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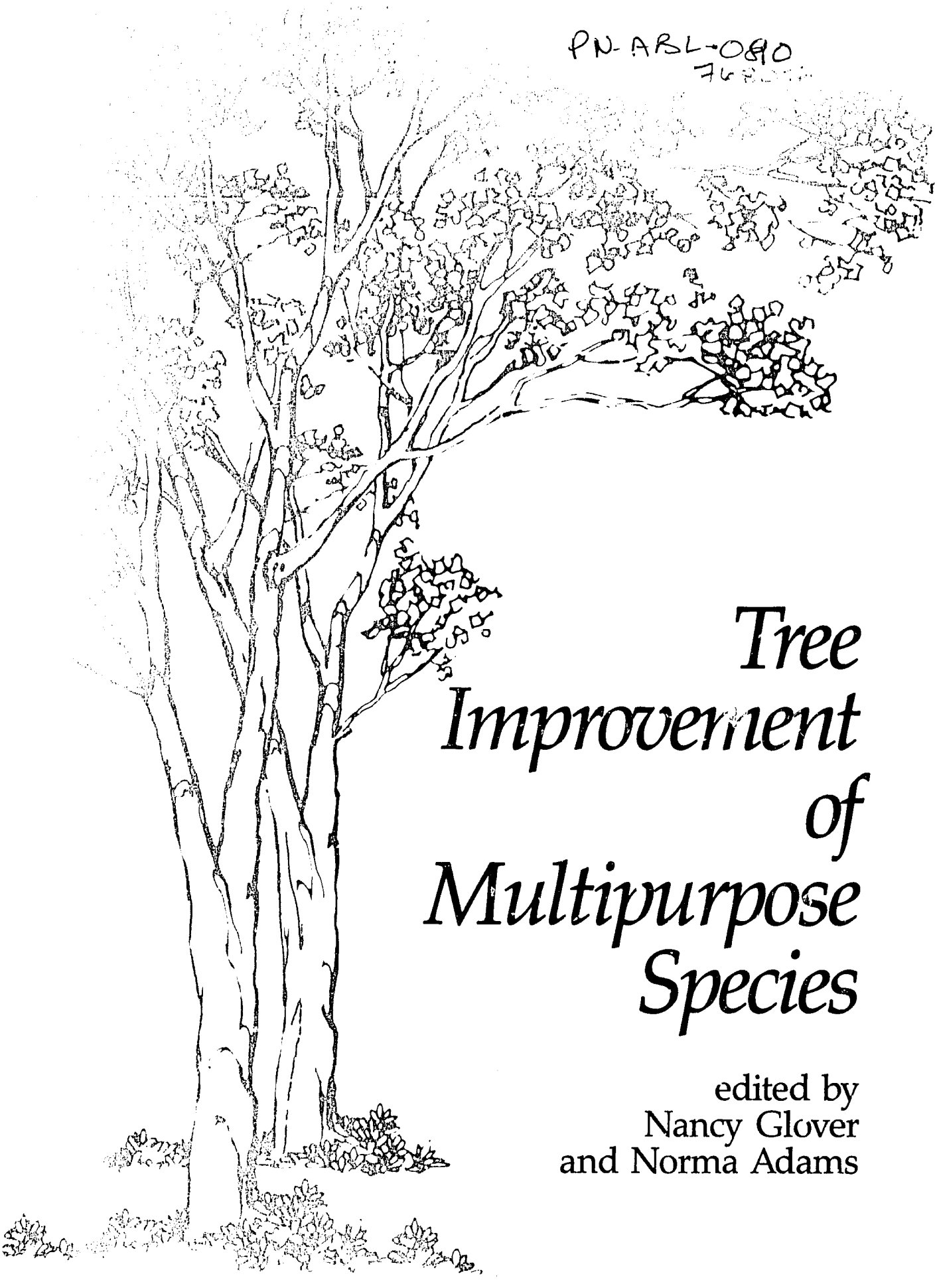
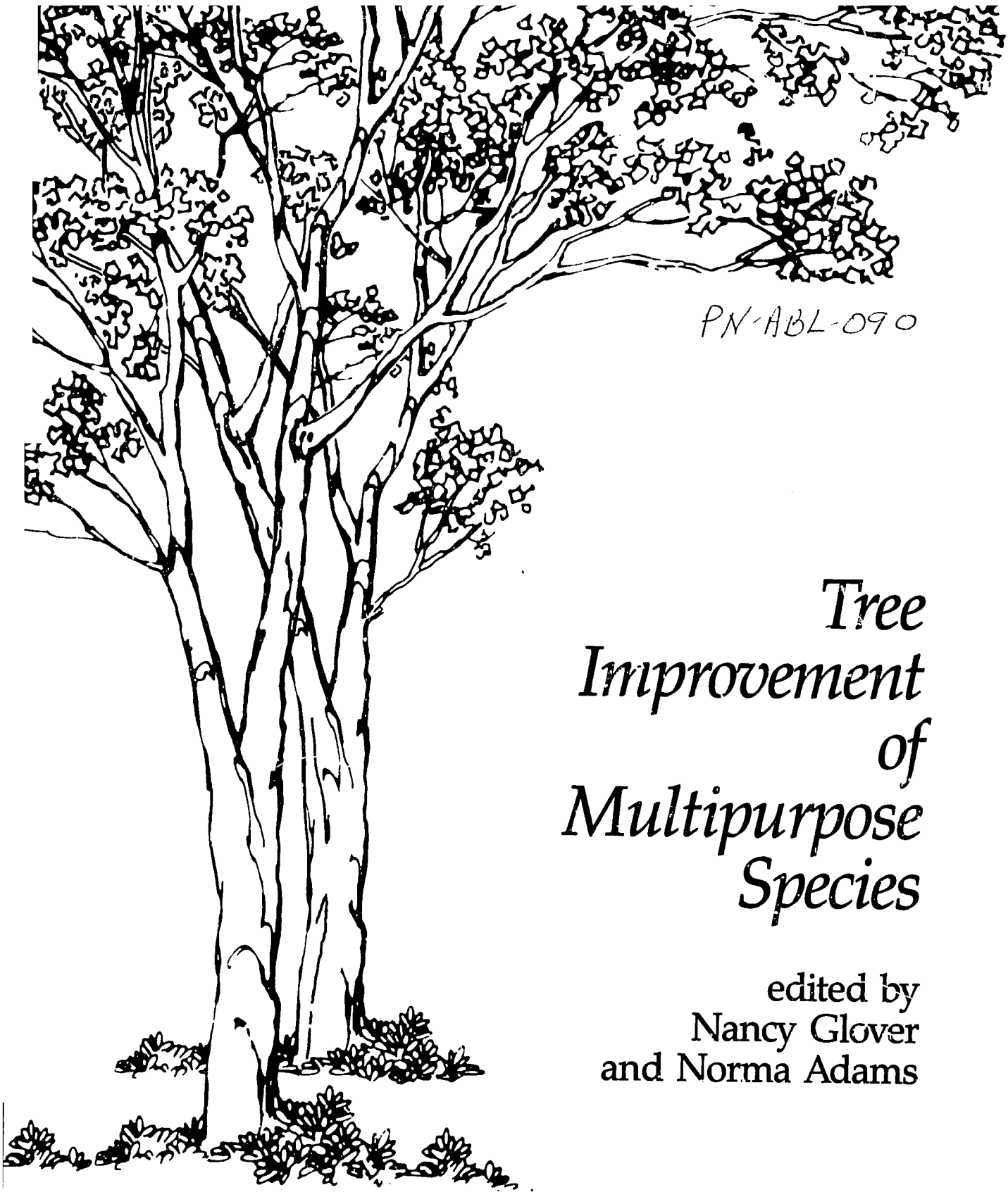


