash-and-burn method, continuously cropped to upland rice (8 crops), without fertilization at Yurimaguas, Peru 1972 (Sanchez 1979).

Yurimaguas is the lack of adapted cultivars that are reasonably tolerant of insects and diseases. Progress has been made in this direction with experiments attaining maize yields of 6-7 t/ha per crop (NCSU 1978). These yields are not consistent enough to be considered a measure of soil productivity in these soils. The upland rice and unshelled peanut grain yields are excellent for anywhere in the world.

The long-term data suggest that continuous cropping of acid, infertile soils of the Amazon is feasible and highly productive under intensively managed rotation systems. The advantages of crop rotations with upland rice at two fertility levels over successive monocultures are clearly shown in Figure 10. The main disadvantage of monoculture is the buildup of pests and diseases; in this case, of mole crickets. Also, the overall rate of yield decline in unfertilized plots was substantially lower when upland rice was rotated with soybean, maize, or peanut. The benefits of rotations in Yurimaguas, however, do not imply that monocultures may not be advantageous elsewhere in the Amazon.

Economic analysis has shown that the intensive fertilization rates used are profitable, with a net return of about $3/$1 invested in fertilizers, lime, and transportation inputs (NCSU 1978). Estimates based on 1980 prices suggest that the net returns are

Table 4. Time of appearance of fertility limitations in an upland rice - maize - soybean annual rotation after a secondary forest in an Ultisol in Yurimaguas, Peru, was burned (Villachica 1978, Sanchez 1979).

Months after clearing	Problem
1	The effect of the ash is an initial increase in pH, inorganic N, P, K, Ca, Mg, S, and micronutrient content, and a decrease in Al saturation to below toxic levels.
8	Inorganic N supply is depleted and N deficiency symptoms appear. Exchangeable K contents decrease below critical level of 0.2 meq/100 g and K deficiency symptoms appear.
10	Organic C decomposition reaches a new equilibrium level. Al saturation increases, surpassing toxicity level of 60% for maize and soybean. Available P decreases to below critical level (12 ppm P via Olsen method). Mg becomes critical at 0.2 meq Mg/100 g for soybean and 0.4 for maize.
12	Liming to pH 5.5 and applications of 80-26-80 kg N, P, K/ha per crop (except N for soybean) increase yields.
	K applications solve K deficiency but create K/Mg imbalance when ratio becomes < 1.2. Mg applications are needed. B deficiency is evident.
	S, Cu, and Mo probably become limiting (S became limiting immediately after clearing in bulldozed plots). Mo deficiency depends on Mo status in seed.
24	Nutrient removal by cropping depletes the soil still further. Rates of N, P, K, and Mg fertilization have to increase.
48	Zn deficiency appears.

Table 5. Suggested fertility maintenance scheme for intensive crop production in Yurimaguas. Three crops a year: preferably rice - peanuts - soybeans or rice - maize - soybeans (Villachica 1978, Sanchez 1979).

Months after clearing	Crop number	Fertilization
0	1	Slash-and-bum clearing. Short-statured upland rice planted without fertilization. Yields 3 t/ha. Soil tested near harvest to determine Al saturation.
5	2	Apply dolomitic lime at 1 x meq/100 g exchangeable AI and incorporate with hand tractor. Apply 50 kg P/ha as single superphosphate to correct P and S deficiencies, and 60 kg K/ha. If dolomitic lime is unavailable, add 30 kg Mg/ha per crop.
12 onward	5	Maintenance applications of 50 kg P/ha, 50-80 kg K/ha, and Mg to keep K-Mg ratio at about 1.2. 1 kg B and 1 g Mo per kg of seed. N rates should be 80 kg/ha for rice, 120 kg/ha for maize, and none for soybean and peanut. Soil testing every 6 months to check for Al toxicity, P, K, Mg, and micronutrients. Apply 2 kg Cu/ha every 3 crops.
24	9	May need to add more lime. Watch for Zn deficiency becoming critical.

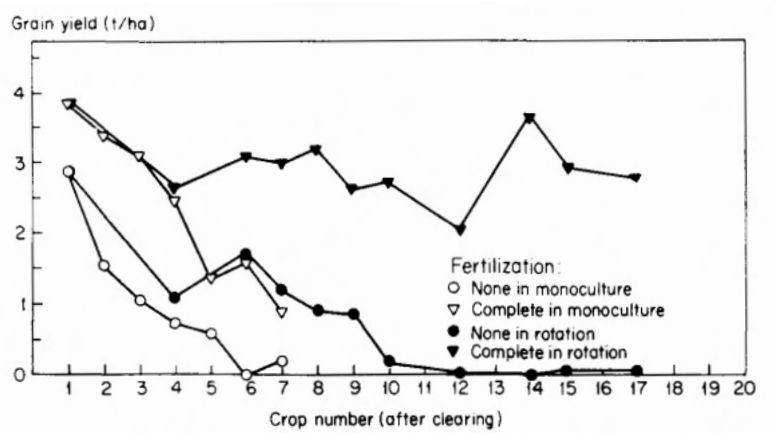
Table 6. Average yields obtained with adequate fertilization levels in two 3-crops-year rotations at Yurimaguas since 1976.

Crop	Av grain yield (t/ha)	Crops (no.)
	Cropping systems 1	
Rice	2.75	7
Soybean	2.70	7
Peanut	2.68	5
Total/year	8.13	
	Cropping systems 2	
Rice	2.96	6
Maize	3.93	8
soybean	2.55	5
Total/year	9.44	

even higher than those at 1978 prices. Different prices in other regions or at other times may affect this relation. This technology is being validated at about 20 farmers' fields in the area, with promising results. Several farmers, with the use of fertilizers, are already in their fourth continuous crop (Valverde and Bandy 1980).

Research on lower input cropping systems has also shown promise in Yurimaguas. Intercropping of cassava with upland rice, maize, soybean, and peanut has produced five crops a year at considerable savings in fertilizer use (Sanchez 1977). The use of mulches and green manures has reduced fertilizer requirements but increased labor costs. Studies to select cultivars for aluminum tolerance, to determine the optimum time of managed fallows, and to incorporate acid-tolerant grass and legume pasture species are expected to develop into a series of alternatives at different levels of input use for validation in farmers' fields.

Some of these low-input systems appear promising. In forage adaptation trials, the grass *Andropogon gayanus* produced a total of 56 t dry matter/ha per year, and the legume *Desmodium ovulifolium* 28.5 t ha on an abandoned Ultisol with pH 3.8,



10. Effects of fertilization and rotation vs monoculture on long-term yields of upland rice on a Typic Paleudult in Yurimaguas, Peru,

2.3 meq Al/100 g, and 75% Al saturation. The forages received only an application of 50 kg P_2O_5/ha as triple superphosphate (NCSU, unpubl. data). Grazing trials to assess the persistence and productivity of such pastures under animal pressure are in progress.

A recent review on perennial crop production in other areas of the Amazon (Alvim, in press) indicates the enormous potential of some species such as oil palm and rubber, that are well adapted to acid infertile soil.

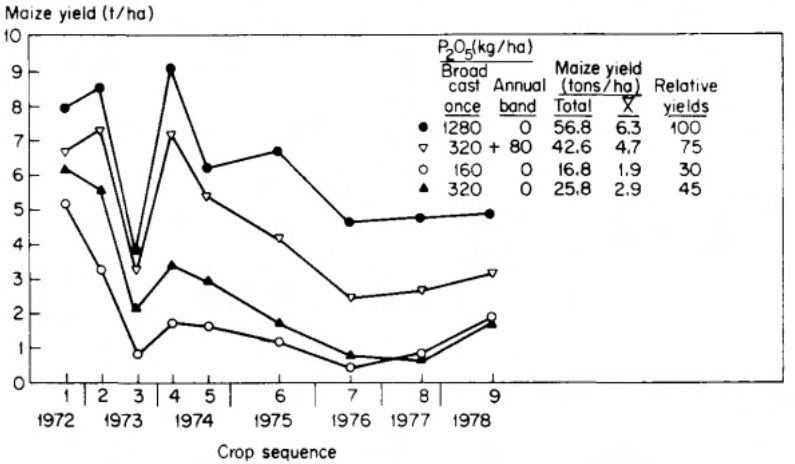
Although the present results equal or surpass yields in temperate-zone Ultisols, the research that has been done in developing technology for the humid tropics is insignificant compared with that done in the temperate zone.

Oxisols in the acid savannas

The Cerrado of Central Brazil is an immense savanna with the largest continuous expanse of Oxisols in the world. At the Centro de Pesquisa Agropecuaria dos Cerrados (CPAC) near Brasilia, a long-term maize trial has been conducted since 1972 to evaluate the residual effects of application rates and placement of triple superphosphate. The soil is classified as a Typic Haplustox, clayey, kaolinitic, isothermic. The average annual rainfall is 1,570 mm but there is a 5-month dry season. The major constraints of this soil are its high fixing phosphorus capacity, aluminum toxicity, low ECEC, low potassium reserves, low zinc, and low available water-holding capacity in spite of its high clay content. The area is essentially devoid of pioneer farming that uses no modern technology, simply because no annual food crops can be produced without fertilization. Figure 11 (drawn from data by NCSU 1975, 1978; CPAC 1978, 1979, 1980; Yost et al 1979; Miranda et al 1980) shows the history of maize grain yields during the nine consecutive crops harvested since 1972. The soil was limed to pH 5.5, fertilized with sufficient amounts of nutrients other than phosphorus, and irrigated throughout the two dry seasons when the second and fourth crops were grown. The most limiting nutrient in this soil is phosphorus because of cost, although some of the other previously mentioned constraints are certainly important.

A maximum average grain yield of 6.3 t/ha per crop can be obtained by broadcasting a massive application of 1,280 kg P_2O_5 ha and incorporating it into the topsoil before the first planting. The residual effect has been sufficient to keep available phosphorus above the critical level of 8 ppm P (N. C. method) for 7 years. Economic calculations by Miranda et al (1980) also indicated that this massive application is the most profitable, assuming a 25% annual interest rate on credit and a price-cost ratio in which 6.7 kg maize is needed to pay for 1 kg P_2O_5.

The high capital requirements, however, suggest a different alternative, which consists of an initial broadcast application of 320 kg P_2O_5 ha, followed by a banded application of 80 kg P_2O_5 /ha per crop, including the first one. This strategy produces about 75% of the maximum yield (4.7 t/ha) at a similar profit level. The high phosphorus fixation capacity of this soil is shown by the poor performance of initial broadcast applications of 320 and 160 kg P_2O_5/ha, which are usually adequate in most other soils. The productivity of these Oxisols for maize, therefore, is similar to that of the North Carolina Ultisol, illustrated in Figure 5, both of which are based on 7 years data.



11. Long-term maize yields on Typic Haplustox near Brasilia, Brazil as affected by phosphorus rate, timing of application, and placement method (sources: NCSU 1975; CPAC 1978, 1979, 1980; Miranda et al 1980).

Considerable variability in the degree of expression of soil constraints in the Cerrado has been well documented by Lopes and Cox (1977). The results of 542 FAO/ANDA/ABCAR simple fertilizer trials on maize in the region from 1969 to 1973 have been evaluated in relation to soil constraints according to the FCC system (NCSU 1974). Although the maize yields were not as high as those being obtained at CPAC. Table 7 shows the impact topsoil texture and high phosphorus fixation had on maximum yields of 228 maize trials. Soils with high phosphorus-fixing capacity, as defined by the *i* modifier (*Ci* and *LCi*), were less productive than those that did not have the *i* modifier (*C* and *LC* soils). Also, clayey soils (*C*) were more productive than loamy ones (*LC*), presumably because of somewhat higher available water-holding capacity.

Data from the other crops show that *C* soils invariably produced higher yields than *LC* soils in the Cerrado. *LC* soils, in turn, were more productive than sandy-over-loamy soils (SL). These differences were as high as 77% for upland rice yields in *C* vs *LC* soils and 47% for cotton yields in *C* vs *LC* soils. The absence of the *e*

Table 7. Mean yields of 228 maize fertilization trials conducted from 1969 to 1973 in the Cerrado of Brazil as affected by 2 FCC[a] modifiers (adapted from NCSU 1974, Couto 1977).

Texture class	i modifier absent (moderate P fixation)		i modifier present (high P fixation)	
	Yields (t/ha)	Sites (no.)	Yields (t/ha)	Sites (no.)
LC (loamy over clayey)	3.60	31	2.39	54
C (clayey throughout)	4.65	85	3.43	58

[a]FCC = Fertility Capability Classification.

modifier (low ECEC) invariably resulted in higher crop yields. The a (Al-toxic) modifier reduced yields in all crops except potato. The yields of potato increased because of aluminum tolerance and fewer disease problems encountered in more acid pH ranges. As expected, Al toxicity, as defined by the *a* modifier, had the most marked detrimental effect on yields of cotton, the most aluminum-sensitive crop in the study (NCSU 1974). Consequently, the effect of specific soil constraints in the Cerrado of Brazil could be judged in the same way as in the more developed farming systems of North Carolina.

In addition to phosphorus, several technology components have been developed to overcome soil constraints and to determine the level of fertilizer and lime input most efficient for continuous cultivation of crops such as upland rice, soybean, maize, sorghum, and peanut. These aspects have been summarized by Sanchez (1977), Miranda et al (1980), Lobato and Ritchey (1980), and Espinoza (1980).

The main components of the technology are:

- Decrease soil acidity by liming to neutralize the exchangeable aluminum in the topsoil, increasing the soil pH up to 5.5, and providing a residual effect for several years. Rates vary from 2 to 4 t/ha (Gonzales et al 1979, NCSU 1978, Miranda et al 1980).
- Increase root volume by applying a combination of broadcast rock phosphate applications and banded applications of superphosphate before each crop. This gradually builds up the phosphorus status of the soil (Lobato and Goedert 1977, Yost et al 1979). The basal or *corrective* applications are about 150-400 kg P_2O_5/ha and the banded applications between 30 and 80 kg P_2O_5/ha.
- Identify, through soil fertility evaluation services, the critical levels for potassium, sulfur, magnesium, zinc, and other elements, and apply the necessary amounts (Lopes and Cox 1977, Galrão and Lopes 1980).
- Decrease the devastating effects of drought stress during peak periods of growth by deep lime application or use aluminum-tolerant cultivars that are capable of exploring a deeper soil volume (Gonzales et al 1979, Salinas 1978). Whenever cheap, gravity irrigation systems are possible, apply supplemental irrigation during these periods. This is the case in a small portion of the Cerrado around Brasilia where a second annual crop, irrigated wheat, can be grown during the dry season. Large areas of the Venezuelan Llanos are now under continuous sorghum-peanut production using center-pivot irrigation systems.

The use of some of these components has permitted a rapid development of crop production in the acid savannas, the most noteworthy being the spectacular increase of soybean production in the Cerrado of Brazil, particularly in areas with topography most favorable to mechanization. The increase in area cultivated to annual crops in the acid savannas during the last 10 years is estimated to be about 5 million hectares, mainly in Central Brazil (Sanchez and Cochrane 1980).

Many serious problems of technology adoption exist. Improper, sometimes excessive, tillage causes severe soil compaction and excess runoff and erosion on sandy Ultisols. Crudely designed irrigation systems often result in serious soil erosion on Oxisols that, because of their excellent structure, have low erodibility. The extent of erosion in parts of Minas Gerais is alarming. Not only is the area eroded but the increased sediment causes environmental damage downstream.

Further erosion should be prevented and the research and extension services strengthened in support of each major crop being grown. The need to increase the efficiency of purchased inputs is also becoming more crucial. Selection of cultivars tolerant of aluminum toxicity and low levels of available phosphorus is a major step; it has resulted in significant reductions in the optimum rates of lime and phosphorus (Spain et a1 1975, da Silva 1976, Salinas and Sanchez 1976, Salinas 1978). More efforts are needed to bring plant breeders and soil scientists together to develop varieties that are high yielding or less risky at lower levels of lime and phosphorus applications.

An interesting sideline of this research is the finding that, over time, there is considerable downward movement of calcium and magnesium from the low ECEC, limed topsoil to the highly acid subsoil. In well-structured Oxisols (Ritchey et a1 1980), such movement is followed by deeper crop root growth and gradual improvement in the soil's productivity with continuous cropping. These results defy the conventional belief that low ECEC is undesirable. Consequently, with good management, soil productivity can increase with time in Cerrado Oxisols.

The principal agricultural activity in the acid savannas of tropical America, however, is beef cattle production. Beef production serves as the wedge for opening new lands in those areas. It is gradually replaced by mixed crop-grazing systems and eventually by intensive cropping systems, as infrastructure improves and land value increases. Although this symposium does not concern beef production, the development of low-input, grass-legume pasture production systems deserves mention as another way of assessing soil productivity. In this case, the emphasis is on solving most of the soil constraints through tolerant germplasm so the necessary amounts of fertilizer inputs can be used as efficiently as possible.

The possibilities of a legume-based pasture production technology for the acid, infertile soils of tropical America seem good at this time. In effect, a management strategy is being developed by CIATs Tropical Pasture Program and collaborating institutions in Brazil, Bolivia, Colombia, Venezuela, and other countries (CIAT 1978, 1979, 1980; Sanchez and Tergas 1979; Sanchez, in press). The main components of this package are:

- Systematically selecting appropriate soils. A computerized land resource inventory of the region has been developed.
- Planting mixtures of locally adapted grass and legume cultivars tolerant of high levels of aluminum saturation and low levels of available soil phosphorus, major pest attacks, drought stress, and burning.
- Supplying nitrogen to the system by inoculating legumes with acid-tolerant *Rhizobium* strains.
- Using low-cost, low-reactivity rock phosphates, which become more available when the soil is kept acid and grown to aluminum-tolerant plants.
- Correcting all other nutritional deficiencies, particularly potassium, sulfur, and micronutrients, through fertilization.
- Reducing pasture establishment costs, where possible, by using low-density planting methods of crops as precursors to pasture establishment.
- Placing about 10% of a management unit in improved grass-legume pastures for COW-calf units under strategic grazing.