Tree Improvement of Multipurpose Species

edited by
Nancy Glover
and Norma Adams

Multipurpose Tree Species Network Technical Series, Vol. 2



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Tree Improvement of Multipurpose Species

edited by
Nancy Glover
and Norma Adams

Winrock International Institute for Agricultural Development

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Multipurpose Tree Species Network Technical Series

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G. sepium, p. 84; *C. calothyrsus*, p. 87; and *L. leucocephala*, p. 94.
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Foreword

Increased productivity of multipurpose trees (MPTs) depends on advances in tree improvement. The improvement process is not easy, however, because MPTs have so many uses. How, for example, does a researcher select superior trees in an evaluation trial without prioritizing uses according to end-user groups?

The range of environmental conditions under which farmers grow MPTs adds to the difficulty. These environments, characterized by soil and weather regimes, are often stress-inducing to trees. Under socioeconomic constraints, farmers may add to the stress by using inappropriate cutting managements, such as excessive pruning. To improve productivity or usefulness, researchers need to understand the causes of stress, as well as the land-use systems and socioeconomic obstacles under which farmers grow trees.

An important component of an improvement program is to evaluate germplasm over a range of field conditions and time. Simple trials suffice in early stages, whereas final evaluation involves multilocational studies with well-characterized sites. Characterizing environments for improved matching of species and management techniques for a specific set of site conditions is a major objective of the Forestry/Fuelwood Research and Development (F/FRED) Project. Under this USAID-sponsored project, being carried out by Winrock International, a network approach to field trials accelerates transfer of technology to end users.

At present, relatively few scientists are engaged in developing MPT improvement strategies. Those represented in this volume focus on procedures and methods for MPT improvement, ranging from seed collection to multiplication of improved genotypes. The authors present the state-of-the-art in MPT improvement, including descriptions of existing programs, and indicate the direction of future improvement.

With an understanding of the status of existing programs, MPT researchers and other interested scientists can better contribute to improvement programs over a wide range of species. It is hoped that a broad base of support will emerge for improved global breeding programs and for collection and distribution of superior seed.

Foster B. Cady
F/FRED Research and Development Director

Preface

The 1980s marked the rapid rise in tree planting in the tropics for non-industrial uses, reaching almost the same planting rate as for industrial purposes. This includes the planting of multipurpose tree species (MPTS), or non-industrial species, for the production of fodder and fuel, sustainable agriculture, land stabilization, desertification control, rehabilitation of degraded lands, and afforestation of wastelands.

The use of appropriate germplasm is fundamentally important for all of the above tree planting activities. Although it is widely understood that tree species differ in site requirements and uses, the extent of genetic variability within species has been less well appreciated. The vast natural genetic variation found within most MPTs is a resource to be wisely used.

Investments in tree improvement programs have proven to be one of the most cost-effective tree planting activities in temperate countries. Tropical field trials have demonstrated that yields can be increased between 10 and 45 percent by simply choosing the best-adapted seed source for a particular site. Further gains are possible from individual selection and breeding.

Tree improvement is a stepwise process involving exploration, collection, evaluation, breeding, multiplication, distribution, and conservation of genetic resources. *Tree Improvement of Multipurpose Species* has been compiled as an overview of the processes involved. We hope that researchers will be encouraged and guided by it to design successful improvement programs for these important trees.

The volume begins with guidance on the collection of genetic resources for species and provenance/progeny trials, as well as for conservation. Willan, Hughes, and Lauridsen highlight the importance of collecting the greatest possible genetic diversity within a species.

A successful tree improvement program begins by defining the traits that need improving. Glover points out that since MPTs are often planted on marginal sites, emphasis should be on producing trees better suited to stress environments. She outlines selection criteria and methods to improve drought resistance, tolerance to mineral stress and aluminum toxicity, and pest resistance. In another paper, MacDicken and Mehl say that MPT selection and improvement should be based on actual needs and preferences. They report results from a study designed to obtain descriptions of ideal MPTs from small-scale farmers in Asia.

Experiments must be properly designed to obtain reliable results. Matheson reviews experimental design from randomization to nested designs. He points out that designing experiments to assess management x genotype interactions, as well as environment x genotype interactions is an essential component of MPT evaluation.

Following evaluation of genetic resources, superior genotypes are bred to ensure that the best genes are transmitted to the next generation. In his second paper, Matheson discusses various breeding strategies and outlines criteria for choosing one strategy over another. A review of various existing MPT breeding programs is presented.

Lastly, Namkoong discusses the practicality of managing seed orchards to ensure reliable quantities of seed. He argues that decisions on orchard size, thinning, design of breeding-block units within orchards, and border or isolation areas require consideration of breeding objectives as well as seed-production efficiency.

Nancy Glover
Coordinator and Co-Editor
Norma Adams
Co-Editor

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Acronyms

ACIAR	--Australian Centre for International Research
ALPHAGEN	--computer program for generating alpha designs
ALPHANAL	--Alpha design analysis (program for analyzing alpha-desings
ARIMA	--Auto-Regrssive Integrated Moving Average (times series model)
BIB	--Balanced Incomplete Block
BIOCLIM	--Bioclimatic Prediction System
BSO	--Breeding Seedling Orchard
CAF	--Chinese Academy of Forestry
CATIE	--Centro Agronomico Tropical de Investigacion y Ensenanza (Costa Rica)
CCNT	--Conservation Commission of the Northern Territory (Australia)
CFI	--Commonwealth Forestry Institute
CLIMSIM	--Climatic Similarity Programme
CR	--Correlated Response
CRD	--Completely Randomized Design
CSIRO	--Commonwealth Scientific and Industrial Research Organization (Australia)
CTFT	--Centre Technique Forestier Tropical (France)
DANIDA	--Danish International Development Agency
DFSC	--DANIDA Forest Seed Centre (Denmark)
FAO	--Food and Agriculture Organization of the United Nations (Rome)
F/FRED	--Forestry/Fuelwood Research and Development (USAID Project)
HYB	--High Yield Bulk
IADSS	--Information and Decision Support System
IBP	--International Biological Program
IBPGR	--International Board for Plant Genetic Resources
ICRAF	--International Council for Research in Agroforestry (Kenya)
IDRC	--International Development and Reserach Centre (Canada)
ILCA	--International Livestock Centre for Africa (Nigeria)
IUFRO	--International Union of Forestry Research Organizations
LSD	--Least Significant Difference
MIRA	--Manejo de Information sobre Recursos Arboreos
MPT	--Multipurpose Tree
MPTS	--Multipurpose Tree Species
NAS	--National Academy of Sciences (Washington, D.C.)
NFTA	--Nitrogen Fixing Tree Association (Hawaii)
NiFTAL	--Nitrogen Fixation by Tropical Agricultural Legumes (Hawaii)
ODA	--Overseas Development Administration (UK)
OFI	--Oxford Forestry Insitute
PNG	--Papua New Guinea
RCB	--Randomized Complete Block
REML	--statistical package using Residual or Restricted Maximum Likelihood method for estimating variance components directly
SAFE	--Spatial Analysis Field Experiments
SASS	--Scottish Agricultural Statistics Service
SED	--Standard Errors of Differences
SISTEM	--Species Information Seed Trial and Environment Management
APA	--Seed Production Area
TREDAT	--Tree Data (information system)
UNEP	--United Nations Environment Program
UNO	--United Nations Organization (New York)
USAID	--United States Agency for International Development
USDA	--United States Department of Agriculture
ViSCA	--Visayas State College of Agriculture (Philippines)

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Seed Collection for Tree Improvement

R.L. Willan,[1] C.E. Hughes,[2] and E.B. Lauridsen[1]
[1]DANIDA Forest Seed Centre and [2]Oxford Forestry Institute

Most MPTs have been neglected until recently. Seeds of many industrial species, both broadleaved and coniferous, have been introduced and transferred between countries and continents, and programs for their genetic improvement have already started. But the potential contribution of exotic MPTs, with superior properties in nitrogen-fixation, use in mulch and soil stabilization, as well as in producing food, fodder, fuel, construction wood, and shade, has only within the last decade been appreciated. Although the flow of information has increased through species monographs, e.g., on *Faidherbia albida* (syn. *Acacia albida)* (CTFT 1988) and specialist studies on reproductive biology, e.g., of *Acacia nilotica* subsp. *subalata* (Tybirk 1988), scientists still have much to learn about MPT distribution, ecology, genetic variation, and breeding systems.