Results from liveweight gain trials and herd management trials *at* Carimagua, Colombia, are promising (CIAT 1979). Swards of the grass *Andropogon gayanus* mixed with the legume *Zornia latifolia* or *Stylosanthes capitata* fertilized with about 50 kg P_2O_5/ ha, 25 kg K_2O / ha, 20 kg S/ ha, and 20 kg Mg ha have increased annual liveweight gains to about 400 kg/ ha and the stocking rate to 2 animal units/ ha (CIAT 1980). These packages appear economically feasible (CIAT 1979). In April 1980, the Empresa Brasileira de Pesquisa Agropecuaria officially released Andropogon gayanus for use in the Cerrado of Brazil.

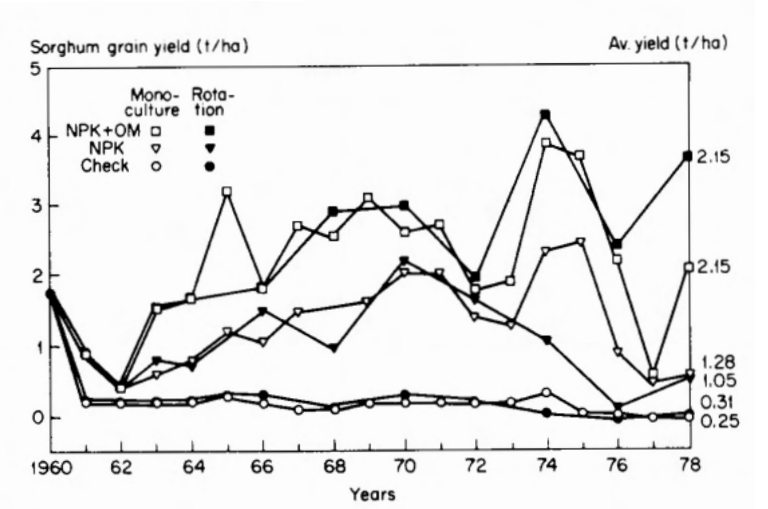
Alfisols in semiarid West Africa

A totally different environment, the Sudano-Sahelian zone of West Africa, has a strong 8-month dry season. The dominant soils of the area are Alfisols. The most serious constraints are soil surface hardening and sealing, which affect seed germination and root growth, and increase runoff and erosion losses (Jones and Wild 1975, Nicou and Charreau 1980). A long-term experiment was initiated in 1960 at Saria, Upper Volta (850 mm annual rainfall), to test the effects of fertilizers, manures, and rotations in a "Sol Ferrugineaux Tropical en Cuirasse," probably classified as an Oxic Plinthustalf, coarse-loamy, kaolinitic, isohyperthermic. Figure 12 shows yield patterns of sorghum when grown in monoculture or in rotation with a legume crop.

Without fertilizers sorghum yields dropped rapidly and remained stable at about 0.2 t/ha. Rotation had no beneficial effect over monoculture in unfertilized plots. With the average NPK fertilization of 60-42-40 kg/ ha, yields remained at about I t/ha but dropped toward 1968 because of increased soil acidity caused by the residual acidity of the fertilizer applied. Lime was applied at this time. The response to lime caused the reversal of the curves after 1968. Rotation with legumes had no beneficial effect in the fertilized plots either. In fact, the average sorghum yields were higher in monoculture than in rotation (1.28 vs 1.05/ha). The application of large quantities of manure plus fertilization increased the long-term yields to 2.15 t/ ha. It is not possible to ascertain whether this increase was due to the additional nutrients supplied by the manure or to an improvement in the soil's physical properties, or to both. Topsoil analysis, shown in Table 8, indicates that manuring prevented potassium deficiency and added significant quantities of calcium, magnesium, and phosphorus. Also, it kept the pH at about 6 and prevented the possibility of aluminum toxicity. The most striking aspect of Table 8 is that organic carbon contents increased from 0.24 to only 0.66% C after 18 years of applying an average of 23 t manure/ha per year. I examined these plots during the 1980 dry season and, although there was a color difference, manured and unmanured plots appeared equally hard. These soils, therefore, are much less productive than the others in the examples because of soil hardening and marginal fertility.

SOIL FERTILITY VS SOIL PHYSICAL CONSTRAINTS

All except the last of the long-term examples described have largely dealt with the conquest of soil fertility limitations. Once the problems are solved, attention gradually shifts to physical soil constraints. In North Carolina the main soil-related concern in soybean and maize production is no longer fertility but how to overcome



12. Long-term sorghum yields on an Oxic Plinthustalf of Saria, Upper Volta. as affected by rotation with legumes and fertilization with NPK and with organic manures (OM) (adapted from Sedogo et al 1979). NPK treatment averaged 60-42-40 kg/ha, organic matter (animal manure) was applied at the rate of 23 t/ha annually.

the detrimental effects of plow pans that form in Ultisols, how to promote deeper root development, and how to overcome periodic droughts (Kamprath et al 1979). In the Cerrado of Brazil, the emerging concern is soil erosion, even though Oxisols are among the least erodible soils of the world. Soil compaction problems are relevant in the Amazon Basin.

Many high-base-status soils, particularly those with 2:1 clays, have less desirable physical properties than the Oxisols and Ultisols. Because of their high native fertility, most Mollisols. Vertisols, and Alfisols are usually preferred by settlers. When the fertility problems in Ultisols and Oxisols are overcome, farmers prefer to work them because the physical constraints are less serious. This has happened in Hawaii. A few decades ago, 1 ha of Vertisol or Mollisol in sugarcane was worth several times 1 ha of Oxisol or Ultisol. Now the situation is reversed (Uehara, pers. comm.). North Carolina is crossed by a Triassic basin with Vertic subgroups of Alfisols. Settlers were attracted to these areas because of the higher native fertility of

Table 8. Topsoil properties in the long-term Saria experiments 6 and 18 years after continuous sorghum monoculture[a] (source: Sedogo et al 1979).

Soil property	1966 (6 yr)			1978 (18 yr)		
	Check	NPK	NPK + OM	Check	NPK	NPK + OM
pH (H_2O)	5.3	4.7	6.2	5.2	4.4	6.0[b]
%C	0.29	0.31	0.53	0.25	0.24	0.66
Exchangeable Ca (meq/100 g)	0.82	0.59	1.75	1.15	0.60	2.37
Exchangeable Mg (meq/100 g)	0.20	0.08	0.54	0.35	0.21	1.07
Exchangeable K (meq/100 g)	0.20	0.05	0.60	0.16	0.15	0.50
Exchangeable Al (meq/100 g)	0.04	0.29	0.00	0.16	0.56	0.04
ECEC[c] (meq/100 g)	1.26	1.01	2.89	1.82	1.52	3.98
% Al saturation	3	29	0	9	37	0

[a]OM = organic matter. [b]Reported as 5.25 KCl. [c]Effective cation exchange capacity.

these soils. Now settlers have essentially moved to the Ultisols, which have better physical properties (less sticky clay), and the Vertic Alfisols are used to grow scientists by housing the Research Triangle Park (Buol, pers. comm.).

I believe that it is easier to overcome soil fertility than soil physical constraints although no data in this paper support the assertion. This brings the overall discussion of soil productivity back to the relation with native vegetation, where physical factors are apparently more important than fertility factors. The highest estimate of productivity I am aware of comes from Ultisols of the tropics that have udic soil moisture regime under intensive fertilization. Vicente-Chandler et a1 (1964) reported annual dry matter production of forage grasses at 60 t/ ha in Puerto Rico. That exceeds by 50% the levels reached by natural ecosystems.

The productivity of soils, in rainfed farming systems, therefore, depends on too many factors to allow a proper concluding statement. It seems more appropriate to emphasize the need for identifying the main soil constraints and developing realistic management practices to overcome them in a way congruent with the prevalent socioeconomic conditions.

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INCREASING CROP PRODUCTIVITY THROUGH CROPPING SYSTEMS

OPTIMUM CROPPING PATTERNS FOR THE DRY TROPICS

S. M. Virmani

In the dry tropics, crop production is low and unstable because of undependable rainfall. Research is aimed at deriving a set of practices for resource development, management, and use that will lead to sustained increases in production while the resource base is conserved and improved. The dry tropics greatly vary in soil type, rainfall, and other climatic factors. Rainfall and soil water storage and release characteristics are the key factors influencing agricultural production possibilities.

This paper reports on an agroclimatic approach involving a simple water-balance model based on rainfall, soil moisture storage, and evapotranspiration used to evaluate the frequency of moisture availability to crops. By comparing the estimated water requirements of crops with moisture availability, approximations regarding suitable crops and cultivars and cropping schemes have been made. The implications for use of this methodology for more efficient crop improvement and farming systems research are discussed.

Agricultural production in the dry tropics is low and unstable primarily because of undependable rainfall. Farming systems research in any agroclimatic region must, therefore, be aimed at deriving a set of practices for resource development, management, and use that will lead to substantial and sustained increases in agricultural production while conserving and improving the region's resource base. Farming systems and crop improvement research should be closely coordinated by developing optimum cropping patterns to capitalize on the synergistic effects in improved farming systems, and by using improved seeds that can serve as catalyst in introducing a complete and integrated set of farming technologies (Krantz and Kampen 1977).

The distinctive characteristics of the tropical environment influence the distribution of the natural endowments soil, rainfall, and climate. The dry tropics are well supplied with radiant energy; however, variations in weather systems and orographic influences produce a variety of rainfall patterns. The effect of differences in

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rainfall on moisture availability to crops in tropical agriculture is especially pronounced because uniformly high temperatures cause rapid and relatively high amounts of evapotranspiration. Variations in the timing and amount of precipitation are key factors influencing the performance of cropping patterns. Therefore, in determining the agricultural potentialities of any dry tropical area, a quantification of the rainfall (timing, amount, and duration), soil moisture (intake, storage, and release), and evapotranspiration characteristics is of fundamental importance. Given the variability of the tropical environment over time and space, such a quantification is among the potentially most rewarding areas for agronomic research.

CLIMATIC CHARACTERISTICS OF THE TROPICS

While in the astronomic sense the term *tropics* refers to the region between the 23°27' North and South parallels, no climatic classification accepts that as the only criterion. Traditionally, climatologists have relied on two basic criteria of the atmospheric climate to delineate the different climatic types. The criteria most often used are thermal (air temperature) and hygric (precipitation).

The thermal characteristics show that tropical climates do not experience temperatures too low for plant growth. Crops requiring considerable heat to mature and ripen can be grown at any time of the year when there is sufficient moisture. Thus, rainfall availability will be the deciding influence on type of vegetation. According to Koppen (193l), the tropical belt has an annual mean temperature of at least 18° C.

The rainfall in the tropics varies widely. Some areas receive more than 400 mm/month, which under all circumstances exceeds the monthly evapotranspiration. At the other extreme are tropical deserts with little precipitation in any month of most years. Between the two are climatic types with alternating wet and dry seasons, and one or two rainfall periods a year. Such areas have agricultural potentialities. Troll (1965) proposed a classification of such dry tropical areas:

Continuous humid months (no.)	General vegetation	Climatic types
7-4.5	Dry savannah	Wet-dry semiarid tropics
4.5-2	Thorn savannah	Dry semiarid tropics
2-1	Semidesert	Arid tropics

A humid month is defined as a month having a mean rainfall exceeding the mean potential evapotranspiration (PE). Troll's classification system is unique because average annual amounts of rainfall are not critical. That represents a strength, because the annual average rainfall indeed suggests little about the agricultural potential in the dry tropics. The time during which water is adequate is important. The number of humid months used in Troll's classification criteria does not describe the entire rainy season; rather, it represents the core of the rainy period, which builds up to and drops from those key months.

DETERMINING OPTIMUM CROPPING SYSTEMS

The early development and implementation of improved cropping systems are crucial for increased and more stable agricultural production. Therefore, the research methodologies must be most efficient. There is little definite information on the long-term behavior of species, varieties, crop management techniques, and combinations of practices. The search for optimum cropping systems and appropriate practices is thus complicated by the need for large numbers of experiments before answers can be obtained. Because the climatic environment is variable, experiments have to be conducted over many years. Agronomists, therefore, aim to narrow the set of practices actually tried to those that appear feasible under a given set of climatic conditions, soils, and other factors.

Experimental research can be focused more systematically on fewer experiments by screening the available climatological, soil-type, and crop information. Such a systematic approach could be an important service to regional research stations by providing them with information on potential crops, varieties, and practices that are adapted to the local conditions. Such a method of focusing research in no way dispenses with the need for local experimentation, because many local factors cannot yet be *modeled* quantitatively. However, focusing research on reduced subsets of *likely* experiments will substantially speed the research process and add to the capabilities of researchers.

CHARACTERIZING CLIMATE IS RELATION TO CROPPING PATTERNS

To test the described methodology, the soil characteristics, rainfall (single day, 1901-70), and weather (evapotranspiration) were studied at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Center, near Hyderabad (India). Dependable rainfall was determined and land preparation schedules were suggested on the basis of a probability analysis of rainfall with respect to its Occurrence and continuity during the rainy and postrainy seasons. By using weekly rainfall as input to soil moisture storage and estimated evapotranspiration as moisture withdrawal, simulation studies on the moisture environment for crop growth, based on climatic water balances, were carried out to evaluate the soil moisture regimes and the amounts of crop-available water weekly. Based on this analysis, the lengths of the crop-growing season, and the variability of available soil moisture in three soil types of the region were estimated.

Dependable rainfall

Annual and seasonal rainfall vary greatly. During the period 1901-70 the Wettest year at Hyderabad received 1,431 mm rainfall and the driest year, 457 mm. The dependable precipitation (at 75% probability) for the early rainy season (18 June- 15 July) is 85 mm; that for the midrainy season (16 July- 12 August), 95 mm; that for the period 13 August-9 September, 81 mm; and that for 10 September-8 October, 72 mm. The amount of dependable rainfall in the postrainy and hot dry summer season is very small. Total annual dependable precipitation is 648 mm.

Probability of weekly rainfall

In dry tropical areas with a short rainy season, short-term rainfall information (weekly or 5-day) provides a better understanding of climatic variability. A study using first-order Markov Chain models to estimate the probabilities of rainfall at a level to satisfy at least one-third of the potential evapotranspiration demand (Virmani et al 1978) found that:

- Dry seeding in early June in anticipation of the rains is feasible in Vertisols.
- The early rainy season (late June to early August) is quite dependable.
- Midseason drought in August is likely in at least 4 of 10 years. This rainless period may extend from 10 days to 30 days.
- The rainy period in September is also dependable.
- The rainy season at Hyderabad may be extended by 2 to 4 weeks beyond the normal date of recession (early October) in about half of the years.

Length of the growing season

A computerized water-balance model (Keig and McAlpine 1974) was used to estimate week-to-week changes in available moisture in relation to potential evaporation. The duration of the crop-growing period, as determined by total available moisture, was estimated. On shallow Alfisols, the growing season fluctuates between 12 and 21 weeks, but on deep Vertisols the duration varies from 20 to 31 weeks (Table 1). Thus soil type plays a dominant role in defining the growing period under a given rainfall-climate situation. The matching of growing-season characteristics to potentially successful crops will greatly help in development of optimum cropping patterns for dry tropical areas.

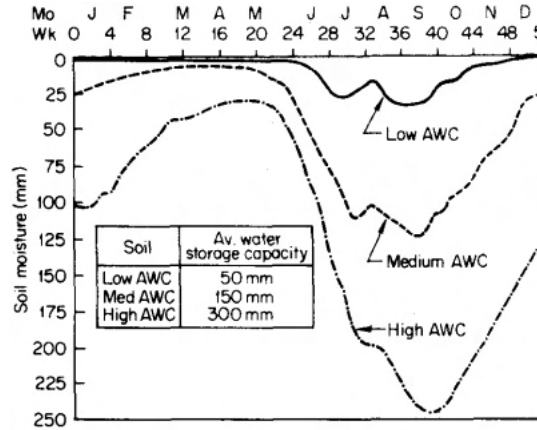
Available profile moisture in three soil types

A reliable estimate of probabilities of water deficits can be provided by estimating soil-moisture variations over the growing season. The median amounts of available water in the root profile of three soil types of low, medium, and high available water storage (AWC) are plotted in Figure 1. The amount of available moisture in the low-AWC soils does not exceed 60-70% of the total available capacity in the first half of August (and may amount to less than 25 mm). Because evapotranspiration during dry periods in the rainy season often exceeds 25 mm/ week, a break in the continuity of rains exceeding one week would be hazardous to crops on the low-AWC soils.

Table 1. Length of growing season[a] in 3 soils differing in available-water storage capacity (AWC).[b]

Probability	Length of growing season in soil whose AWC is								
	Low (50 mm)			Medium (150 mm)			High (300 mm)		
	Period		Wk	Period		Wk	Period		Wk
Mean	25 Jun-29	Oct	17	25 Jun-25	Nov	21	25 Jun-25	Nov	75
90%	25 Jun-30	Sep	12	25 Jun-21	Oct	16	25 Jun-18	Nov	70
75%	25 Jun- 7	Oct	13	25 Jun- 4	Nov	18	25 Jun- 2	Dec	22
Median (50%)	25 Jun-21	Oct	16	26 Jun-18	Nov	20	25 Jun-23	Dec	25
25%	25 Jun-11	Nov	19	25 Jun- 9	Dec	23	25 Jun-14	Jan	28
10%	25 Jun-25	Nov	21	25 Jun-23	Dec	25	25 Jun- 4	Feb	31

[a] From the sowing rains until the week when availability of profile moisture reduces. [b] Shallow Alfisols exemplify a low AWC situation; deep Vertisols, a medium AWC situation; and deep Vertisols, a high AWC situation.



1. Weekly soil-moisture storage in 3 soils. 1901-1970 data, Hyderabad, India.

These results emphasize the need for developing alternative water sources to break intraseasonal droughts and to increase and stabilize crop production in such regions. According to Kampen (1979), one alternative is to collect runoff during periods of excess rainfall and use the collected water through a farm water-storage and application facility. [1]

Risk to dependable cropping

Because of rainfall variability and soil-related management problems, nearly 20 million ha of Vertisols are presently fallowed in India during the rainy season. These soils are difficult to manage — extremely hard when dry, and very sticky when wet. Also, the period within which they can be prepared and planted is short (Krantz et a1 1977). Binswanger et a1 (1980), using agroclimatic approaches, have quantified the risk of either rainy or postrainy season cropping, or both, for three typical locations in similar soil-ecological zones of semiarid India (Table 2).

The probabilities of a 90-day rainy season crop's encountering good growth conditions throughout the crop season vary widely at the 3 selected locations. At Sholapur, growth conditions are good only in roughly one-third of the years, and for similar Vertisols in Hyderabad and for medium-deep Vertisols in the higher rainfall zone (represented by Akola) only in two-thirds of the years. The most serious drawback in Sholapur arises from a much lower probability of successful and timely crop emergence. All subsequent conditional probabilities show that the crop encounters higherrisk in Sholapur than in the two other areas at every growth stage, even if it has successfully completed earlier growth. A 33% probability of a favorable soil moisture regime is too low for encouraging annual rainy season cropping. The loss of seed and cultivation expenses in some years, and the low return in others would almost certainly mean no profit or actual losses.

The probability of adequate soil moisture for a postrainy season crop after rainy season fallow at Sholapur (80%) exceeds that for good growth conditions for rainy

[1] ICRISAT is developing appropriate technologies in this direction. The decision to apply small quantities of water is made on the basis of conditional probabilities of rainfall.

Table 2. Reliability of a 90-day rainy season crop on Vertisols [a] of 3 areas in semiarid India.

Location, soil	Annual rainfall (mm)	Probability (% of years)				
		Emergence (%) before 15 July	Seedling survival	Good growing conditions throughout	Adequate soil moisture for postrainy Season sorghum	
					After rainy season crop	After rainy season fallow
Sholapur – deep Vertisols	142	65	49	33	60	80
Hyderabad – deep Vertisols	761	85	76	62	50	83
Akola – medium-deep Vertisols	840	92	80	66	n.a. [b]	n.a. [b]

[a] Available water-holding capacity of deep Vertisols is assumed at 230 mm; that of medium-deep Vertisols at 120 mm.
[b] Not applicable. The water-holding capacity is far too low to meet the water needs of postrainy season sorghum.

season crops in Hyderabad or Akola. However, if a rainy season crop is taken in Sholapur, the chances of the postrainy season crop maturing on the residual profile moisture are reduced (by 20%). Consistent rainy season cropping would not only be unprofitable but endanger the profitability of the more important postrainy season crop. There is thus need for breeding postrainy season sorghum with high yield potential for such regions.

Crop yield simulation models

Dynamic crop weather models based on crop physiology are now available. They could be used to:

- develop a quantitative understanding of the crop response to the environment and lead to yield prediction;
- plan alternative strategies for cropping, land use, and water management to increase and stabilize production; and
- identify areas of research where quantitative knowledge is lacking.

Modeling is useful to answer the classical *what if* questions and to suggest priorities for applied research and development to aid in making crop management decisions.

ICRISAT has computerized *SORGF* — a dynamic grain sorghum growth model developed by Arkin et a1 (1976). It presents an approach for calculating the daily growth and development of an average grain sorghum plant in a field stand. Agronomic, climatic, soil, and location data are the inputs required.

Sorghum yield on a deep Vertisol receiving different amounts of supplemental water was simulated in the postrainy season (Table 3). The results indicated that if no supplemental water were available, it would be best to grow short-duration types (70 days to physiological maturity) rather than long-duration types (90 days to physiological maturity). It would also be more advantageous (in terms of production) to apply small amounts of supplemental water to larger areas than to apply greater quantities of water to a smaller area.

Table 3. Yield simulations of sorghum with the use of postrainy season data for International Crops Research Institute for the Semi-Arid Tropics Center.

Amount of water (cm)		Grain yield (t /ha)	
In soil profile	Supple-mental	Long duration	Short duration
10	0	1.34	2.10
10	5	4.10	3.10
10	10	4.66	3.16
10	15	4.72	3.16

SELECTING SUITABLE CROPS AND CROPPING PATTERNS

The probabilities of certain levels of crop-available water over the growing season, when compared with the water requirements of the crops, give an initial idea of the suitability of the crop in the given soil-climate environment. The discussed agroclimatic quantification techniques give an integrated index of rainfall, soil, and evapotranspiration. Because these techniques quantify the crop-growing periods and their characteristics in terms of water stress or sufficiency, selecting crops with the required phenological characteristics for any specific location becomes easier. This approach should substantially reduce the time and effort required to arrive at suitable crops and cropping patterns for various locations. It also permits identification of ecologically similar isoclimes, thus facilitating the transfer of appropriate farming systems technology.

Sorghum can serve as an example to illustrate an application of the analysis. The crop is sown in the last week of June. Traditional 130- to 150-day varieties will flower in late September and reach physiological maturity in late October or early November. On soils with low to medium available water-holding capacities, the crop will be caught in a water-deficit situation at the reproductive stage in most years. The high-yielding, shorter duration (90 to 110 days) hybrids will flower in the last half of August and reach physiological maturity in late September. Considering the rainfall probabilities, the long-duration varieties will be caught in heavy rains at harvest time in 3 years out of 10; the short-duration hybrids may face this situation 6 years out of 10. Thus, while the present varieties are subject to serious drought risk, hybrids lacking mold resistance may not provide a sufficiently attractive alternative.

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LOW INPUT CROPPING SYSTEMS

Ch. Krishnamoorthy

To the vast majority of farmers in developing countries low inputs are a necessity, to others they are prerequisities to high input agriculture. Traditional low input systems are low-productivity, low-risk systems and our interest is to improve productivity without increasing the risk.

This paper examines the individual effects of choice of crops and varieties, sowing dates, plant density, weed control, and their combinations. Except when soil is very low in fertility, responses to good husbandry practices are of the order of 50-100%.

Some recent improvements in intercrop systems achieved by using optimum plant density and proper crop geometry are described.

It is not enough to make recommendations and conduct demonstrations. It is necessary to convince the farmers that the recommendations can be implemented under their conditions and with their resources. This is the objective of operational research projects.

Using low inputs, sorghum production programs have been started in India, and the impact has been striking. During the 5-year period 1971 to 1976, sorghum production in India increased from 7.7 to 10.4 million tons.

This paper analyzes and reviews from a practical point of view low input systems, both experimental ones and those practiced by farmers. The paper draws heavily on evidence and experience from India and Thailand and, to a limited extent, on material from Malaysia and Sri Lanka.

Attention is confined to rainfed field crops other than rice. However, I believe that the approaches and practices are equally applicable to all crops including rainfed wetland rice.

The aim of the paper is to bring out some of the more widely applicable principles in the hope that specifics suitable to the physical, social, and economic environments will be developed locally.

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LOW-INPUT SYSTEMS

Although farmers have been practicing low-input systems for ages, scientists have only recently gained a proper perspective and appreciation of such systems which, in the past, were dismissed lightly as being primitive. Some enduring qualities in such systems compel our attention. It should be made clear that we are not going back to the traditional systems as they were practiced, but rather trying to understand their strengths and weaknesses and to improve them.

Low inputs are less than the high inputs used at the experiment stations and recommended for highest attainable yields, but more than zero. Low inputs occupy a large range between high and zero inputs and we cannot hope to deal with the whole range (Winkelmann and Moscardi 1979).

We are concerned with not only the low inputs but also their management, and the objective is to improve the efficiency of low inputs. The majority of farmers in developing countries have limited access to credit and institutions supporting agriculture. They have to make do mostly with their individual resources and sometimes resources available in the village (Norma 1976). Farmers tend to use low input systems to minimize risk and practice them on lands to which they are unable or unwilling to give the needed attention. It is assumed that farmers are prepared to put in additional effort once they are convinced of the benefits.

To improve and stabilize crop productivity, changes should be introduced into traditional agriculture. The options are either to disregard entirely the existing framework and convert it into high investment agriculture or to recognize the constraints and bring about small but critical changes easily implemented over a large area.

High energy systems are essentially unstable unless they are built on a sound foundation and infrastructure support is made available. Curiously, returns to an external input are maximum when the system is least dependent on it, i.e. when the external input is used as a critical supplement to the internal resources, and not as a substitute. An apt illustration is water. Water is considered the most limiting factor in semi-arid tropics. The approaches open to us are 1) to improve rainfall use efficiency or 2) to seek additional water. I maintain that unless rainfall use efficiency is improved, additional water, even if available, would not be put to optimum use.

The first concern then is how well the natural resources of the area and internal resources of the farmer are utilized and how they can be improved by overcoming the more critical or limiting factors. Ideas of this kind lead to the emphasis on low inputs (Krishnamoorthy 1977). The concept does not deny the need for external inputs but insists that to optimize the use of external inputs, low monetary inputs are prerequisites. Up to this point there is general agreement.

Some researchers doubt whether low monetary inputs by themselves are capable of giving visible and attractive yield increases. There are two aspects to consider. One relates to the quantitative aspect of the yield increase and its economics. The other relates to the subjective judgment of what constitutes a visible yield increase. A 20% yield increase is not easily demonstrable on a farmer's field because the variation in productivity among farmers is of that magnitude. Yield increases of 200% are rarely

possible, if at all, with low monetary inputs alone. The Indian Dryland Project defines, as a first approximation, a 50-100% yield increase as visible and attractive.

The low monetary inputs are actually good farming practices that are necessary to raise crops, and that emphasize the timing and the quality of the operations. These practices are implicit whether the objective is to make the best use of normal to good rainfall years or to cope with drought.

LOW-INPUT SYSTEMS COMPONENTS

Low monetary inputs consist of choice of crops and varieties, early sowing, optimum plant density and row spacing, and weed management through year-round tillage.

Cropvarieties

Choosing varieties suitable for a given environment and the farmer is the first step. Multilocation tests and on-farm testing enable us to identify them. The superior performance of high yielding varieties is well known. However, in some areas opinions on HYVs differ. First, the HYVs have performed worse in some cases than local varieties and their acceptance by farmers has been low. I believe this is a reflection on testing and identification rather than a point against the HYV concept. Second, there is the question of genetic vulnerability. What is needed is a wider genetic base and varietal diversification within a maturity zone. Third, the eating quality of HYVs is poor in some cases. Experience has shown that the farmers' resistance wears down rapidly and is an important issue only for export where quality is a premium and there is a price differential.

For many reasons the seed industry is interested only in hybrids, while the majority of small farmers prefer straight varieties because of their lower cost and because the farmer can produce and retain his own seed. Because of the difficulties of producing large quantities of F_1 hyrid seed and supplying it to farmers at the proper time and at reasonable cost, large-scale development programs should be based initially on straight varieties even though their yield potential may be 10-20% less than that of the best hybrids.

Sowing date

Tables 1 and 2 illustrate the effects of sowing dates on yields. It is best to start sowing rainy season sorghum at the earliest opportunity and complete sowings within 2 weeks of the first to minimize shoot fly incidence. Early sowing of postmonsoon crops (Table 2) increases yields because crops sown on the normal date run out of moisture during flowering and grain formation stages. Early sowing is one of the few successful recommendations for such postmonsoon crops.

There are a few exceptions to the rule of early sowing. Some crops such as castor *(Ricinus communis),* cluster bean (*Cyamopsis tetragonalobus),* and some varieties of maize grow tall and vegetative when sown early in the rainy season when the temperatures are high (40° C).

No amount of sowing date tests at a single site will enable us to identify the "optimum" sowing date for a crop variety, even for that location. Multilocation yield

Table 1. Effect of sowing date on grain yield of rainy season sorghum.

Hyderabad (1973)		Indore (1970)	
Sowing date	Yield (t/ha)	Sowing date	Yield (t/ha)
9 Jun	5.41	Dry sowing	3.6
23 Jun	4.62	With the first soaking rain	3.7
2 Jul	1.72	7 days after soaking rain	2.4
21 Jul	0.09	14 days after soaking rain	1.6
4 Aug	0.08	21 days after soaking rain	2.8
19 Aug	0.07	CD (0.05)	3.0

Table 2. Effect of sowing date on grain yield of postmonsoon crops, Sholapur Station, India, 1971.

Sowing date	Yield (kg/ha)			
	Sorghum	Safflower	Chickpea	Wheat
8 Sep	880	1240	840	470
20 Sep	540	990	740	460
7 Oct[a]	420	720	440	210
20 Oct	150	400	410	200

[a]Normal sowing date.

data should be supplemented with an analysis of historical rainfall data to estimate the growing season weather hazards. Very early sowing may be successful in one year but it cannot be recommended because of the high probability of a rainless period of 2 weeks or more immediately after sowing.

Early sowing is advantageous due to better utilization of mineralized nitrogen which occurs rapidly with the first rains; better utilization of moisture including rainfall; early seedling vigour which helps to overcome nonspecific pests, diseases and weeds; and avoiding specific pests, as in the case of sorghum.

Plant density (seed rate)

The adage "sow thin for grain and thick for fodder" was true for tall traditional varieties that were selected for performance at an individual plant level. With the short-statured HYVs which have been selected for performance as a population, a higher plant density is needed. The height and width of yield plateau are larger for HYVs. For example, HYV sorghum yield does not vary significantly with plant density in the range of 180,000 to 360,000 plants ha.

The optimum plant density for rainy season and postmonsoon crops is worth discussing. For rainy season crops the optimum plant stand is the same whether the crop is rainfed or irrigated. There is no need to cut down seed rate for a rainfed crop simply because it is likely to suffer from intermittent drought stress. Thus, for rainfed or irrigated rainy season sorghum, the recommended seed rate for HYVs is 10 kg/ha. For postmonsoon crops which are raised on moisture stored in the soil with little or no rainfall during the crop season, optimum plant density is lower and varies with stored moisture. For example, in Parbhani area (deep Vertisols, mean annual rainfall 800-900 mm) the optimum density of postmonsoon sorghum is 150,000 to 180,000 plants/ha, whereas in Bellary area (medium deep Vertisols, mean annual rainfall 500-600 mm) it is 90,000 to 135,000 plants/ha.

Besides plant density, plant distribution is an important consideration. The best arrangement — even stand with uniformly spaced plants — is difficult to attain without a precision planter. Our studies indicate that yield loss is not significant even if the plants are not uniformly spaced, provided the gap between any two plants in the row is not greater than twice the normal plant-to-plant spacing; in sorghum planted 45 × 15 cm, gaps up to 30 cm can be tolerated.

Row widths

Recent studies on row widths at an optimum plant density reveal that the optimum range is larger than indicated earlier. For sorghum, pearl millet, and other millets, yield is constant from 30- to 75-cm row spacing; 90-cm rows yield only 10% less. Studies in Thailand show row spacing of kenaf may be 30 to 50 cm and of cassava 80 to 200 cm. In castor, pigeonpea, and cotton the range is much wider (45-135 cm).

Some implications of wider row spacings will be discussed in later sections. The immediate implication is for weed control within the row and improving fertilizer efficiency. With wider row spacing and the resulting narrow spacing within the row, weeds within the row tend to be fewer, and less labor is needed to control them than with narrow rows.

Weed control

It has been estimated that the yield losses of crops due to weeds are of the order of 30% and may be as high as 65%.

A more recent finding is that timing of weed control is as important as thoroughness (Table 3). Data show that, if the first weeding is delayed beyond 3 weeks after seedling emergence, the damage is irreparable. Once the crop canopy closes, weeds are less of a problem. Then weeds become a problem again when the crop canopy opens up towards maturation of a sole crop or when an intercrop is harvested. The importance of weeding within the rows either manually or by band placing of herbicides is recognized.

If properly done, hand weeding, mechanical interculture, and herbicide are equally effective. The choice of method depends on local availability of labor, power, herbicides, and their relative cost. In general, weed management through tillage and interculture is more appropriate to the majority of farmers in developing countries.

Year-round tillage

One of the simplest recommendations of low input is early sowing. Farmers know its advantage but are unable to practice it because their lands are not ready for sowing.

Table 3. Crop-weed competition studies on pearl millet HB3, Sholapur, India.

Treatment	Yield (kg/ha)
Weed infested for first 10 days	1420
Weed infested for first 20 days	1380
Weed infested for first 30 days	540
Weed infested for first 40 days	270
Weed infested for first 50 days	130
Unweeded check	130
CD (0.05)	3.6

A set of tillage operations, collectively called year-round tillage was developed to facilitate early sowing. The basic operations are:

1. Begin field preparation for the next crop immediately after the harvest of the previous crop or intercrop. The field should not be abandoned in the fallow season to allow weeds to flourish and produce seed. In some cases postharvest primary tillage can be hastened by harvesting the crop at physiological maturity. If the soils have a tendency to cake or harden, open furrows at 60- to 100-cm intervals to facilitate harrowing for secondary tillage.
2. Because there is no advantage to inverting the soil, do primary tillage with a native (local) plow which has chisel action.
3. Plant a short-duration crop for grain or forage after postharvest tillage if soil moisture permits. This crop serves as a cover protecting the soil from weed growth and erosion.
4. Plow and blade the fields in preparation for seeding, taking advantage of summer rains and premonsoon showers. No amount of plowing with a native plow alone can be expected to make the field weed-free so blading should be introduced as early as possible. This helps to firm the seedbed and is particularly important in sandy soils.
5. Use surface (blade) tillage again before seeding to remove fresh weed growth. Final shallow cultivation instead of deep plow will help to conserve moisture and facilitate early seeding and uniform emergence of vigorous seedlings.
6. Use blade harrow or wooden peg-harrow immediately after sowing to cover the seed and remove small weeds that emerged after the last blading.
7. Begin interrow tillage and hand weeding as early as possible and certainly within 3 weeks after sowing. Do not delay this operation. Continue intertillage and weeding as required throughout the season.
8. Begin field preparation for the next crop immediately after harvest of the crop or intercrop.

It may take two to three seasons to realize the full benefit of year-round tillage in fields that are heavily weed infested. Perennial weeds require specific treatment and their control should be considered a part of land reclamation. All those operations could be done effectively with local plow and blade (harrow) using animal power.

Crop response to year-round tillage in moderately fertile red soil is given in Table 4.

Seeding and stand establishment

Seeding methods include broadcasting, sowing in the furrow behind a country plow, and native- or tractor-drawn seed tubes and seed-drills. Broadcast sowing has the advantage of rapid coverage; its greatest disadvantage is that all subsequent operations must be done manually. In some areas furrows are made before the sowing season. When soaking rains come, seed is broadcast and dragged lightly toward the furrow with thorny brush. After the plants are established, the spaces between the rows are harrowed to remove weeds and unwanted crop plants.

Sowing is usually practiced in light soils that tend to harden or crust rapidly However, in light soils, soil slides into the furrow from the sides and seed falls on dry soil, and stands are adversely affected. This can be remedied by attaching a seed tube

Table 4. Effect of year-round tillage on grain yield of rainy season sorghum, Hyderabad, India, 1978.