Much research is needed on the positive and negative correlations between desirable MPT traits. For example, one would hope that a genotype superior in nitrogen-fixation efficiency would also produce superior quality and quantity of fodder. In practice, some desirable traits will be negatively correlated. Thus, a genotype eminently suitable for maximum production of leaf biomass is unlikely also to yield a tall, straight pole. An example is *Leucaena leucocephala*, of which the Hawaiian Giant varieties are preferred for wood production and shrubby varieties with low mimosine content for fodder production (Venkatesh 1988).

Improvement strategies can differ within a single industrial species, such as the long-fiber and short-fiber seed orchards of *Pinus taeda* (for strong packaging papers and fine quality papers, respectively) in the southern United States. Since MPTs have more possible combinations of interesting traits than do the average industrial species, the range of possible improvement strategies are correspondingly greater. After some generations of breeding, one may expect to find, within a given MPTS, a number of distinct populations, each with a single or dominant purpose, e.g., separate seed stands of *Gliricidia sepium* for (a) poles and fuelwood and (b) fodder and green manure. Because of the diverse traits to be improved, MPTs exploration and collection should be planned to include the fullest possible range of genetic and ecological variation. Sample phenotypic diversity, not phenotypic superiority, should be the rule.

Agroforestry presents additional complications. When trees and agricultural crops are grown together, their interaction is as important as their discrete potential. A vigorous genotype that adds $100/ha to the tree yield but causes a loss of $150/ha in agricultural crop yield is no advantage. An additional range of genetic variation may be required to suit the agricultural crop partners and the likely management regimes (Burley 1980).

Reproductive Biology

The reproductive characteristics of species can affect collection strategy. Unfortunately, precise information on the reproductive biology of most MPTs is lacking. Many leguminous MPTs have desirable characteristics when viewed from seed collection. They tend to start flowering at an early age, e.g., one to four years for most *Acacia* spp. (Doran et al. 1983). Under suitable conditions, they bear regular and heavy seed crops, although in areas of low and irregular rainfall there is marked periodicity. For *Acacia aneura*, good crops depend on a suitable pattern of summer and winter rainfall and, on the average, occur less than one year in ten (Doran et al. 1983). The seed-harvest period can be inconveniently short, but may be compensated for by differential ripening dates due to environmental variation. For *Gliricidia sepium*, the harvest period at any one site is typically about 20 days, but the peak can vary from late February at sea level to late April at 950 m altitude (Hughes 1987b). As the collector's experience of phenology

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increases, so the efficiency in planning annual seed collections can be improved.

Most leguminous MPTs have hard-coated seeds that retain viability over a long period, so seed storage presents no problem. Seed collection can, if necessary, be concentrated in good years, when costs per kg collected are reduced and collection from the full range of genotypes, including the normally shy seeders, is possible. A major problem for many leguminous species is the infestation of seeds by bruchid borers, which may destroy the greater part of the crop. Research on the biology and control of this pest and on the practicability of collecting pods while still unripe and uninfested is a high priority.

Most *Leguminosae* are insect-pollinated, mainly by bees. In Kenya, Tybirk (1988) identified six genera of solitary bees pollinating *Acacia nilotica* subsp. *subalata*. Birds and bats sometimes contribute to pollination, e.g., hummingbird pollination of *Erythrina* (Neill 1988). Other important MPTs, such as the *Casuarina* spp., are wind-pollinated. Although few detailed studies have been done, it is thought that most MPTs are strongly self-incompatible and outbreeding. Estimates of natural outcrossing in *Acacia mearnsii* range from 67 to 98 percent (Moffett 1956, Sherry 1971, Doran et al. 1983). Other genera containing strongly self-incompatible species include *Albizia*, *Enterolobium*, *Cercidium*, *Gliricidia*, *Pithecellobium*, and *Prosopis* (Kalin Arroyo 1981; Burley, Hughes, and Styles 1986; Hughes 1987b). Obligate outcrossing occurs in fully dioecious species, which include many *Casuarina* spp.

For many species in the subfamily *Mimosoideae* of the *Leguminosae* family, pollen grains are transported by insects in clumps known as polyads (Guinet 1981). The polyad commonly has sufficient grains to fertilize all the ovules within a flower. Thus, all the seeds within a pod may be full sibs. Studies of this phenomenon in *Acacia melanoxylon* showed that the probability of a single father fertilizing all ovules in a pod was over 0.9 (90 percent), all ovules in a raceme was 0.46, all ovules on one side of the crown was 0.23, and, for different trees in one population, was 0.07 (Muona and Moran 1988). To maximize genetic variation in the seed in such a case, fruits should be collected equally from all sides of the crown.

Many *Leguminosae* have rather large, unwinged seeds. Seed dispersal from the parent tree is limited, with the important exception of those with palatable pods, of which the seeds may be widely distributed by wild and domestic herbivores. Where seed dispersal is limited, regeneration close to a parent tree is likely to contain a high proportion of half-sibs. When this regeneration produces seeds, inbreeding depression can be present in the following generation. The common rule for natural stands is to avoid collecting from a high proportion of half-sibs by having a minimum distance of 100 m between every tree collected. The same applies more so to species that regenerate from root suckers, e.g., *Acacia albida* near the northern limits of its range, where suckers may arise up to 22 m from the parent tree (CTFT 1988, Doran et al. 1983). In such a case, apparently independent trees may have all originated from a common ortet.