Treatment	Yield[a] (kg/ha)
Farmers' variety + farmers' tillage	620
Farmers' variety + year-round tillage	830
HYV + farmers' tillage	930
HYV + year-round tillage	1340

[a] Mean of 4 trials on farmers' fields.

to the country plow. Sowing may then be done on the side or in the middle of the furrow depending on soil moisture, It is preferable to sow on the side of the furrow in crusting soils. Using the seed tube, a 50% increase in stand establishment of sorghum was obtained on crusting soils of Hyderabad.

Native seed drills can be used only when the primary tillage is good and the seedbed is firm and weed-free. Pressing the seed lines is advantageous with postmonsoon crops.

Farmers raise only a single crop in the wet season in several areas with double-cropping potential. Although there is enough moisture in the soil profile, the surface soil has dried out and farmers find it difficult to sow. When surface soil moisture depletion is extreme (10-15 cm of dry soil overlying a good soil moisture reserve), the lister seeder should be used. Seed is placed in a deep furrow opened to the moist soil layer and the furrow is not covered.

Early sowing of the whole farm

The farm-level questions related to early sowing are:

1. How does one sow all the crops as early as possible?
2. What are the relative losses suffered by the different crops when sowing is delayed?
3. What crops and varieties are suited to aberrant weather?

Year-round tillage makes possible early sowing of the whole farm. Large areas can be sown in a day by doubling row widths. No significant yield reduction results if the optimum plant density is maintained. Short time moisture carryover in the seeding zone and extension of the sowing time are achieved by organic or soil mulch.

Farmers are well aware of the order in which to sow crops to minimize yield losses when they cannot sow all the crops within a given rainfall period.

CROP RESPONSES TO LOW MONETARY INPUTS

High monetary inputs such as fertilizers, pesticides, and tractor power have given such spectacular results that low monetary inputs have not generally received the research attention due them. In developing countries this presents a dilemma: the farmers are too poor to use high cost inputs but the need for rapid increase in food production is great. Modest increases over large areas by large numbers of farmers are relevant to developing countries. Low monetary inputs become particularly relevant in this context; therefore, it is appropriate to examine their contributions to yield increases.

Earlier the question was raised whether low monetary inputs are capable of giving yield increases sufficiently visible to enthuse the farmers.

In the Hyderabad area, where the soils are extremely deficient in phosphorus and low in nitrogen, mean response of HYVs to low monetary inputs (without fertilizer) was 0.3 t/ha, which may appear small and unattractive (Table 5). However, considering that the mean farm yield with farmers' variety and practices was only 0.5 t/ha, the yield increase was nearly 65%. The response increased to 1.5 t/ha when low inputs were combined with HYVs and fertilizer.

At Bellary Station where soil fertility is not as low, the response to low monetary inputs was striking, 0.7 t/ha with farmers' variety and 1.7 t/ha with improved variety (Table 6). Response to fertilizer was not impressive because of limited moisture.

In the Indore area (Deep vertisols, medium fertility, mean annual rainfall 900 mm), a large number of sorghum trials on farmers' fields gave average yields of 0.5-0.6 t grain/ha with farmers' varieties and practices, and 1.0-1.2 t/ha with HYV and low input.

Unless soil fertility is very low, low monetary inputs alone can give visible yield increases; when low monetary inputs are combined with fertilizer the responses are spectacular.

HIGH-COST INPUTS

Manures and fertilizers

Manures (green manure, farmyard manure, compost, and tank (pond) silt) supplied plant nutrients in the past. With the introduction of chemical fertilizers, interest in manures began to wane. The practice of green manuring has practically disappeared because of increasing population pressure on land. Because fertilizer is expensive and production has not kept up with demand, interest in organic manures has been reviewed. The remarkable feature — robustness and virility — of Indian soils, even after centuries of cultivation, has been attributed, among other things, to the legumes grown in rotation, or in cropping systems with cereals, and integration of livestock with crop husbandry. It is becoming increasingly difficult to meet the needs for food, shelter, and clothing without the use of fertilizers. Current research, therefore, is on improving fertilizer use efficiency and the synergistic effects of combining organics with fertilizer.

Table 5. Contribution of inputs to grain yield of rainy season sorghum, Operational Research Project, Hyderabad, India.

Treatment[a]	Grain yield (t/ha)				
	1976	1977	1978	1979	Mean
Farmers' variety + farmers' practices	0.4	0.7	0.2	0.6	0.5
Farmers' variety + low inputs + fertilizer	1.3	1.3	0.6	1.1	1.1
HYV + low inputs	0.5	1.2	0.4	0.9	0.8
HYV + low inputs+ fertilizer	1.6	2.6	1.4	1.3	2.0

[a]Low inputs are year-round tillage, early seeding, optimum plant density, and weed control. Fertilizer consists of 40 kg Nand 30 kg P_2O_5 per ha.

Table 6. Contribution of inputs to yield of postmonsoon sorghum, Bellary Station, 1975.

Treatment [a]	Yield (t/ha)	
	Grain	Straw
Farmers' variety + farmers' practices	0.7	2.3
Farmers' variety + low inputs	1.4	6.9
Farmers' variety +low inputs + fertilizer	1.6	7.3
HYV + farmers' practices	0.7	1.6
HYV + low inputs	2.3	4.9
HYV + low inputs + fertilizer	2.7	4.8

[a]Low inputs are year-round tillage, early seeding, optimum plant density, and weed control. Fertilizer consists of 30 kg N and 30 kg P_2O_5 per ha.

Fertilizer use efficiency

Fertilizer response is greatest when fertilizers are used in combination with HYVs, optimum sowing date, adequate plant population density, and thorough weed control. Table 7 shows the superiority of this combination is consistent irrespective of annual weather fluctuations.

One advantage of early sowing is better utilization of mineralized soil nitrogen that occurs rapidly with the first rains. In addition, a small dose (5-10 kg N/ha) is recommended as a starter to promote seedling vigor to enable the crop to outgrow nonspecific pests and diseases. Split applications and adjusting subsequent doses to the progress of the growing season minimize risk. For rainfed rice in northeast Thailand, basal nitrogen is not recommended because of uncertain weather early in the season. Just before panicle initiation, when adequate rainfall is more likely, 15 kg N/ha is recommended.

Placement is more effective in improving fertilizer efficiency than broadcast application, particularly in the case of phosphorus. An ingenious traditional practice in some parts of India (Gujarat and Rajasthan States) has been the use of semipermanent set furrows. That practice combines the principles of minimum tillage and fertilizer placement. Manures (and fertilizers) are applied only in the furrows. The interrow spaces are harrowed to control weeds and keep the soil open. Immediately after harvest, furrows are opened by plowing only the crop rows.

Used alone at the recommended rates, organic manures can maintain yields at 3 t/ha for rice and about 1-1.5 t/ha for dryland cereals. The main problem, however, is the production and transport of sufficient quantities of organic manure, particularly in countries where there is a high aversion to the use of human excreta. Just as there is renewed enthusiasm for increasing the production of farmyard manure and compost, so is the role of legumes in cropping systems being reevaluated.

Cereals perform better after a fodder legume than after a nonlegume. But information is meager on the immediate and long-term effects of cereals following legumes or being intercropped with legumes that are grown for grain.

Before closing the discussion on fertilizer use. mention may be made of the effect of fertilizer on moisture demand. Data from Hoshiarpur Station (not reported in the paper) showed that yield increases of fertilized crops were 50 to 100% and that the crops took up about 20% additional moisture, mostly from lower depths of the soil that remain untapped by unfertilized crops. The deeper root penetration of fertilized

Table 7. Stability of sorghum grain yield at 2 levels of inputs, Bellary Station, postmonsoon crop.

Year	Yield[a] (t/ha)	
	Level 1	Level 2
1971	0.5	1.5
1972	1.2	3.4
1973	1.7	3.0
1974	0.2	1.1
1975	0.7	1.6
1976	0.3	1.2
1977	0.7	1.2
Mean	0.8	1.9

[a] Level 1 is farmers' practices; level 2, low monetary inputs plus 30 kg N and 30 kg P_2O_5 per ha.

crops enables them to withstand intermittent dry spells better than unfertilized crops.

CROP SUBSTITUTION AND DIVERSIFICATION

Most dryland farmers in India are subsistence farmers: their first priority is to produce food for their families and cattle. Their yields can be increased by accepting the crops they grow and introducing yield-increasing practices. Another way to increase the farmers' yields is to replace the traditional crops with more efficient ones.

Table 8 lists the yields of some traditional crops and their substitutes. Farmers accept all of the substitute crops. They continue raising traditional crops because these satisfy a specific need, even if their yields are low.

In the Bellary region, cotton is still grown because the stalks are a valuable source of fuel in the treeless black soils. Wheat is a staple wherever it is grown. Green gram (mungbean) is produced for human consumption and soybean for cattle. The strategy to promote more efficient substitute crops is to convince the farmer that his primary and secondary needs can be met from a smaller area, and that in the rest of his field it is more profitable to grow substitute crops. The government can also make it attractive for farmers to grow oilseed crops and food legumes, both of which are in short supply in India.

IMPROVED INTERCROP SYSTEMS

Intercropping is of both theoretical interest and practical utility because of the strong competition effects between the component crops. The object is to reduce such effects. Intercropping is possible in space (differences in root depth, canopy, etc.) and in time (crop duration). In a biological system, space and time factors are difficult to separate because the space requirement varies with plant growth (time). The peak demand of the component crops for moisture, nutrients, and light should not coincide. Although there are no clear-cut data, it appears there should be a difference of at least 45 days in duration between 2 crops and they should draw moisture and nutrients from different soil depths.

Table 8. Some examples of crop substitution.

Region	Year	Traditional crop	Yield (t/ha)	Substitute crop	Yield (t/ha)
Bellary	1973	Cotton	0.2	Sorghum	2.7
Indore	1971	Green gram	1.2	Soybean	3.3
		Wheat	1.1	Safflower	2.4
	1972	Wheat	0.5	Safflower	3.5
Agra	1972	Wheat	1.0	Mustard	2.0
Hissar	1973	Wheat	0.3	*Eruca sativa*	1.6
Varanasi	1971	Wheat	0.9	Chickpea	2.9
Ranchi	1973	Upland rice	2.9	Maize	3.4
				Sorghum	3.4

Phenotypically the component crops should have an erect growth habit and should be short-statured to reduce shading effects (competition for light).

In an intercrop system, the interspecific competition should be less than the intraspecific competition. That is, varieties should be chosen on the basis of performance in a population rather than performance of individual plants. High-yielding varieties are more amenable than traditional ones to an intercrop system in this respect.

It is customary to speak of intercropping in terms of crop species such as cassava + mungbean, sorghum + pigeonpea. From what has been stated it is clear that the system is better described in terms of *varieties.* It is equally clear that varieties, and the package of practices recommended for sole cropping, are not necessarily the best for intercropping. Breeding varieties for intercropping is an area that has received little attention.

Bases for intercrop improvement

The practical bases for improved intercrop systems are 1) the plant population density-yield relation, and 2) the relative insensitivity of yield to other parameters of crop geometry.

Manipulation of the parameters of crop geometry is a means to reduce mutual competition in an intercrop system. Wider row spacing is necessary to accommodate an intercrop. This may be accomplished by replacing some of the rows of crop A with rows of crop B (replacement series) or by reducing hill spacing within a row to make up for wider row spacing (full population series). Alternatively, the rows of one or both crops may be paired to achieve wide interrow spaces.

Optimum plant density generally higher than that of sole crops and better crop geometry have led to substantial yield increase of component crops and land equivalent ratio (LER) of the systems (Thailand Department of Agriculture, Field Crops Div., Upland Crops Improvement Project 1980). Thirty percent yield increases of mungbean and soybean have been achieved by adopting a hill spacing of 10 cm instead of 20 cm when the crops are intercropped with cassava. By doubling plant density and pairing the rows of the component crops, LER of 1.60 has been obtained for kenaf - mungbean and kenaf - peanut intercrop systems. Shelke (1977) reported optimum row ratios of 1:1, 1:2. 2:1, and 2:2. LER values of 1.5-1.6 have been reported for sorghum - pigeonpea intercropping full populations series compared with 1.2-1.3 for replacement series.

For attaining high yield and high LER it is necessary to have optimum population density of each of the component crops and a duration difference between *any two* species of about 45 days. It becomes progressively difficult to satisfy simultaneously these two conditions with more than two component crops. There is no experimental evidence, but there is reason to believe that, as the number of species for seasonal field crops increases beyond 2, LER decreases and approaches a value of 1.20 to 1.30. That is, as in traditional replacement series, a number of crops can be mixed if one is satisfied with low LER. By combining perennial crops and seasonal field crops, it appears possible to have more than two crops while maintaining a high LER.

Assessment of intercrop systems

The criteria commonly used for assessing intercrop systems have been LER and net returns. In our view LER, a measure of intercrop system efficiency, is essentially a research criterion. Net return assumes that the component crops are interchangeable and the farmer has no particular preference for one crop or the other.

Additional criteria are needed to enable farmers to make decisions. If one of the components is a food crop, farmers would not agree to any reduction in its yield compared with a sole crop. That is, partial LER of the food crop should not be significantly different from unity. Yield from the other component crop is considered a bonus. In India, this is true of the sorghum - pigeonpea intercrop system. It is also true when one of the crops is an export crop with an established market, i.e. cassava- and kenaf-based intercrop systems in Thailand.

When both the components are grown for export, as the maize - soybean intercrop system in Thailand, net return is a sufficient criterion provided the risk is not higher than that of the previous crops.

Doubts have been expressed whether intercrop systems are appropriate for high productivity systems. They are no longer valid in view of the data presented at the International Symposium on Intercrop Systems at Morogoro, Tanzania, 1976 and, more particularly, the recent data from India.

Farmers and scientists believe that the productivity of intercrop systems is more stable than that of sole crops. Rao and Willey (1979) of the International Crops Research Institute for Semi-Arid Tropics examined the data of 89 sorghum - pigeonpea trials in India in which optimum population of both the crops was maintained and the row ratio of sorghum to pigeonpea was 2:1 or 1:1. Their analysis of yield data is given in Table 9 and that of returns and risk in Table 10. They concluded: "The relative advantage of intercropping remained more or less similar at different levels of fertility. Regression analysis showed that the intercrop is superior to sole crops at all levels of yield and is more widely adoptable." At the usual range of price levels of the two commodities, the probability of returns falling below a given disaster level was always less for the intercrop system than for sole crops (Table 10). The coefficient of variation (CV) of returns (Table 10) although least for the intercrop system, was still high (35.44%). This finding does not negate the value of the system because in this case, CV was more a measure of the variations among the environments (sites) than of variations among the treatments.

Improved intercrop systems are more productive, more efficient, and more stable than either the replacement series of the traditional systems or sole crops.

Table 9. Stability parameters of fitted regression and relative yields based on sole crop mean.[a]

System	Yield (kg/ha)				Relative yields			
	X	b	S^2di	r^2	X	b	S^2dr	r^2
Sorghum, sole crop	3278	1.39*	22.06	0.91	1.00	1.00	0.070	0.63
Pigeonpea, sole crop	1450	0.28*	24.36	0.18	1.00	0.78	0.109	0.45
Intercrop	3687	7.32*	4.59	0.98	1.44	1.2*'	0.012	0.95
Mean	2805	1.00			1.15			
SEM ±	64.2				0.04			
LSD (0.05)	178				0.19			

[a]Data of 89 trials in India, courtesy of M. R. Rao and R. H. Willey, agronomists, ICRISAT. * = significantly different from 1.00 at 5% level

Table 10. Risk associated with sorghum and pigeonpea in sole and intercrop systems at specified levels of returns.[a]

System	Mean income[b] (%/ha)	Standard deviation	Coefficient of variation (%)	Probability of income falling below disaster levels ($/ha)		
				125	190	250
Sorghum, sole crop	360	1528	52.95	0.11	0.18	0.28
Pigeonpea, sole crop	520	1958	46.80	0.05	0.08	0.13
Shared crop[c]	425	1308	38.56	0.03	0.07	0.14
Intercrop	620	1753	35.44	0.01	0.02	0.04

[a]Data of 89 trials in India, courtesy of M. R. Rao and R. W. Willey, agronomists, ICRISAT. [b]Valued at Rs 100/100 kg of sorghum and Rs 300/100 kg of pigeonpea. US$1 is rougly Rs 8. [c]0.61 ha of sorghum and 0.39 ha of pigeonpea, that is, the same proportion as the mean proportions of sorghum and pigeonpea in intercropping.

DRYLAND CROP PRODUCTION PROJECTS

Operational Research Projects (ORP) in 1975 were initiated to understand farmers' traditional practices, discover their strengths and weaknesses, and develop with the farmers simple, innovative solutions to field problems as the farmers see them. No inputs other than those available to similar farmers through existing agencies were introduced. Models of hand tools and bullock-drawn equipment were supplied for testing, adaptation, and where possible, fabrication by the village blacksmith. Seeds of suitable varieties were supplied to farmers so they could produce their own seed.

Base line surveys were conducted so farmers' responses to suggested low input technology could be measured. Farmers were unable to follow the recommendations because neither they nor the scientists had devised ways to implement the recommendations within the limited resources of the farmers and the villages.

For example, farmers in the Hyderabad region are well aware of the advantages of early sowing. But because the soils harden rapidly after harvest in October-November, farmers delay plowing until the premonsoon showers in May. Often, primary tillage and sowing are done on the same day that soaking rains are received and the result is very weedy fields. The introduction of harrows made year-round tillage practicable and it is now accepted in ORP villages. Sorghum yields from year-round tillage, in 1978 and 1979, were 1.24 t/ha compared with 0.49 t/ha under the plow and plant system.

Sorghum stands in the Hyderabad region were improved by using bamboo seed tubes attached to the native plow instead of dropping the seed in the furrows,

The advantage of early planting of dryland crops, even if it means slightly delayed transplanting of irrigated rice, is now recognized by the OR P farmers. ORP farmers are presently studying ways to implement the improved sorghum - pigeonpea intercrop system.

The ORP agricultural scientists have come to realize that there is much to learn from the farmers and every traditional practice is not necessarily outdated. Farmers have compelled scientists to reorient their research by insisting upon practical solutions to their problems.

DEVELOPMENT IMPACT

Until recently the impact of dryland research and development in India was hardly noticeable, although dryland research was initiated in 1923. During the last 5 years spectacular gains have been made in the production of dryland sorghum in the States of Maharashtra, Karnataka, and Andhra Pradesh, although 2 of the 5 years were not conducive to growing sorghum.

Although sorghum production programs were begun in India in the early seventies, sorghum production actually declined. Sorghum was grown in patches scattered among local varieties, and it was never planted on more than 20% of the total sorghum land. CSH 1 escaped ear midge because it is early-maturing, but local varieties were severely damaged. Although CSH 1 yielded 150-200% more than local varieties, there was a net loss of production. The problem was solved by growing CSH 1 in large blocks and introducing straight varieties with growth duration comparable to that of the hybrid. Early sowing, optimum plant density, weed control, and the application of 10-25 kg N/ha were incorporated into the strategy. Within 3 years the State of Maharashtra, once chronically deficient in sorghum, became nearly self-sufficient. The gains made in sorghum production so far have been with the rainy season crop. Attempts are being made to increase production of postmonsoon sorghum in the States of Maharashtra, Karnataka, and Andhra Pradesh.

Production of pearl millet increased appreciably with the introduction of hybrids HB 1,3, and 4. A serious setback due to severe incidence of downy mildew caused us to temporarily lose the confidence of farmers. With the introduction of BJ 104 and other mildew-resistant cultivars, the pearl millet program is recovering.

There has been little increase in the production of food legumes and oilseed crops. The strategy for increasing production of food legumes is to intercrop and sequence food legumes with dryland cereals during the rainy season. In improved intercropping systems, the yield of the cereal is not significantly reduced compared to that of a sole crop, and the legume yield is higher by 0.4-0.8 t ha.

The major dryland oilseed crop in India is groundnut and the yields are low and unstable. Because high annual rainfall fluctuations in the 500-750 mm zones are in 30 to 35% of the crops area, it has not been possible to increase yields or stability. To increase groundnut yield potential, the strategy is to grow groundnut on irrigated lands after rainy season rice.

APPLICABILITY TO OTHER COUNTRIES

Several of the ideas presented in this paper are generally applicable to countries in South and Southeast Asia with similar physical environments. Examples are:

- year-round tillage for dry seeding rainfed rice in Thailand and weed control in the Dry Zone of Sri Lanka;
- the paired-row technique for improving efficiency of cassava-, kenaf-. and cotton-based cropping systems in Thailand: and
- on-farm testing in Thailand, Sri Lanka, and Malaysia.

The causes of low groundnut yield in Andhra Pradesh are delayed sowing, absence of seed selection and treatment, inadequate crop stand, and poor weed control (Andhra Pradesh Agricultural University 1978). These are common causes of low yields for most upland crops in South and Southeast Asia.

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HIGH-INPUT CROPPING SYSTEMS

Kuang-Chi Su

Depending on availability of water, the farmlands in Taiwan are divided into different cropping areas, including double rice, single rice, rotational rice, and dryland cropping. Growing two or more crops in the same field in a year to increase farm income has been attained by growing short-growth-duration crops or cultivars, and adopting special cultural practices such as relay-intercropping, ratooning, no tillage, older seedlings, or the raised-bed method.

Some very efficient and productive cropping patterns have been developed through combining widely adapted cultivars and physical and chemical treatments.

The trend of labor shortage by migration of rural labor to urban-industry sectors has induced changes in cropping systems, depending on farm size. Farmers of small farms (less than 0.5 ha) continue to intensify land use. Two to three harvests of fruit, or seven to eight vegetable crops in a year are practiced extensively on such farms. Small farms of around 1 ha or larger cannot be managed with family labor alone. Owners have to cut down on crop acreage which requires much labor input. Group farming operations as a means of accelerating farm mechanization have gradually been adopted. Thus, diversified multiple cropping systems tend to change to monoculture and multiple cropping index will decline as more farmers join group farming.

This paper discusses recent changes in high-input cropping systems and consequent technical change in Taiwan agriculture.

The practice of annually growing two or three crops sequentially or simultaneously on the same field is common in Taiwan. A favorable subtropical climate, good irrigation facilities, and technological experience accumulated over generations of farming experience make multiple cropping feasible for increasing productivity of land and labor on small farms.

Multiple cropping indexes show a gradual increase from 116 in 1911-15 to 190 in 1964-68. Subsequently, they declined gradually until the late 1960s, when rapid

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industrialization caused considerable migration of rural labor to urban-industrial areas. Farm labor shortages and high farm wage rates resulted. These trends induced changes in cropping systems, from labor-intensive to capital-intensive or labor-extensive. Labor shortages also caused farm families to reduce acreage in crops that required a large labor input. The acreage in field and special crops decreased from 679,274 ha in 1962-66 to 550,495 ha in 1972-76. But acreage in fruits, vegetables, and fishponds expanded rapidly.

CROPPING SYSTEMS IN TAIWAN

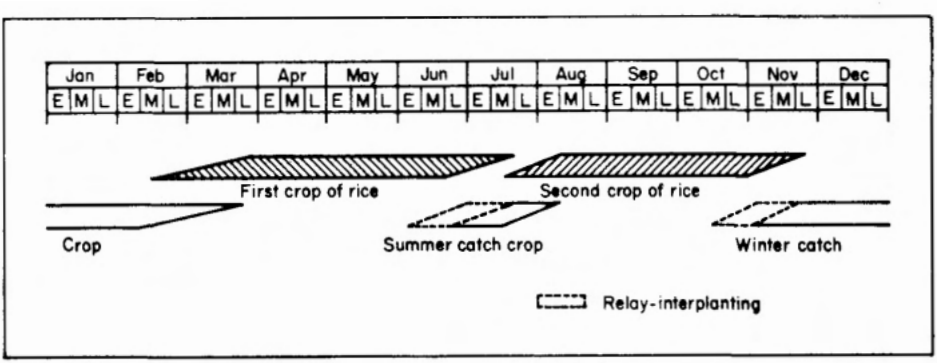
Arable land in Taiwan totaled 918,143 ha in 1978. Paddy fields amounted to 517,061 ha (56.32%), and dry farming fields 401,082 ha (43.68%). Cropping patterns in paddy fields are determined mainly by the reliability of water supply. Paddy fields in fully irrigated areas, which can grow 2 crops of rice a year if they have adequate water for year-round irrigation, accounted for 396,010 ha (40.19%). Partially irrigated and rainfed areas can be used for single rice cropping or rotational cropping of rice with other crops, depending on water supply. Paddy fields with a single rice crop per year accounted for 49,984 ha (5.45%). Rotational cropping areas with a single rice crop every 2 or 3 years amounted to 98,067 ha (10.68%).

Fully irrigated double-cropped rice

Growing two winter or vegetable crops and one summer vegetable crop with two rice crops constitutes the most intensive land use in Taiwan (Fig. 1).

Two fallow periods occur between the year's rice crops — a winter gap of about 120 days from late October through the following February and a summer gap of 30-40 days. If the growing time of the vegetable crops is short enough, two crops may be grown in sequence during the winter gap. The main crops are sweet potato, wheat, tobacco, flax, rape, soybean, azukibean, maize, and sunflower. Vegetables commonly planted are Irish potato, carrot; onion, cabbage, cauliflower, peas, beans, tomato, radish, lettuce, and garlic. The few vegetables suitable for the summer gap are pai-tsai, edible amaranth, yellow melon, and oriental pickling melon.

Some special techniques, such as relay-intercropping and no-tillage planting with short-growth-duration crops or cultivars, are adopted by industrious farmers. Two-



1. Double-cropping rice pattern.

week-old melon seedlings are transplanted 2 weeks before rice harvest, or melon seeds are planted 4 weeks before harvest in the space which occurs every 10 rows in the rice field. Melon can be harvested within 70-80 days after seeding in summer. The same procedure of relay-intercropping is used for tobacco, maize, sweet potato, and sugarcane before the harvest of the second rice crop.

This practice allows the production of crops which are otherwise impossible to fit into the multiple cropping system. The adverse effect on rice, usually a 3-10% decrease in grain yield, is more than made up for by the multiple cropping returns as a whole.

No-tillage planting is practiced with relay-intercropping. In southern Taiwan, a winter soybean crop to follow the second rice crop is sown by opening shallow holes close to the rice stubble and placing two or three seeds in each hole. No land preparation is involved. After sowing, rice straw from the preceding crop is spread over the field and left as a mulch. In central Taiwan some no-tillage planting is used for wheat or peas immediately after harvest of the second rice crop. The advantages are savings in time and labor. Several studies have shown that yields from no-tillage fields can equal or surpass those from fields under conventional tillage.

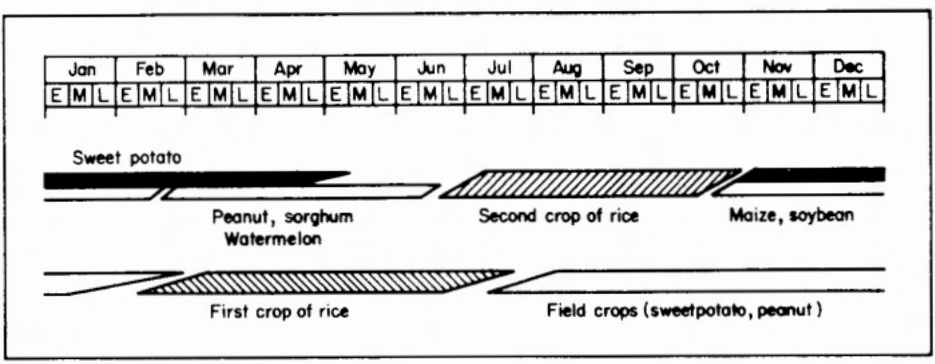
Rainfed and partially irrigated rice

Rice is grown with supplemental irrigation during the rainy season. Cropping patterns can be classified into three types based on the amount of supplemental irrigation available:

- one rice crop, one other crop per year.
- one rice crop every 3 years.
- two rice crops every 3 years.

A single crop of rice grown with supplemental irrigation during the rainy season is followed by another crop (Fig. 2). Depending on the rainfall pattern, rice may be the first crop or the second crop of the year. On slightly more than 9,000 ha, rice is the first crop; on more than 40,000 ha, it is the second crop.

Paddy fields along the west coast formerly were fully irrigated. But to escape strong seasonal winds from October to March, transplanting of rice as a first crop is now delayed until the end of March with harvest at the end of July. Because a second



2. Single–croppingrice pattern.

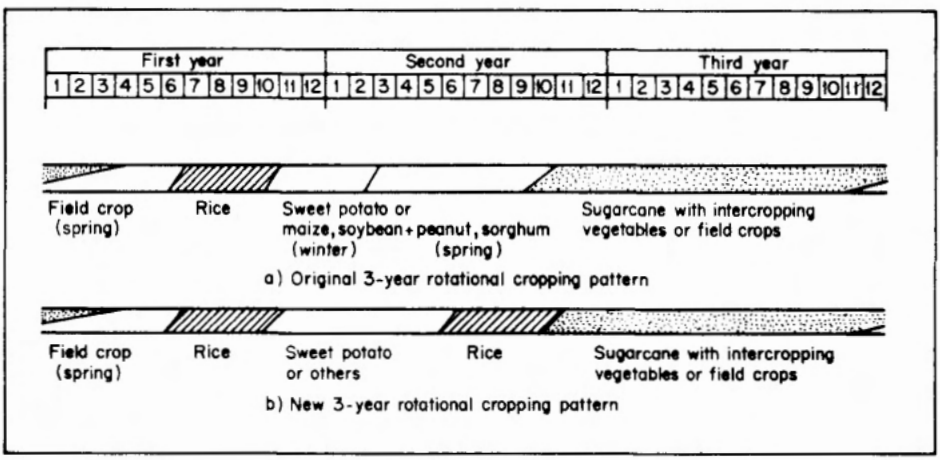
rice crop would be damaged by winter winds, peanut, sweet potato, or watermelon is recommended as the second crop.

Dryland crops planted first, with rice as the second crop, usually are long-duration and drought-tolerant sweet potato or processing tomatoes.

One rice crop every 3 years in rotation cropping is practiced because of uneven distribution of rainfall. In the dry winter and spring, water resources are insufficient to cover the entire irrigation area throughout the year. On about 120,000 ha, 3-year rotational irrigation has been practiced 50 years (Fig. 3). Farmlands are divided into crop-rotation units of 150 ha each. Each unit is again subdivided into three 50-ha subunits. The three kinds of crops planted in rotation over a cycle of 3 years are rice; dryland crops such as maize, peanut, sweet potato, sorghum, soybean, and vegetables; and sugarcane.

A spring dryland crop or green manure as the first crop is harvested by June to have the land ready for rice transplanting. Rice may be harvested by October, and then followed by two more dryland crops. After the last harvest the next September, sugarcane is grown for about 18 months before another cycle of spring dryland crop starts. The rice crop and the sugarcane crop are irrigated with a total of about 180 mm water. The dryland crops either are not irrigated or are irrigated only once with 90 mm during the growing season, depending on surplus water in the reservoir.

Two rice crops every 3 years became possible after completion of the lining of the irrigation canals and the construction of Tsengwen Reservoir. Sufficient water became available for full irrigation of 2 rice crops and for adequate irrigation of sugarcane (6-7 irrigations during the growing season) and dryland crops (2-4 irrigations) in a 3-year rotation. A winter or spring dryland crop can be harvested by June followed by paddy rice to harvest in October. Two successive dryland crops occupy the land for about 7 to 8 months. Then a second rice crop is transplanted and harvested in October. Sugarcane is planted after the rice harvest or relay-interplanted before the harvest. Another 3-year cropping cycle is initiated after the sugarcane is harvested.



3. Rotational cropping pattern.

Sugarcane is the main crop in rotational cropping. Since it is a long-duration crop (18 months), farmers are accustomed to relay-interplant about 50 days before the rice harvest to fit the multiple cropping system. Cane interplanted with the first rice crop is called spring paddy sugarcane. Cane interplanted with the second rice is called autumn paddy sugarcane.

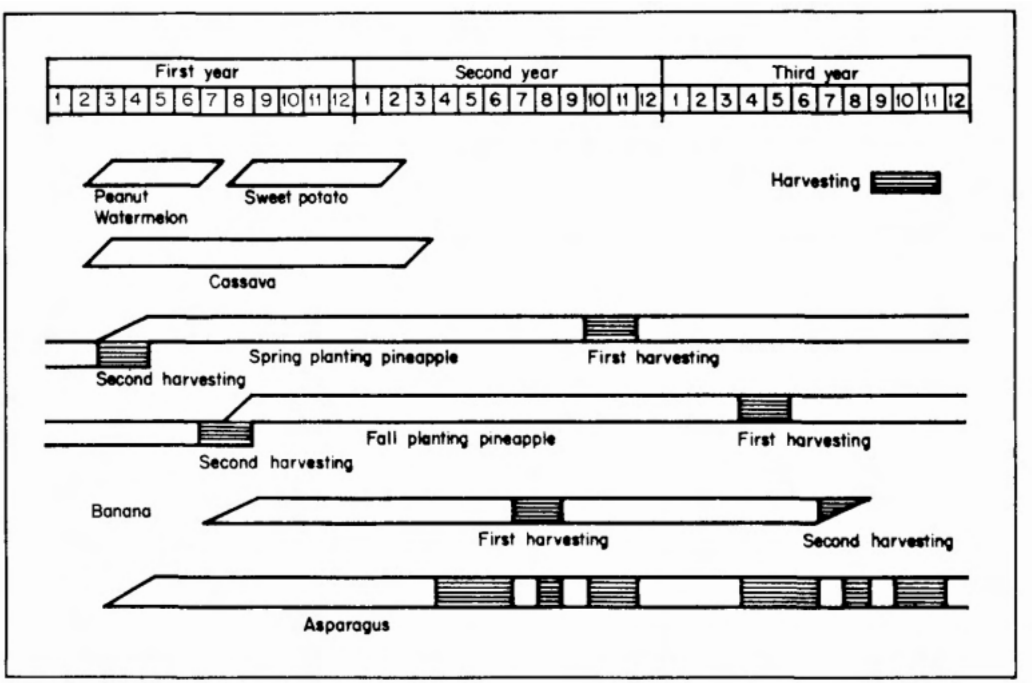
A general interest in a shorter growing period for cane is revealed by extended ratooning and by choice of spring paddy sugarcane. With these practices, spring cane needs only 8-12 months to mature. Spring paddy sugarcane has no significant effect on rice yield.

Farmers interplant other crops with sugarcane to get some additional financial return before the cane harvest. Sweet potato, peanut, soybean, maize, tobacco, rape, tomato, seed melon, and vegetables such as cauliflower, cabbage, and radish, are intercropped either at the same time or after sprouting of the sugarcane.

Dryland cropping patterns

Dryland fields are on rolling hills, table terrace land, and other areas where irrigation is economically impossible or soils are low in water-holding capacity. Prevailing cropping patterns (Fig. 4) are annual dryland crops and perennial dryland crops.

Annual dryland crops grown in spring and summer are followed by sweet potato during autumn and winter. A crop of peanut, sorghum, maize, soybean, sesame, mungbean, or watermelon is planted in February or March and harvested in July. Then sweet potato occupies the field for 5-6 months.



4. Dryland cropping pattern.

Long-growthduration crops, such as cassava or sugarcane, are rotated with other dryland field crops or with green-manure crops. A typical cassava pattern might be planted February-April and harvested after 12 months, with a spring crop of peanut, and an autumn crop of sweet potato. Another rotation is green-manure crops in spring, fall sugarcane harvested in 18 months, and spring ratooned sugarcane harvested in 12 months.

Perennial dryland crops are grown in the rolling hill region of the lower mountainous area below 1,000 m. Tea and citrus are the main crops in the north; tea, citrus, mulberry, pear, grape, loquat, lichi, banana, and pineapple in the center; and banana, pineapple, sisal, longan, and mango in the south. Sandy soils along the west coast and the river banks in central and southern Taiwan are given over to asparagus.

INCREASING CROPPING INTENSITY

In the last few years we have faced these problems in crop production: 1) rice overproduction promoted by a high guaranteed price and advanced technology, 2) maize, soybean, and wheat supplies lagging behind a rapidly growing demand for livestock feed and industrial uses, 3) increasing export and domestic markets and prices for vegetables and fruits, and 4) labor shortages and depressed agricultural prices relative to inputs.

To cope with these problems, new cropping patterns have been developed.