For any outcrossing species, a considerable degree of genetic variation is to be expected within a given population. To obtain an adequate sample of this variation, provenance seedlots should be collected from several to many trees. Precisely how many trees may be expected to provide an adequate sample is still largely guesswork. Few studies have been completed, and the optimum number can be assumed to vary a good deal among species and provenances. A common rule of thumb is to prescribe a minimum of 25 mother trees per seed source. This may be difficult to achieve, particularly if a species occurs as widely scattered individuals. Not all individual trees will have good seed crops in the same year. Dry-area *Acacia* spp. often fall into this category, for which Doran et al. (1983) suggest an arbitrary minimum of five trees.

It is important to balance the parent tree contributions to a bulked provenance seedlot. An initial step is to collect the same quantity of fruits from each tree, but this does not take account of variable seed yield between trees. If possible, parent tree seedlots should be kept separate until after seed extraction, then mixed to include the same number of seeds from every parent. The fewer parent trees sampled, the more important it is to balance their individual contributions. For special investigations, it may be desirable to defer mixing until the results of germination tests are known and then mix to obtain the same number of seedlings per parent. But this is impractical as a routine procedure.

Apart from ensuring a balanced parent contribution in a provenance seedlot, maintaining the separate identity ofindividual parents confers the following additional benefits:

- combined provenance and progeny trials can be established for important species and provenances that may give valuable insights into heritabilities and the potential for accelerated genetic gain;

- seed can be used in isoenzyme, chloroplast DNA or phytochemical studies of patterns of genetic variation; and

- if both stand size and seed yield from individual trees are limited, it is acceptable to collect from neighboring trees less than 100 m apart, using seed from one for the bulked provenance seedlot and from the other for the combined provenance and progeny trials.

A few MPTs are known to be self-fertile; *Leucaena leucocephala*, a tetraploid, is one (Brewbaker 1983, 1987). An isolated tree of a monoecious but normally outcrossing species may be forced to develop an increased level of self-compatibility. Where collection is from self-fertile trees, the seed of each tree should be kept separate and the subsequent trials made to compare progeny rather than provenance.

Inter- and intra-specific hybridization occurs in several leguminous genera, e.g., *Prosopis* and *Leucaena* (Burley, Hughes, and Styles 1986). Among the *Acacia* spp., *A. laeta* is considered to have originated as a hybrid of *A. mellifera* and *A. senegal*. Hybridization between subspecies of *A. nilotica* in Pakistan has given rise to wide morphological variation in that country. Vigorous hybrids of *A. auriculiformis* and *A. mangium* have been found in plantations in Sabah (Doran et al. 1983).

Hybridization can be a valuable tool in tree breeding, especially if the desirable characteristics can be maintained through vegetative propagation. The casuarina widely planted in Thailand by vegetative propagation has been identified as a sterile hybrid of *C. junghuhniana* and *C. equisetifolia* (National Research Council 1984). It makes splendid uniform plantations, but would be at serious risk if attacked by pest or disease. The high degree of crossability between species in the genus *Leucaena* is notable. It implies that, provided the hybrids can be successfully propagated, the whole genus can be treated as a potential gene pool for tree improvement. In all cases where seedlots are suspected of hybrid origin, this fact should be noted on the seed origin form so that forest staff handling trial plantings are forewarned of possible aberrant growth in the next generation.

Purposes of Seed Collection

The main purposes of seed collection are evaluation, conservation, and utilization (Palmberg 1985). Since tree improvement programs with most MPTs are still at an early stage, this paper concentrates mainly on seed collection for species and provenance trials--that is, for evaluation of comparative performance at the population rather than individual level.

Two other types of collection that may require urgent action at an early stage are (1) collection for the *ex situ* conservation of provenances seriously endangered in their natural range and (2) collection for research on the seed biology of an otherwise promising species in which seed viability is a serious problem, e.g., *Azadirachta indica*.

Seed collection for large-scale tree planting programs is not directly related to tree improvement but likely affects it indirectly in the long-term. A country that has identified one or more exotic superior provenances for local conditions may wish to import seed in bulk for large-scale plantings. Whether in fuelwood blocks or agroforestry rows, the plantings will form the basis for selecting individuals and breeding material for the continued improvement of subsequent generations. If bulk seed supplies are not available, it may be necessary to import enough seed for the establishment of local seed stands (10-20 ha) and use seed from these stands for later large-scale planting. Both the bulk seed for planting and the semi-bulk seed for the seed stand contribute to the introduced populations that will provide the genetic base for a national tree improvement program.

Seed Collection and Evaluation

In the manual on species and provenance research (Burley and Wood 1976), a full, idealized

sequence for species and provenance trials was conceived as comprising the following phases:

- arboretum,
- species elimination,
- species testing,
- species proving,
- rangewide provenance,
- restricted provenance,
- provenance proving,
- pilot plantations, and
- commercial plantations.

The authors noted that the complete idealized sequence is rarely practiced (Burley, Wood, and Lines 1976); more often, one or more phases are omitted, combined, or overlapped. In the last decade, a trend towards simplification has been emphasized and is applicable to MPTs.

In this paper, species trials correspond to the species-testing phase of Burley, Wood, and Lines (1976); they provide useful comparisons of survival, health, and growth up to half rotation age. Both arboretum and elimination phases may be omitted, provided that the number of species is limited by a meticulous matching of environments and end uses. On the other hand, it may be permissible and desirable to include more than one provenance in species trials with an especially favorable prognosis, treating the provenances as if they were separate species (see section below, "Seed Collection for Species Trials").