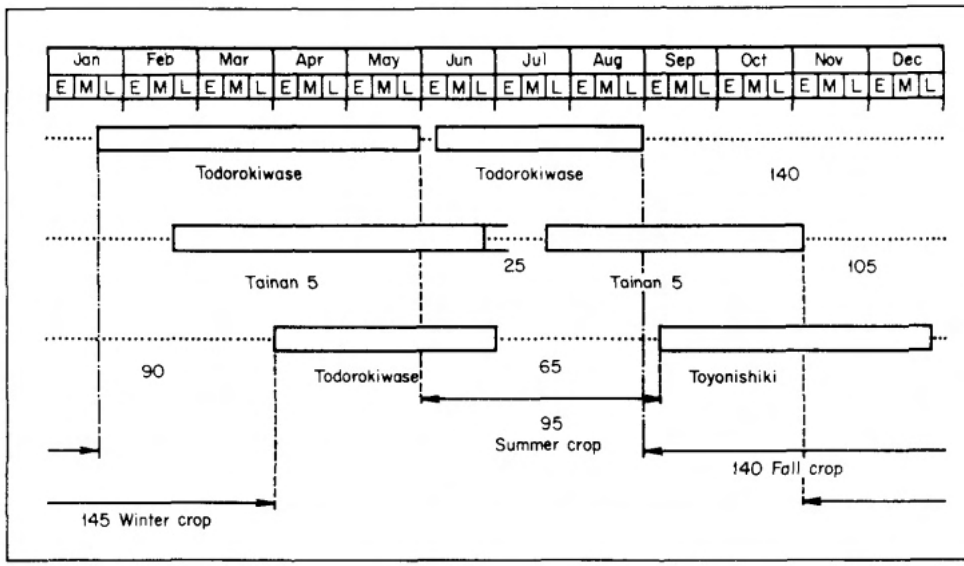
Diversification in fully irrigated paddy areas

Successful introduction of early-maturing and cold-tolerant Japanese rice cultivars has extended the planting season from the conventional late February through mid-August to early January through early September. Choosing early-maturing cultivars and adopting ratoon or older-seedling methods could shorten the growing period of rice without significant yield loss. Ratooned indica type cultivars mature 22 days earlier than under conventional transplanting, but grain yield is 13% lower. Planting older seedlings shortens the growth duration by about 10 days but decreases grain yield by 3-5%. However, older seedlings planted at closer spacings have yields similar to those under conventional plant spacings.

By combining rice cultivars which mature at different times, ratooning, and older-seedling treatments, diversified cropping patterns can be adopted.

Maintaining the two-rice-crop patterns. The two rice-crop pattern can be maintained while extending the summer vegetable season, extending the winter crop season, or advancing the winter crop planting time (Fig. 5).

Common vegetables are difficult to grow in the hot, humid, and short summer fallow period and only a few varieties are suitable. But if this fallow time can be extended from 1 to 2 or 3 months through early harvest of the first rice crop and late planting of the second rice crop, many leaf and cucurbit vegetables can be grown without labor-intensive relay-interplanting. Watermelon (15 days nursery + 85 days), melon (60 days), vegetable soybean (75 days), Chinese cabbage (heat- tolerant, 20 days nursery + 45 days), water convolvulus (90 days with 4 harvests), oriental pickling melon (50–70 days), edible rape (45 days), edible amaranth (45 days), and



5. New double-cropping rice pattern.

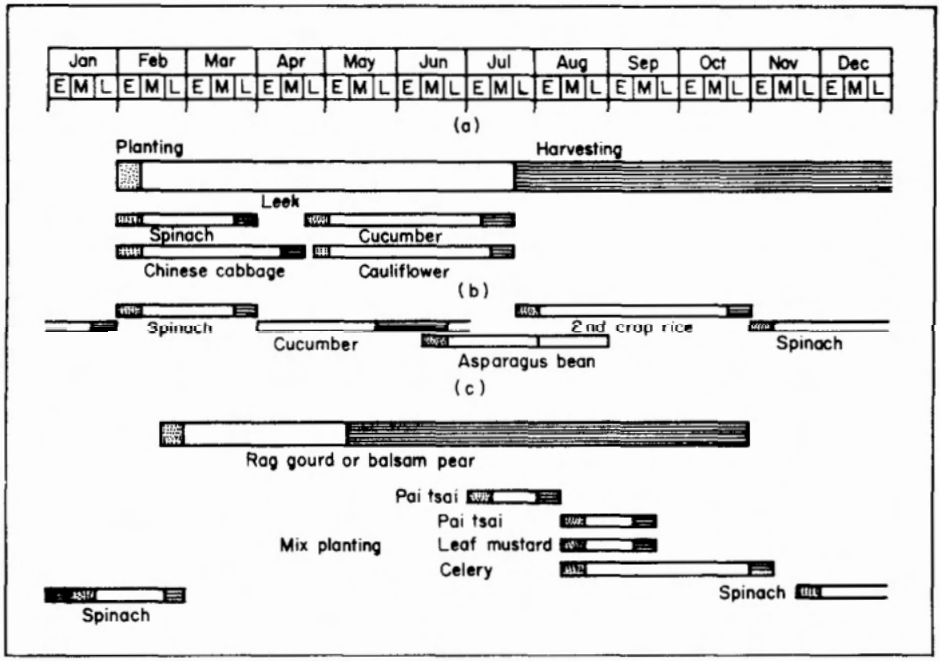
radishes (50 days) command high market prices in the summer vegetable shortage period.

Some long-maturation vegetables have been widely grown in paddy districts in recent years. Since the maturation periods of pea, tomato, strawberry, and garlic exceed 120 days after the second rice crop, early-maturing cultivars or older seedlings may be used after the winter crop harvest in late March or early April. The first rice crop could be harvested before mid-July.

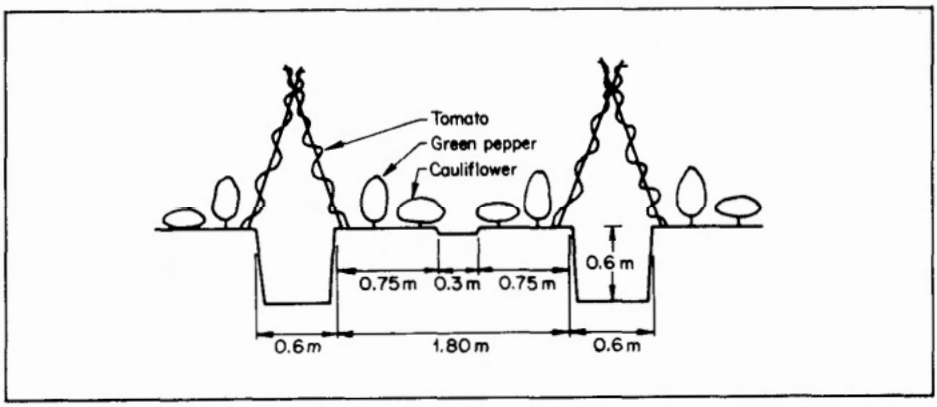
Soybean grows poorly during November to February and crop maturity is delayed because of the cool dry weather in central Taiwan. However, planting maize or soybeans early, before mid-September in the central region or mid-October in the south, has resulted in shorter growth duration and higher yields than late planting. Shifting the two rice crops from February-October to January-August by adopting early-maturing and cold-tolerant cultivars may be the most suitable cropping pattern for rice and field crops.

Replacing one rice crop with another crop. If unfavorable climates or soil conditions cause low yields or unreliable yields of the second rice crop, vegetables or field crops could replace the second rice crop to be harvested before the seasonal wind. Whenever the profit from other crops or land uses is higher than that of rice, progressive farmers adopt such crops or land uses even on highly productive paddy land. Four cropping patterns are practiced:

- First rice crop in March-July, watermelon for 60 days, and Chinese cabbage or minimaize (young ears harvested as vegetable about three days after silking) for 70 days.
- First rice crop and fishery pond.
- First rice crop (February to June) and tomato (July to January).
- Second rice crop (July to October) and strawberry (November to May).

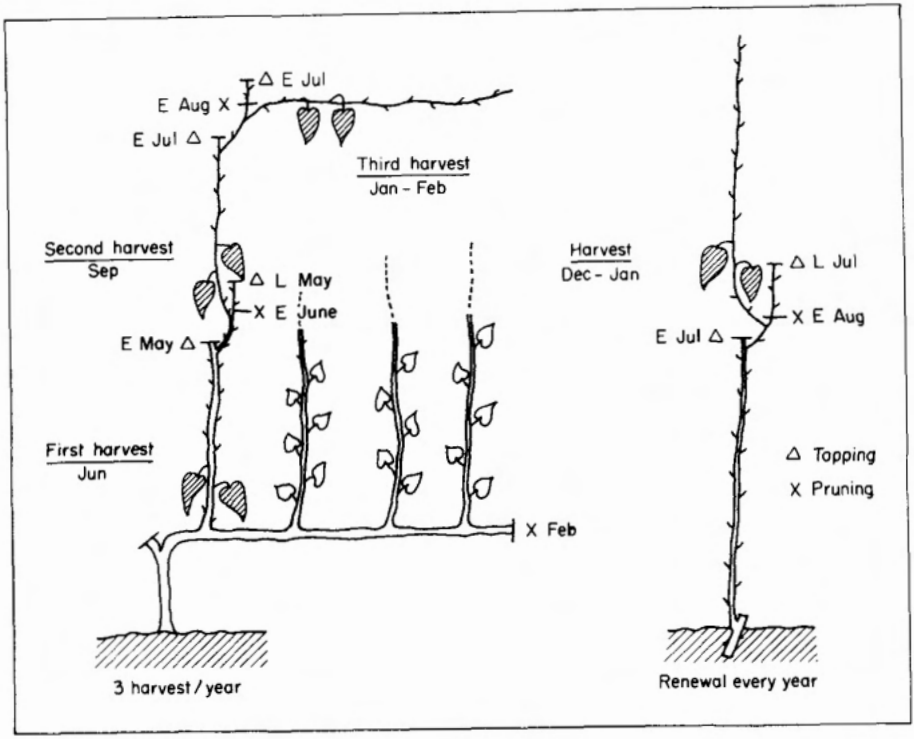


6a. Vegetable farm in paddy field.



6b. Intercropping of vegetables on the raised bed system.

Shifting the paddy land to fruit or vegetables. On small farms around 0.5 ha in size, continuous vegetable production on raised beds with furrows for drainage is common in fully irrigated areas of central Taiwan. Leek, spinach, cucumber, tomato, asparagus bean, cauliflower, and a second rice are interplanted sequentially (Fig. 6). Other patterns are rag gourd or balsam pear plus pai-tsai, then mixed pai-tsai, leaf mustard and celery plus spinach and leek plus intercropped spinach and Chinese cabbage plus intercropped cucumber and cauliflower.

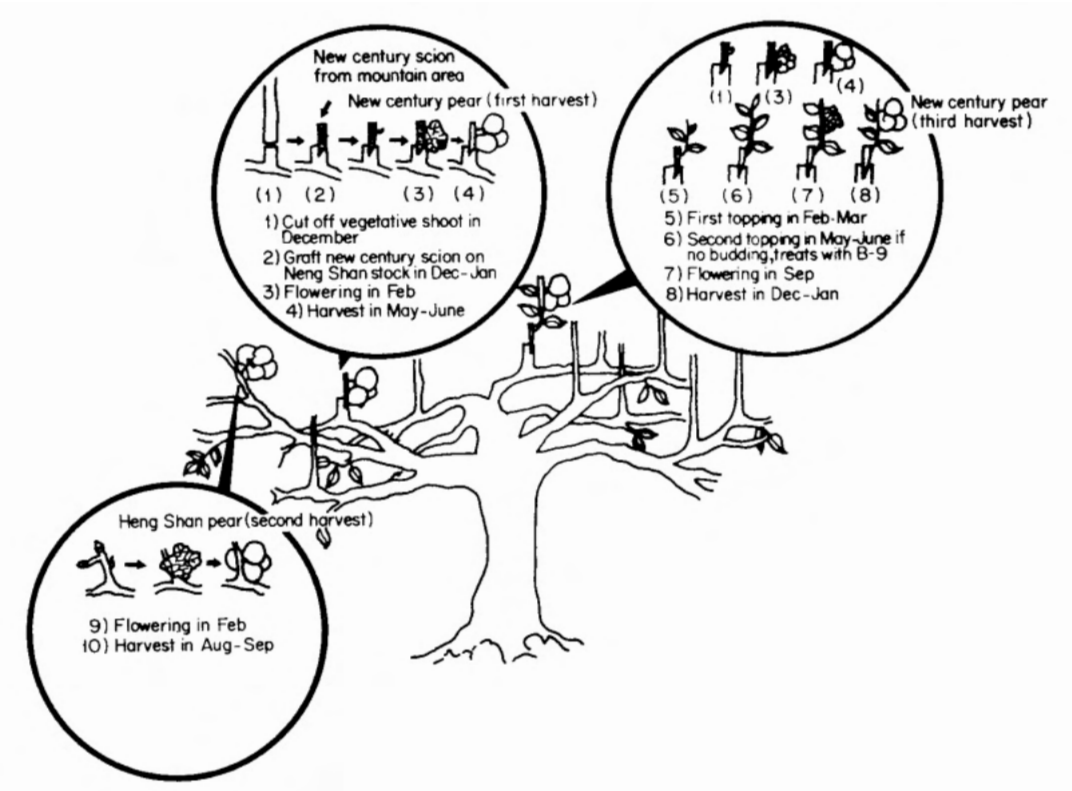


7. Methods for 2 to 3 grape harvests or renewals a year. E = early, L = late.

Harvesting two or three crops of temperate fruits

Grapes for table use and wine are an important temperate fruit in Taiwan. The growing areas, totaling about 4,000 ha, are distributed over the slope land and paddy areas of central Taiwan. Generally, grapes are harvested once a year between mid-July and mid-August. Since grape farms are small, about 0.5 ha growers adopt topping and pruning and chemical control for growth regulation and defoliation to adjust the harvest season, to prolong the market season, and to increase productivity with two or three harvests a year (Fig. 7).

Pear is grown on lowlands and mountains (above 1,500 m) in central Taiwan. Cool weather in the mountain areas is suitable for high quality pears such as the New Century cultivar. In subtropical lowland areas, the heat-tolerant but low-quality cultivar Heng Shan is grown. But if New Century scions are grafted to Heng Shan shoots in December, a first harvest of New Century fruit will set on Heng Shan branches in early June. Then, Heng Shan trees set on their own fruit in August to September, providing a second harvest. New Century scions on Heng Shan branches can be topped during April and May or treated with B-9 (×800) during May and June to promote flower bud differentiation. After pruning in August, the flower bud can be treated with ethylene chlorohydrin to promote flowering in August or September. Additional New Century fruits can be harvested December to January, making a third harvest (Fig. 8).



8. Method for three pear harvests: year.

FUTURE DEVELOPMENT OF CROPPING PATTERNS

The relative importance of agriculture in Taiwan's national economy has declined considerably because of accelerated industrial development and other activities. As a result, farmers face such difficulties as the shortage of farm labor, the high costs of small-scale farm operations and essential production methods, and the low rates of capital return from agricultural investments. Labor-intensive cropping systems have gradually changed to other patterns.

Farmers of small farms with less than 0.5 ha continue to intensify land use by adopting short-duration crops, cultivars, or cultural practices. The management of 7 to 8 sequential crops on raised beds or two to three crops of temperate fruits can be done with the labor of a small family (probably by a couple).

Small farms of around 1 ha or more cannot be managed by such limited family labor. The need for high-cost employed labor during the busy farming season has forced many to become part-time farmers, seeking nonfarm employment at the expense of their farming operations. Because they cannot afford to invest in farm machines or to purchase the land necessary to increase farm size, such farmers may give up labor-intensive crops or winter and summer cash crops.

Some efforts have been made to promote joint or group farming operations by small farmers as a means of accelerating farm mechanization. Group farming leads

to technological agreements, joint operation of farms, and use of machinery, and to entrusting part or all of the work to others. In general, group farming is a device to enlarge the scale of farm operations and to promote farming efficiency, and hence to increase unit yield and reduce production costs without changing ownership of the land. Diversified multiple cropping patterns tend to change to monoculture. The multiple cropping index will decline as more farmers adopt group farming.

CROP PRODUCTION UNDER SHIFTING CULTIVATION AND MAINTENANCE OF SOIL FERTILITY

D. J. Greenland and B. N. Okigbo

Shifting cultivation includes a wide range of crop production practices in which crops are grown for a few seasons and then the land is allowed to revert to natural vegetative cover for several years.

When adequate land is available, the system stabilizes over time, soil fertility is maintained, and satisfactory yields for subsistence farming are attainable. If land is insufficient for fertility to be restored during fallow, then a degradative cycle may develop.

During cultivation, soil acidity increases and there are decreases in available plant nutrients, organic matter, storage of plant available water, and infiltration capacity. Yields are reduced if cultivation extends beyond one or two cropping cycles and fallow periods are reduced. Under natural fallow, forest regions will be rapidly covered by redeveloping vegetation, but the regeneration of savanna and grassland is much slower.

In forest areas, a suitable combination of trees with fertilizers, zero tillage, and mulch farming can lead to a stable, continuously productive system, with relatively low inputs. The natural grass savanna fallow is a poorer means of restoring soil fertility, because grass stores only small amounts of nutrients and maintains a chronic shortage of available nitrogen.

Stable, economic, high productivity may be attained in the humid tropics through a combination of natural rotation cultivation systems with some inputs characteristic of modern farming systems. Some form of rotational grassland farming with modern inputs is probably essential to raise the productivity of savanna and grassland zones.

Although shifting cultivation is more productive than many other systems considering the total energy requirement per unit of food produced, its high human labor requirement rules it out as an alternative to high energy input systems. In areas where shifting cultivation is practiced, yields are not sufficient to adequately maintain current populations.

Shifting cultivation and the many related natural fallow rotation systems are usually thought of as systems of low productivity. This is correct if yields are considered in

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terms of kilograms per hectare or kilograms per hectare per annum. However, where shifting cultivation is practiced, land usually is not the limiting factor. Labor and other energy demanding inputs are. Therefore, productivity should be considered in relation to energy used. In terms of the human labor required to produce a certain quantity of food, shifting cultivation is still low in productivity. But when total energy requirements per unit of food produced are assessed, then shifting cultivation is seen to be very much more productive than many other systems in current use (Table 1).

Shifting cultivation is a successful low input production system because energy from sunlight can be stored in the natural ecosystem for several years to be exploited when the land is cultivated. But because it can only be successful where plenty of land is available, it is unrealistic to think of it as an alternative to higher energy input systems if the present population of the world is to be fed. In many areas where shifting cultivation is currently practiced, it cannot adequately sustain the current and rapidly increasing populations.

Calculations of the total population that the soils of the world can sustain with high energy input farming systems, such as that made by Buringh and Van Heernst (1977), are also unrealistic in terms of currently exploited energy resources. The energy needed to generate the inputs required if all potentially arable soils of the world are to be farmed intensively cannot be met over a long period of time from existing resources.

Table 1. Productivity of different agricultural systems, energy inputs, and energy output/energy input advantages (E_r) (data from Leach 1976).

Area	Crops	Energy (GJ/ha per annum) Output	Input	E_r
Shifting cultivation systems				
New Guinea Highlands[a]	Yam, sweet potato, cassava (total kg)	41	2.5	16.5
Congo	Cassava, plantain, rice (total 2,600 kg)	15.7	0.24	65
Mexico	Maize (1,900 kg)	29.4	0.96	30.6
Partially mechanized systems with fertilizers				
Mexico	Maize (93 1 kg)	14.2	2.90	4.9
Philippines	Maize (931 kg)	14.2	2.8	5.0
Uttar Pradesh, India	Wheat (756 kg)	11.2	6.6	1.7
Philippines	(Rainfed) Rice (1,500 kg)	22.9	4.2	5.4
Fully mechanized with all necessary inputs for high yields				
Surinam	(Irrigated) Rice (3,400 kg)	51.5	41.1	1.3
USA	(Irrigated) Rice (5,700 kg)	84.1	65.5	1.3
USA	Maize (5,100 kg)	76.9	29.9	2.6
UK	Wheat (3,900 kg)	56.2	17.8	3.3
UK	Maize (5,000 kg)	61.7	26.4	2.3
UK	Potato (26,300 kg)	56.9	36.2	1.6

[a]Leach (1976) gives much lower figures for output and input calculated per ha of total land including the fallowed areas, Rappaport (1971) gives higher figures calculated for cultivated land and for the whole 120 wk of the cropping period.

Shifting cultivation in some form probably supports 200-300 million people now, most of them in Africa. Around 40 million are in Asia (Spencer 1966 estimated 50 million) and 40 million are in Latin America. Shifting cultivation farmers cultivate about 50 to 100 million hectares each year and their fallow land covers between 250 and 500 million hectares, assuming 4 years of fallow for each year of cultivation.

The lands under shifting cultivation amount to a very significant proportion of the potential arable area of the world, estimated by Buringh et al (1975) as 3,419 million hectares, by Kellogg and Orvedal(1969) as 3,182 million hectares, and by the Ceres staff (Ceres 1978) as 2,495 million hectares. In South America, Asia, and Africa, where shifting cultivation is currently practiced, it is an even more significant proportion of the total potential arable lands, estimated by Buringh et a1 as 1,400-2,200 million hectares. In fact, the fallow lands of shifting cultivation areas constitute a very high proportion of the so-called unused areas of the world available for agricultural expansion. When discussing the future of these areas it is important to recognize the traditional rights of the users of these lands, although they use such lands infrequently.

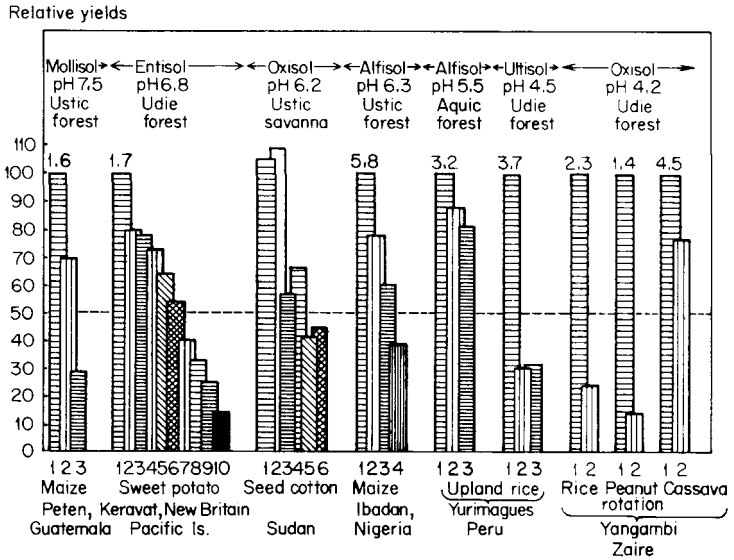
Here we review shifting cultivation and related fallow systems as they currently are practiced and the maintenance of soil fertility and hence productivity under natural fallow rotation systems. We also discuss the ways in which high productivity per unit input might be introduced to turn shifting cultivation into a more continuously productive system.

CLASSIFICATION OF SHIFTING CULTIVATION SYSTEMS

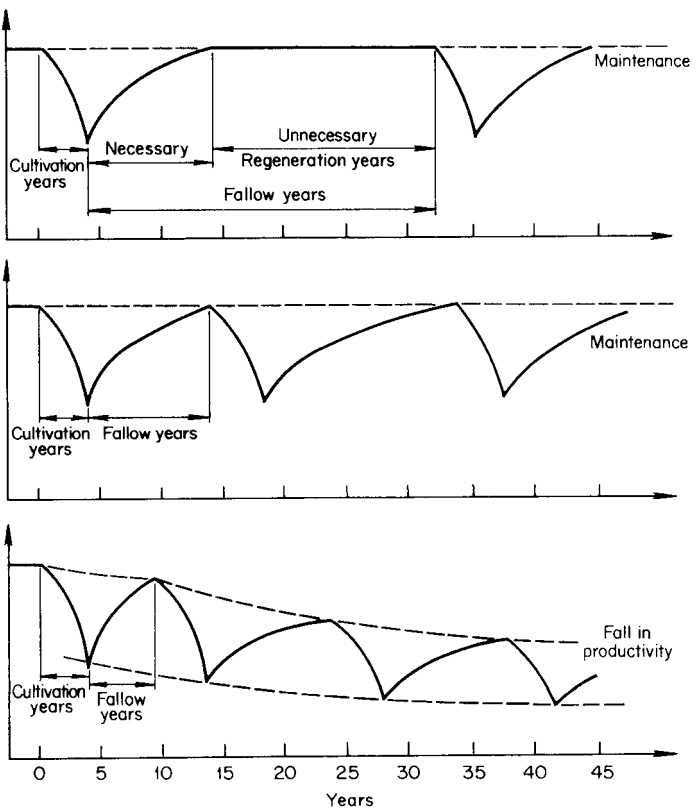
Shifting cultivation as a generic term includes a wide range of crop production practices. The basic pattern is crops grown for a few seasons, after which the land is allowed to revert to a cover of natural vegetation for several years before it is again cultivated. Soil fertility tends to improve under natural vegetation. Immediately after clearing, a satisfactory crop is obtained. Subsequent yields decline rapidly and the land is abandoned after a few harvests (Fig. 1). The system has been very widely practiced in Europe and North America (Grigg 1974, Sigaut 1975) as well as throughout Africa (Allan 1965), Latin America (Watters 1971), and Asia (Spencer 1966).

Where socioeconomic circumstances have allowed the system to establish an equilibrium with the physical environment, it is practiced with considerable sophistication. Different cropping systems are utilized for different soil types. The length of the fallow is determined by the appearance of certain indicator plants in the natural succession, which shows that fertility has attained a level where good yields will again be obtained. De Schlippe (1956) gives an excellent account of such a system. Many other examples can be found in the literature (Nye and Greenland 1960, Spencer 1966).

When adequate land is available and the area has been utilized for shifting cultivation for many years, the system tends to be stable and soil fertility is maintained over a long period. However, if the amount of land is insufficient for fields to be left in fallow until fertility is fully restored, then a degradative cycle may develop (Fig. 2). Dramatic gully erosion may result in some areas. The result is that these



1. Yield decline of successive crops after clearing and burning natural vegetation (from Sanchez 1976).



2. Soil fertility changes in stable and unstable shifting cultivation systems (after Guillemin 1956, Sanchez 1976).

areas become unable to support their populations. This is happening in many of the more heavily populated parts of Africa (Prothero 1972). Outward migration to major cities is one result, contributing to the general rural/urban migration. Concentration on food crops at the expense of cash crops to ensure survival is another. The recent rapid decline in the export of groundnut from Nigeria can be attributed at least in part to this process.

Degradative processes in fallow systems also occur as a result of displacement of a community from one environment to another, less favorable one. Commonly, invasion of their territory involves displacement of people from lowland areas to highland areas. Sometimes shifts from well-tried or traditional production systems to cash crop production systems have the same result (Okigbo 1977). Traditional lowland cultivation methods not adapted to steep slopes inevitably result in severe erosion. The system typically becomes a slash-and-burn in which the land is so severely degraded following clearing and the taking of one or two crops that it has to be more or less permanently abandoned:

Nakano (1978) described an interesting example of stable and degradative systems existing in the same area of Thailand. Well-established and stable systems of shifting cultivation have been practiced by the Karen and Lawa people, among others, in northern Thailand for many years. They cultivate hill slopes on a pattern of 1 year of cultivation followed by about 10 years of fallow. Valley bottomland is cultivated as terraced rice paddies in a continuous system (Gibson 1976).

However, their lands have recently been penetrated by Meo, Yao, Lahu, and other groups who by preference clear old or primary forest. They grow upland rice and opium on the cleared land until yields become negligible and the land is essentially ruined in 3 to 10 years. Regrowth after such a relatively long cultivation period is very slow indeed and further erosion inevitably ensues. The pioneer swiddeners, as Gibson calls them, do not expect to cultivate the same land again.

The same areas also are being penetrated by lowland rice growers from other parts of Thailand who have been forced by population pressure to move into areas where they have to farm the hillsides. These incipient swiddeners grow only dryland rice, on a rotational basis with natural fallow. But because they are not accustomed to farming hilly areas, they also cultivate in such a way that soil degradation occurs.

In discussing the productivity of fallow systems, it is essential to have some understanding of the different ways in which shifting cultivation is practiced.

Allan (1965), Ruthenberg (1976), Greenland (1974). and others have discussed the evolution of different types of shifting cultivation. Where some fields are cultivated on more fertile soils, for example, where animal manure and household refuse are used as soil improvers, the system usually includes both continuous cultivation on land around homesteads and closely settled areas and shifting cultivation on outlying land. This system is a late phase in the transition from true nomadic shifting cultivation, where the houses as well as the fields of cultivators shift regularly, to fully permanent cultivation (Table 2). The FAO Classification of Cultivation Systems (Table 3) divides them into normal and accelerated (or degraded) systems according to the relative length of crop and fallow and the nature of the fallow vegetation.

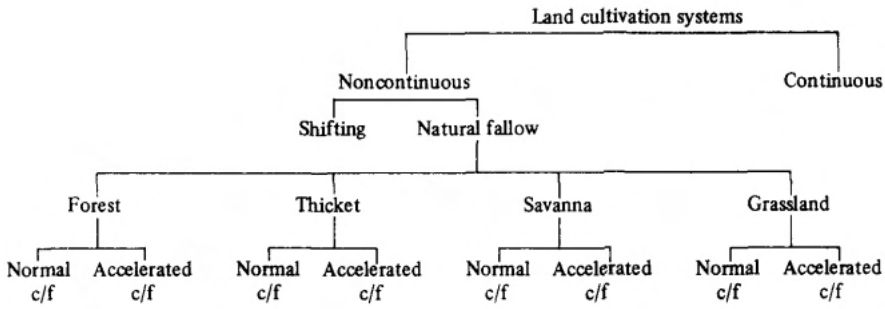
Only on highly fertile soils, such as the Rhodustalfs derived from basaltic rocks and the Eutrandepts of volcanic regions, is a high frequency of cultivation possible

Table 2. The phases and categories of land cultivation systems (Greenland 1974).

	Phase I	Phase II		Phase III	Phase IV
Land cultivation phases	Simple shifting cultivation	Recurrent cultivation		Recurrent cultivation with continuously cultivated plots	Continuous cultivation
	Dwellings and cultivated area shift together	May be complex with several field types		Always complex with several field types	May involve alternate husbandry with planted and cultivated pastures or fallow crops
Land categories	Shifting cultivation land L> 10[a]	Recurrent cultivation land			Permanent (L<2) and semipermanent land L<2-3
		Long-term recurrent cultivation L = 7-10	Medium-term recurrent cultivation L = 5-7	Short-term recurrent cultivation L = 3-5	
Principal soil order with which associated (very tentative)	Any	Alfisols Ultisols Oxisols	Alfisols Deeper Ultisols	Alfisols Deeper Ultisols Andepts	Rhodustalfs Andepts

[a] L = land use factor, defined as $L = \frac{C+F}{C}$ where C = length of cropping period in years, F = length of fallow period in years (Allan 1965).

Table 3. The FAO classification of cultivation systems (UNESCO 1979).



Note 1. An initial division into *continuous* and *noncontinuous* cultivation systems.

Note 2. *Continuous* systems include all those where some form of management is continuously applied, e.g. planted fallows, planted tree crops, managed grassland, and *taungya* cultivation.

Note 3. *Shifting systems* are those in which the homes of the cultivators are moved when the cultivated area of land is moved. *Nutural fallow systems* are those in which the homes of the cultivators are not normally moved when the cultivated land area is moved.

Note 4. *Natural fallow systems* are very widely practiced and further subdivisions are necessary:

a. The type of fallow vegetation: *forest* comprises woody vegetation with trunks and a closed canopy in which the trees are ecologically dominant; thicket comprises dense woody vegetation without trunks; *savanna* comprises a mixture of fire-tolerant trees and grasses in which the grasses are ecologically dominant; *grassland* comprises grasses without woody vegetation.

b. The length of the fallow: normal is used when land availability is unrestricted; *accelerated* is used when the length of the fallow period is less than would be voluntarily chosen because of population pressure or other factors.

c. Duration of crop and fallow periods shown as c/f, where c is the length of the cropping period in years and f the length of the fallow period in years, the end of the cropping period being taken as the time when the cropped land is no longer maintained.

Natural fallow systems can be described in these terms:

normal or accelerated	forest or thicket or savanna or grassland	fallow system, c/f

e.g. an accelerated forest fallow cultivation system, 2/5.

without serious loss of yield. On the other hand, in many highly acid soils (Oxic Paleudults and Oxisols) of forest areas, a substantially longer fallow period normally is necessary. Allan (1965) described this in terms of the Land Use Factor (L) defined as:

$$L \quad \frac{C + F}{C}$$

where C is the number of years of the cultivation period and F the number of years of fallow.

Different intensities of cultivation are associated with different soil and climatic conditions, so that different categories of recurrent cultivation (Table 2) are associated with different land types. Ruthenberg (1976) has proposed a rather different basis for the classification of shifting cultivation. His system classifies according to the natural vegetation, with subdivisions related to migration, rotation practice,

clearance methods, cropping sequence, and tools used. Moormann and Greenland (1980) attempted to analyze the relation between land use intensity, and soil and climate characteristics, but found no simple relationship which was also widely applicable.

CROP PRODUCTION UNDER SHIFTING CULTIVATION

Because shifting cultivation is practiced in a very wide range of physical and social environments, it is difficult to describe crop production within the system without a great deal of detail. Nevertheless, some generalizations can be made. In Phase I systems, yields of cereals are almost invariably very low and substantially less than 1 t/ha equivalent grain yield is commonly obtained. In Phase II and III systems (forest areas), different rotations will normally be practiced in outside fields and near fields, and compound gardens and wetland sites may be more or less continuously cultivated.

Outside fields, often with a land use factor of 10 or more, are cultivated for only 1 or 2 years. In the first year, a mixed stand of a cereal and root crop may be planted, followed by cassava interplanted with plantain. The cereal may yield 1-2 t/ha, the root crop 5-10 t/ha, and the plantain 2-10 t/ha. Forest will regenerate through the final cassava and plantain crop. Such systems are common in much of West and Central Africa and those parts of Thailand, Indonesia, the Philippines, and New Guinea where shifting cultivation is practiced.

On near fields, a rather more complex rotation may be practiced, involving legumes and vegetables and possibly a longer cycle. On the compound or home garden, up to 50 or more species may be planted (Okigbo and Greenland 1976) and cultivation may continue for 50 years or more.

In all the field types, several varieties of each species may be grown to mature at different times and so spread the harvest. This also reduces loss from failure of an individual crop or variety and provides more continuous soil cover than a single arable crop. Individual crop yields tend to be low, although the productivity of a compound farm which is manured may be a substantial per year total (Table 4). On the basis of energy produced per unit of energy input, yields are very high (Table I).

A detailed study of the effects of population pressure on Phase III shifting cultivation in eastern Nigeria has been reported by Lagemann et al (1976), Lagemann (1977), and Flinn and Lagemann (1980). Land use factor L varied for outer fields from 6 to 2 as the population increased from 100 to over 500 persons/km^2 (Table 4).

There have been few critical studies to isolate the contribution of different factors to the rapid yield decline after the first year of cultivation. Undoubtedly depletion of available nutrients and increasing weed incidence are of major importance, as the work of Kanget al (1977) at Ibadan in Nigeria has demonstrated (Fig. 3). On poorer soils, multiple nutrient deficiencies have been encountered, for example at Nsukka (Fore and Okigbo 1974). Deterioration of soil physical conditions is probably important, especially where soil erosion occurs. But Kang demonstrated in his experiment at IITA, Ibadan, that yields can sometimes be restored on areas where they have fallen to near zero simply by introducing appropriate fertilizer and weed

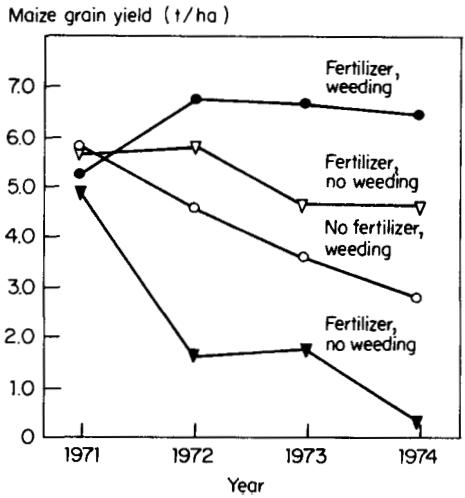
Table 4. Effects of population pressure on cropping intensity and soil properties in eastern Nigeria (Lagemann et al 1976).