Provenance trials, as defined here, correspond to the rangewide provenance phase of Burley, Wood, and Lines (1976). It is assumed that many countries will wish to proceed directly from successful rangewide provenance trials to the establishment of seed stands using the best provenances and to genetic improvement through individual selection. They will be prepared to omit restricted provenance trials, whereby stands in the general area of the best provenances identified in the rangewide provenance trials are sampled at closer intervals.

Provided that the rangewide trials are based on efficient sampling of the species genetic variation, the additional stage of restricted trials may well be superfluous. For example, in a situation where (1) rangewide provenance trials give 15 percent gain, (2) restricted provenance trials give an additional three percent gain but take at least five years, and (3) individual selection and progeny testing give an additional 20 percent gain, it is preferable to forego the three percent gain from (2), saving five years, and proceed directly to the individual selection of (3), which will yield 20 percent.

A strong case for supplementary trials may, however, arise if the rangewide collections fail to sample a significant portion of the genetic variation of the species. This may result from inadequate knowledge of new MPTS or because known areas are inaccessible for physical or political reasons. If the missing provenances become available later, the subsequent supplementary trials could well yield more valuable results than the incomplete provenance sets of the initial trials.

It is possible to simplify the evaluation phases further by combining species and provenances in a single set of trials. The practicability of doing this depends on the number of species and provenances involved. If using a few well-known species on similar sites, it may be possible to include a number of provenances of each. For example, fuelwood trials in a dry, tropical climate might combine six provenances each of *Cassia siamea*, *Azadirachta indica*, and *Eucalyptus camaldulensis*. As the number of species or provenances increases, the size of the trial becomes excessive and soil heterogeneity introduces an uncontrolled source of variation into the experimental data. When seed is available of 25 to 30 species, as from Central America (Burley, Hughes, and Styles 1986), and of 25 to 30 provenances of just one of them, *Gliricidia sepium* (Hughes 1987b), it becomes essential to separate species and provenance trials. One source-identified provenance per species is then normal in a species trial, with a maximum of three (see section below).

Seed Collection for Species Trials

International and intercontinental transfer of MPTS seeds is a recent concept. Only a few species, including *Gliricidia sepium* and *Leucaena*

leucocephala, have spread worldwide. Some of those introductions were from a narrow gene pool. Moreover, the early introductions resulted more often from casual selection, e.g., as ornamentals, than from systematic investigation of the full potential of a species. Thus, the spread of *G. sepium* rather than *G. maculata* and of *L. leucocephala* rather than other species in the genus was due to historic chance, not innate superiority.

For many MPTs, therefore, species exploration and species trials are the essential first steps in any genetic improvement program. Exploration and seed collection of one useful species frequently lead to the identification of others. Thus, among industrial species, extensive collections of *Pinus caribaea* in Central America led to an increased awareness of the importance of *P. oocarpa* (*sensu lato*) and then to the differentiation of *P. patula* var. *tecunumannii* as a separate taxon. Similarly, *Leucaena* collections have led to the discovery of a new taxon in Southeast Guatemala (Hughes 1986) and *Gliricidia* collections to recognizing the potential value of the closely related *Yucaratonia breaningii* (Hughes, in press).

The number of MPTs involved may be large. The FAO/IBPGR/UNEP Project on Genetic Resources of Arid and Semi-arid Zone Arboreal Species for the Improvement of Rural Living coordinated seed collection of 43 species (including 20 *Acacia* spp. and 15 *Prosopis* spp.) from 11 countries in Africa, Asia, and America (FAO 1988). In Central America, the OFI/ODA Programme on Tropical Hardwoods for Dry and Semi-arid Zones included 25 MPTS initially (Hughes and Styles 1984) and was later expanded to 27 (Burley, Hughes, and Styles 1986). Brewbaker and Styles (1984) listed 43 economically important nitrogen-fixing tree species. Boland and Turnbull (1981) listed many Australian, non-eucalypt species with fuelwood and multipurpose potential in the tropics (36 for the humid tropics, 35 for the tropical highlands, and 40 for arid/semi-arid regions). Of these, 12, 7, and 6, respectively, were considered high priority for seed collection and testing overseas.

In 1984, joint seed-collecting operations of CSIRO (Canberra), CTFT (France), and CCNT (Northern Territory) had made available for international trials seeds of 62 arid/semi-arid species (45 of them *Acacia* spp.) from Northern Australia (Thomson and Cole 1987). Later revision of the Australian list reduced the number of preferred species but it still contains 100 species, including 54 acacias and 8 eucalypts. The total number of MPTs appearing in the various lists must run into the thousands. It is a formidable task to select the most promising species for exploration, let alone explore and collect them.

The many species of potential value, little known and sometimes closely related, make essential early involvement of experienced taxonomists in the exploration and collection phases. Especially in the neotropics, major MPT genera suffer from a severe lack of taxonomic revisions. Not only is there no stable taxonomy to follow but new taxa in these genera are still being discovered, e.g., *Calliandra* and *Leucaena* (Hernandez and Sousa 1988, Hughes 1986). Natural hybridization and the occurrence of intermediate forms are not uncommon among MPTs, e.g., in *Acacia*, *Cercidium*, and *Prosopis* (Ebinger and Seigher 1987, Leach and Whiffen 1978, Carter 1974, Hunziker et al. 1986). This makes careful taxonomic studies still more important.