Village	Owerre-Ebeiri	Umuokile	Okwe
Persons/km^2	> 500	350-500	<350
Cultivated ha/farm	0.23	0.27	0.40
Compound field	Very intensively used	Very intensively used	Less intensively used
Outer fields land use factor	2	2.5-5	3.5-7
Useful trees and shrubs (no./ha)[a]			
on outer fields	406	354	93
on near fields	523	340	312
Arable crop density (plants/ha)[b]			
on outer fields	36,516	19,012	12,175
on near fields	40,368	21,125	13,522
Yields from principal crop associations in outer fields (kg/ha)			
Maize	100	600	800
Cassava	2,000	4,000	10,000
Egusi melon	160	–	300
Groundnut	–	440	–
Yam (*Dioscorea* sp.)	1,100	–	–
Total grain equivalents (in 16 mo)	3,000	4,500	9,700
Soil fertility indicators			
Compound fields			
Organic C (%)	1.06	2.06	–
Total N (%)	0.09	0.17	–
pH	5.1	5.1	–
Exchangeable Cat Mg (meq/100g)	2.8	3.5	–
Exchangeable K (meq/100 g)	0.21	0.14	–
Extractable P (Bray 1) (μg/g)	19	36	–
Outer fields			
Organic C (%)	1.4	2.1	2.4
Total N (%)	0.10	0.16	0.17
pH	4.4	4.7	4.5
Exchangeable Ca + Mg (meq/100 g)	1.2	1.8	1.2
Exchangeable K (meq/100 g)	0.1	0.06	0.09
Extractable P (Bray 1) (μg/g)	9.7	9.1	14.9

[a]Principal useful trees were oil palms and fruit trees, including plantain. [b]Principal crops in compounds were cocoyam (*Xanthosoma*) and yam (*Dioscorea*). These were increasingly replaced by cassava in near and outer fields.

control methods (Table 5). However, his experimental plots were on level ground and carefully managed to minimize physical deterioration.

Nye and Greenland (1960), Sanchez (1976), Qureshi (1978), Lal and Cummings (1979), and others (Table 6) have documented several measurable changes in soil characteristics which occur during the cultivation period. These include increased acidity, decreased levels of available plant nutrients, loss of organic matter, greater compaction, decreased storage of plant available water, and decreased infiltration capacity. Marked changes in the faunal population and microbiological activity (Critchley et al 1979) also occur. These detrimental changes undoubtedly influence yields increasingly as cultivation is extended beyond one or two cropping cycles and the length of the fallow period is reduced.



3. Maize yield changes in successive years after forest clearance at IITA, Ibadan, Nigeria, and the response to fertilizers and weeding (Kang et a11977).

Table 5. Maize yields in 1975 after 5 years of cultivation with and without fertilizer and in 1976 (first season) when fertilizer was applied to all plots on the Egbeda series, Oxic Paleustalf, at IITA, lbadan, Nigeria (from Kang and Fox 1980).

Treatment before 1976		Rotation		Maize yield (kg grain/ha)	
Fertilizer[a]	Weeding[b]	First season	Second season	1975	1976
–	–	Maize	Sweet potato	356	5735
–	+	Maize	Sweet potato	2466	5865
+	–	Maize	Sweet potato	4369	5985
+	+	Maize	Sweet potato	5877	6031
+	+	Maize	Cassava	6283	6031
+	+	Maize	Cowpea	6061	5883
+	+	Maize	Pigeonpea	6603	5994
LSD 0.05				1221	ns

[a]– indicates no fertilizer used before 1976. +indicates 120-30-30 NPK applied to each crop other than legumes before 1976. Legumes received 30-30-30 NPK. In 1976 all plots received 120-30-30 NPK. [b]– indicates no weeding before 1976 but plots were plowed and harrowed before planting. +indicates hand weeding was done whenever sufficient weeds made it desirable. All plots were hand weeded as necessary in 1976.

SOIL IMPROVEMENT UNDER NATURAL FALLOWS

Forest regions

Provided the cropping period is not extended and significant soil erosion does not occur, the topsoil normally will contain sufficient viable seeds and residual rooted stumps for the soil to be rapidly covered by redeveloping vegetation as soon as it is abandoned. In forested areas of Zaire (Bartholomew et a1 1953) and Colombia (de las Salas 1978), quantitative measurements have shown how rapidly nutrient accretion occurs in young forest vegetation (Table 7). Other studies of nutrient storage in tropical forests (Table 7) have shown that large quantities of plant nutrients become locked in the vegetation.

After clearing, provided a good burn is obtained, all nutrients other than nitrogen and sulfur are added to the soil, mostly as carbonates. Consequently, there is a rise in the soil pH and an increase in the levels of available nutrients, including micronutrients, which may persist for several crop cycles (Table 6). In the wettest forest

Table 6. Changes in soil properties following clearing and burning of natural vegetation and during subsequent cultivation. [a]

Changes in chemical properties	Site	Before	Immediate	After 1 yr	After 2 yr	After 3 yr
pH	1	5.2	8.1	6.8	6.6	–
	2	6.6	9.0	–	–	–
	3	4.0	4.5	4.5	4.1	4.4
Exchangeable Ca (meq/100 g)	1	7.2	21.2	20.5	14.5	–
	2	9.4	33.5	–	–	–
	3	0.2	0.9	0.8	0.8	0.5
Exchangeable K (meq/100 g)	1	0.5	2.5	0.6	0.3	–
	2	0.5	11.8	–	–	–
	3	0.1	0.3	0.1	0.1	0.1
Total N (%)	1	0.26	0.25	0.24	0.19	–
	2	0.35	0.41	–	–	–
	3	0.1 2	0.14	0.09	–	–
Readily estimated P (μg/g)						
Truog	1	10	30	–	–	–
Bray 1	2	5	–	–	–	–
Olsen	3	5	16	11	15	5

Changes in physical properties	Site	Before	After Immediate	After 1 yr	After 2 yr
Bulk density (s/cm^3)					
Hand clearing	2 (0-3 cm)	0.63	0.94		
	(3-5 cm)	0.80	1.17		
Bulldozer clearing	2 (0-3 cm)	0.63	1.11		
	(3-5 cm)	0.91	1.46		
Infiltration (cm/h)					
Hand clearing	2 Capacity [b]	88	44		
	rate [c]	21	–	21	22
Bulldozer clearing	2 Capacity rate	115	17		
Hand clearing	3 Rate	(210)	19		
Bulldozer clearing	3 Rate	(210)	0.5		

[a] Site 1 = Kade, Ghana (Nye and Greenland 1960, 1964). Site 2 = IITA, Ibadan, Nigeria (Lal and Cummings 1979). Site 3 = Yurimaguas, Peru (NCSU 1975, Sanchez 1979). [b] Capacity refers to water entry when lateral flow above B horizon prevented. [c] Rate refers to water entry when lateral flow above B horizon prevented. Rate data are for a similar site near Ibadan, reported by Wilkinson and Aina 1976.

areas, the bum may be incomplete so that some of the accumulated nitrogen and sulfur is incorporated with the soil in organic form (Table 8). Although it is sometimes suggested that the bum will lead to losses of soil nitrogen through oxidation, the experimental evidence is that this does not occur, or at least that the loss is too small to be measurable, except in spots where dry plant residues are piled and when high and excessive temperatures persist for some time.

Organic matter accumulates in the soil during the development of the forest vegetation. Speculation on the rate of accumulation (Greenland and Nye 1959) has been supported by subsequent measurements (Jaiyebo and Moore 1964, Jenkinson and Ayanaba 1977). Now evidence confirms a generally high rate of nitrogen

Table 7. Biomass and nutrients accumulated in tropical forest vegetation.

Location	Approximate age (y.r)	Biomass (t/ha)	Nutrients (kg/ha)					soil
			N	P	K	Ca	Mg	
Kade, Ghana[a]	40	330	1797	123	804	2419	340	Ultisol
Yangambi, Zaire[b]	5	86	383	23	338	287		Ultisol
	18	143	549	76	391	551		
Cerare, Colombia[c]	5	68	351	22	320	181	40	Aeric Ochraquox
	16	203	712	55	495	558	156	
	"Virgin"	184	140	27	277	431	133	
Marafunga[d] New Guinea	40 (montane thicket)	592	1415	74	1227	2060	452	Andept
Manaus, Brazil[e]	"Virgin"	504	3294	67	500	528	275	Orthaxic Paieudult
Merida, Venezuela[f]	"Virgin" montane	462	1085	62	1470	894	253	Aquic Humitropept

[a]Greenland and Kowal(1960). [b]Bartholomew et al (1953). [c]De las Salas (1978). [d]Edwards (1973). [e]Fittkau and Klinge (1973). [f]Fassbendet (1974).

Table 8. Nutrient content of ash and partially burned residues added to the soil after clearing and burning a 17-year-old forest (Seubert et al 1977).

Element	Composition	Total addition to soil (kg/ha)
N	1.72%	67
P	0.14%	6
K	0.97%	38
Ca	1.92%	75
Mg	0.41%	16
Fe	0.19%	7.6
Mn	0.19%	7.6
Zn	137 ppm	0.3
Cu	79 ppm	0.3

buildup in the soil-vegetation system under redeveloping forest (Bartholomew 1977).

Much organic matter returns to the soil in the form of litter (Nye and Greenland 1960, John 1973) and leads to the redevelopment of an active soil fauna. Their activities create an open porous soil structure which the forest cover protects from direct raindrop impact. A large volume of information relating to changes in forest composition and associated fauna and flora has been collected in a recent state-of-knowledge report on tropical forest ecosystems (UNESCO 1978).

Savanna and grassland regions

The regeneration of soil fertility is much slower under savanna and grassland than under forest. One reason is the bum of vegetation during the annual dry season. This implies not only that the increase in total vegetative biomass is restricted, but also that a considerable amount of nitrogen is lost to the atmosphere through conversion to oxides of nitrogen during the burn. The loss of sulfur which occurs is undoubtedly a major contribution to the widespread sulfur deficiencies in these regions (see Jones and Wild 1975).

Nevertheless, some accumulation of the nutrients in the vegetation does take place (Table 9). The annual biomass production by savanna vegetation varies widely. Some of the data recently collated and reported in the State-of-Knowledge Report on Tropical Grazing Land Ecosystems (UNESCO 1979) is given in Table 9.

In addition to the accumulated vegetation nutrients released on burning, the amount of organic matter in the soil also increases under vegetation. Jones (1973) gives the organic matter carbon in noncultivated soils of West African savanna areas an average value of 1.03% and that in cultivated and recently cultivated soils as 0.58%. Soil organic matter levels are generally low, especially on the sandy soils typical of many savanna regions (Jones 1973, Kowal and Kassam 1978).

In some areas of the savanna zone of Central Africa, nutrient accumulation in the vegetation is so low that it is inadequate to support even one or two reasonable crops. To overcome the problem, the Citimene system of collecting and piling vegetation from surrounding areas in large or small circles on the area to be cropped before burning it has been developed (Allan 1965). More commonly animals serve to accumulate nutrients. They graze on the fallow land and are herded into pens at

Table 9. Biomass and nutrients accumulated in savanna and grassland vegetation.

Location	Principal spp.	Rainfall (mm/yr)	Biomass (t/ha)	Nutrients (kg/ha)				
				N	P	K	Ca	Mg
Ejura, Ghana[a]	Andropogonaceae	1,320	8.7 grass 53.3 trees	26	8	45	34	25
	Imperata cylindrica	1,320	3.9 grass	16	6	34	7	13
Southern Ghana[a]	Coastal thicket	780	57	216	28	213	433	102
Zambia[a]	Miombo woodland	1,100	99	–	50	168	386	99
Marandellas, Zimbabwe[a]	Natural grassland	800	2.4	22	2	30	14	–
Bambesa, Zaire[a]	*Pennisetum purpureum*	1,600	40	321	22	440	98	138
Sahelian zone[b]	*Erapostis* and *Aristida* spp.	250-500	0.5-2.0					
Sudan-Zambezi zone[b]	*Andropogon* and *Themeda* spp.	500-1000	2-12					
Guinea[b]	*Andropogon*	1000-1600	5-20					
Congolese zone [b]	and *Loudetia* spp.							
Northern India[b]	*Dichanthium* and *Cymbopogon* spp.	900	5					
Northern India (Varanasi)[b]	*Cynodon* and *Dichanthium* spp.	1,200	20					

[a] Nye and Greenland (1960). [b] UNESCO (1979).

night. The manure which collects is used on household fields and other fields close to the house (Allan 1965, Ruthenberg 1976). The manured fields are usually cultivated with a higher land use factor than the others.

Although many legumes are included in the crop and fallow phases of the cycle (Okigbo 1977), nitrogen fixation under savanna and tropical grassland conditions appears to be generally slower than under forest vegetation (Greenland 1977). This is probably due largely to the lower supply of energy for the nitrogen fixing organisms. The leguminous trees common in savanna regions may have nitrogen fixing rhizobia associated with them (cf. e.g. Radwanski and Wiekens 1967), but their contribution to the nitrogen economy appears to be small.

Organic matter increases in more humid savanna area soils under grasses such as *Pennisetum purpureum* (elephant grass) and *Panicum maximum* (Guinea grass). Rates of nitrogen accumulation of the order of 50–100 kg/ ha a year have been commonly observed (Greenland 1977). Presumably these high rates of nitrogen accretion are associated with the presence of nitrogen-fixing organisms in the rhizosphere. By contrast, much lower rates of accumulation appear to occur under the *Andropogonae* grasses of the drier regions.

BASIS OF THE ENERGY-EFFICIENCY OF SHIFTING CULTIVATION SYSTEMS

Where shifting cultivation is practiced without undue land constraints and the cropping period is not prolonged, satisfactory yields can be obtained, at least in terms of subsistence farming. Rappaport's calculation (1971) of the energy required for crop production included that involved in clearing, fencing, burning and land preparation, planting and weeding, other maintenance, harvesting, and cartage. His total was 5.78 GJ/ha for the 120-week cultivation period. Harvested material provided the equivalent of 95 GJ (also for 120 weeks), or a favorable 16:1 return in energy. Most of the harvest was root crops. The return would have been lower if cereals had been a major component, but still much more favorable than the range of 1:1 to 1:3 calculated for many agricultural production systems in temperate regions (Table 1).

The system is successful because the work of nutrient accumulation and pest eradication is done by the fallow vegetation, utilizing energy derived from the sun during the fallow period. Essentially, sunshine falling on land not used for crop production is being employed to gather nutrients and provide the energy required for the cropping phase. The soil fauna living under the fallow vegetation conducts much of the soil loosening for which a great deal of energy is expended in tillage operations in many modern agricultural systems. Of course, the energy expended per ha and returned per ha is very low if expressed on the basis of cultivated plus fallow land.

As population pressure causes the land use factor to fall, crop yields also will fall unless fertilizers and pesticides are introduced into the system. The calculations in *Agriculture 2000* (FAO 1979) suggest that by the end of this century most of the fallow areas of the shifting cultivation lands will need to be cultivated if even present inadequate nutritional standards are to be met. But is it possible to retain at least some of the advantages of natural fallow rotation systems while this occurs?

In fact a population density of 500 persons/ km^2 is currently maintained on very poor, highly acid soils in southeastern Nigeria under a system with a land use factor of 2. Root crop production is part of an agroecosystem of arable crops and oil palms approximating a tropical forest ecosystem (Okigbo 1974. Lagemann 1977). The palms cycle nutrients and enable a relatively closed system of crop production to be maintained. Other combinations of trees with crop production also may minimize the need for external energy inputs. Leguminous trees and shrubs combined with food crops may be particularly advantageous (Mongi and Huxley 1979).

Zero or minimum tillage systems, at least for the forest areas, can be combined with mulch farming practices to produce a stable production system in which high yields can be obtained for relatively low inputs (Lal 1976, 1980; Okigbo and Lal 1979). The importance of the mulches commonly employed in traditional farming systems is hard to overestimate. They maintain a cover on the soil which prevents erosion, helps to retain moisture in the soil, suppresses weeds, aids seedling emergence, and prevents excessive temperatures (Lal 1974, Falayi and Lal 1979, Harrison-Murray and Lal 1979). Live mulches of slow-growing prostate legumes also provide a suitable cover for arable crops (IITA 1979).

For forest regions, suitable combinations of trees with fertilizers, zero tillage, and mulch farming methods can lead to a stable and continuously productive system (Greenland 1975).

For savanna and grassland regions, the success of such systems is less certain. Mulches are difficult to maintain and yields often are seriously reduced by soil compaction if no-tillage systems are used (Charreau and Nicou 197 la, b, c, d; Nicou and Chopart 1979). Some type of grassland rotation needs to be developed for these areas (Nye and Greenland 1960, Ruthenberg 1976, Jones and Wild 1975).

A common result of increasing the length of the cultivation period in forest areas is that grass species enter. When the forest area is abandoned, grasses may be established in place of woody species. If the grass vegetation is burnt at the end of the dry season, as often happens, the remaining woody species of the forest area are destroyed and a change from forest to less productive savanna occurs (Nye and Greenland 1960). This is equally true where the conversion is to grassland dominated by alang-alang *Imperata cylindrica,* as frequently occurs in the shifting cultivation areas of Asia.

If productivity is maintained, as it can be by proper use of inorganic fertilizers, and if undesirable species are controlled by mulches or proper weeding, then the disappearance of forest is not necessarily a disaster. Lal (1976) and Juo and Lal (1977) have shown that, given proper management of crop residues, an adequate level of soil organic matter can be maintained by continuous cultivation systems, even in areas of high rainfall erosivity.

Stable and economic high productivity may be attainable in the humid tropical areas through a combination of some features of natural rotation cultivation systems with some of the inputs characteristic of modern farming systems. For the drier savanna and grassland zone, a few features of traditional cultivation systems may be useful. Some form of rotational grassland farming, again with some modern inputs, is probably essential to raise the productivity of these areas.

However, to develop more productive farming systems for the humid and sub-

humid tropics, it is as true now as it was in 1960 that "what is needed is critical experiment that will convert what is so often mere assertion into established fact" (Nye and Greenland 1960).

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