Identification of seed sources is essential, even at the stage of species trials. No longer acceptable are haphazard supply standards, where seed was identified only to species, information on precise origin was lacking and, in some cases, the seed may have been a bulked mixture of several disparate sources. Likewise, the need for accurate and detailed description of ecological conditions applies no less to species than to provenance or seed-source trials. Using seed of unknown origin is of little value in establishing trials comparing species X with species Y, especially if both are widely distributed over a range of environments. The comparison should be between clearly identified sources of each species. If the seed source of the best performers is known, further collections from the same seed source can be arranged. The results will also help guide the planning of subsequent provenance trials of the successful species.

If a single provenance is to be used, it should usually come from an area where the species reaches its finest development (Edwards and Howell 1962). This is commonly near the center of its natural range. This strategy may be altered to suit the range of sites over which the species is to be tested. In Central America, seed collection under the OFI/ODA Programme on Tropical Hardwoods

for Dry and Semi-arid Zones was designed to supply MPTs suitable for dry-zone planting. Provenances from the drier parts of the species range were favored (Hughes and Styles 1984). At this stage, care should be taken to collect from apparently natural stands and to avoid manmade plantations within the natural range. The latter may, however, play an important role in the later stage of provenance trials.

Because so many MPTs are widely distributed and less known, extensive sampling of provenances is better delayed until fewer promising species can be studied more thoroughly through provenance research. Single collections of little-known species may, however, be combined with collection of several provenances of better-known species (*Acacia aneura* in Australia, *Leucaena leucocephala* in Central America). Thus, the Australian collections described by Thomson and Cole (1987) were mainly of single seedlots per species, but for several species there was more than one seedlot.

Edwards and Howell (1962) suggest a rule of three provenances when introducing a well-known species to a new site, to include a range of provenances: (1) the closest environmental match to the new site, (2) the area where the species reaches its finest development, and (3) a provenance that extends the range sampled in an important direction. Although MPTs are little-known, it is still worth considering the potential of category 3. MPTs often play an important role under harsh conditions. The range should extend into more difficult environments than average for the species, e.g., a calcifuge ecotype in an otherwise calcicole species or an isolated occurrence in much drier-than-average conditions for the species.

In practice, constraints of time, finance, and access usually determine how much can be collected and, equally important, evaluated. Often one representative sample from the middle of the species range can be considered adequate. On occasion, a single provenance may give a misleading impression of the species' potential. In the OFI collection of *Prosopis juliflora* for the trials of Central American dry-zone species, the Honduran provenance proved to be an unusual form with an initially prostrate growth pattern, quite unlike the form previously and successfully introduced into India. Had the prostrate form been the first introduced into that country, the entire species might well have been eliminated from further consideration.

Such cases are rare and can usually be corrected in the subsequent phase of provenance trials, provided there is an effective international system for communicating information. Exploration and seed collection of species and provenances should be considered a continuous, integrated process. Experience gained during the species phase will assist in the efficient planning of the provenance phase.

Since species trials are to be conducted with the seed source clearly identified, the same prescriptions should be followed for numbers of parent trees, distance apart, etc., as in the case of provenance trials (see section below).

Collection for Provenance Trials

Provenance trial results have shown that much genetic variation exists at the infraspecific level. For tropical industrial species, volume yields of the fastest growing provenances commonly exceed the average by 5 to 15 percent. For species with an extensive range covering a rich variety of environments, the difference may be more than 20 percent, whereas gains as low as two or three percent are likely to cover the cost of the research needed to identify these provenances, assuming normal interest rates and a fairly substantial planting program (Willan 1988).

Although many provenance trials of MPTs are still at an early stage, there is already evidence that variation is likely to be no less than for industrial species. Several authors have reported results for *Gliricidia sepium*. In Ibadan, Nigeria, some newly introduced Central American provenances outperformed the local, earlier introduced source (Atta-Krah 1987). The mean of the four best among the new introductions showed 45 percent greater height growth than the "Ibadan local" at six months and 28 percent greater after one year, while the biomass yield over seven pruning harvests averaged 32 percent more.

In the Philippines, as in Nigeria, the new introductions were superior to the local land race, which was the slowest growing of any under trial. After two years, the best introduced source had over 60 percent greater height growth and over 75

percent greater diameter growth than did the Philippines source. Results of trials in the Philippines, Hawaii, and Costa Rica indicated that, in general, the same provenances appeared among the best performers as at Ibadan (Bumatay, Escalada, and Buante 1987; Glover 1987). Some sources were more sensitive than others to variation in site quality; thus, seedlots ILG 1 and 8 were consistently good over a range of sites, while ILG 14 performed relatively better on good sites than on poor ones (Glover 1987).

The four best provenances identified in the above trials were planted together in a seed stand, and the seed collected from it was designated as High Yield Bulk (HYB). Subsequent trials tested HYB against the range of *Gliricidia* provenances collected by OFI (Atta-Krah 1990). Results confirmed the considerable variation between provenances, the best in terms of dry fodder productivity being twice as productive as the poorest. HYB was among the best performers but was less productive than several of the OFI provenances, notably ILG 55 (CFI 14/84) from Guatemala.

Results in Sierra Leone (Amara 1987) showed that height growth and fodder production are not always closely correlated. ILG 63 (CFI 31/84) yielded 49 percent more fresh fodder than ILG 62 (CFI 30/84) at one year, although the height growth was almost identical (1.78 m versus 1.77 m). In one trial at Ibadan, Nigeria, ILG 58 (CFI 17/84) proved to be the poorest provenance in height growth, below average for wood production, but the highest yielder after HYB for dry-leaf matter production (Atta-Krah 1990). Final choice of provenance clearly depends on end uses best suited to local needs.

Any genetic improvement program for a promising MPTS must involve research into heritable variation between provenances or populations at an early stage. Not only will the identification of superior provenances for local conditions confer a direct benefit through immediate use in operational planting, but will provide a surer genetic base than inferior provenances for additional gains through individual selection and breeding. Some guidance on an appropriate strategy of seed-source sampling is given below.

Morphological Variation

Taxonomy can sometimes help distinguish not only closely related species but also infraspecific variants. A good example is the differentiation within some *Acacia* spp. Nine named subspecies of *A. nilotica* and four named varieties of *A. senegal* have been recognized, while there are two unnamed but well-marked geographical races of *F. albida* (Brenan 1983). A prostrate form of the Australian *A. ampliceps* is potentially usable as an ornamental ground cover, which differs from the typical fast-growing, small tree valued for fuelwood and fodder production in the wet/dry tropics (Thomson and Cole 1987).

The distinction between the spineless *Prosopis* var. *inermis* and the spinescent *P.* var. *horrida* is significant for the management and use of this species. Such clear morphological variants that show promise should be sampled separately. Large, infraspecific variation can occur in seed size. In Australia, nine provenances of *Casuarina cunninghamiana* had a range of 1.3 to 3.1 million seeds per kg (Turnbull and Martensz 1983). Recognizable differences of this type are not necessarily associated with differences in economic or social value.

Important differences in physiological characteristics, such as growth rate or drought resistance, which have been revealed in provenance trials, cannot always be associated with detectable differences in morphology. Where morphology gives no guidance, ecology may help.

Ecological Variation

In the absence of distinguishing morphological features or of genetic differences demonstrated by earlier provenance trials, provenance seed collectors must rely on their ability to detect environmental variation within the range of target species. They must assume that it is reflected in a corresponding genetic variation due to the ability of populations, over a period of time, to adapt to their habitats, i.e., that the influence of natural selection, working on random mutations within the local gene pool, outweighs that of gene flow from external and distinct populations to produce a gene pool well-adapted to the specific habitat in which it occurs.

The strategy for exploration and collection is therefore to seek seed-source areas with apparent environmental differences and to sample each separately. This contrasts with the homoclime strategy for preliminary selection of species/provenance for planting, which seeks environmental similarities (see section below, "Seed Storage and Distribution," p. 28).

For a little-known species, the first step in assessing the pattern of environmental variation is often to determine and map the natural distribution. Good examples are the recent distribution maps for *Gliricidia sepium* (Hughes 1987b) and *Acacia mangium* (Nicholson 1981). Maps become still more useful if isohyets, isotherms, or elevation contour sand soil-type boundaries are included or superimposed. The combination of natural distribution and environmental parameters can lead, in turn, to delimiting seed collection zones, which are commonly a compromise between the ideal system of climate and soil and the practical problems of access and communications. Frequently, they are related to major physiographic systems, e.g., *Pinus caribaea* and *P. oocarpa* in Honduras (Robbins and Hughes 1983). Since there is commonly little knowledge about variation patterns at the time of seed-source collections, sampling can be done at rather widely separated intervals.

For flat land, a sampling grid can be adapted to the clinal type of environmental variation expected, e.g., a gradual increase of temperature from poles to equator or a gradual decrease in rainfall from coast to interior. Where sharp discontinuities occur, e.g., sudden changes in soil type or elevation, the intensity of sampling must be increased to detect, from subsequent trials, any associated genetic variation between neighboring populations. Geographic proximity does not always signify genetic identity.

Although genetic diversity within populations is generally largest in areas optimal for the development of the species, at the limits of its range outlying populations may be exposed to extreme temperature, rainfall, or edaphic conditions. Such populations may possess adaptive characteristics of great potential for particular environments. For this reason, peripheral and isolated populations should be included among those sampled (Turnbull 1975b, Palmberg 1985).

Dyson (1974) recommended for *in situ* conservation five separate populations: one central, representing optimum growth and variation, and four peripheral (or isolated), representing extremes of specialization to environmental limits (altitude, rainfall, latitude, etc.). This is also a useful guide to the absolute minimum number of provenances in first-stage trials. For species known to have extensive and ecologically diverse ranges, considerably more are advisable. Recent examples are 29 provenances of *Gliricidia sepium* (Hughes 1987b), 12 of *Acacia aneura* (Midgley and Gunn 1985), and 21 of *Eucalyptus microtheca* (FAO 1979).

Seed-source sampling is usually guided by climatic and physiographic features rather than by soil variation, but sudden and marked changes in soil type or geology may call for additional sampling. Vegetation is sometimes a valuable guide to site conditions since it should result from all environmental factors. It is important, however, to distinguish between long-term, natural and short-term, manmade factors.

A particular problem for many MPTs is distinguishing between truly natural populations and those moved within or close to the natural distribution. *Gliricidia* is a good example. It has been used, cultivated, and transported by people over many centuries in Central America. This makes its true natural range uncertain and has also created numerous land races through cultivation (Hughes 1987b).

No matter what system of sampling is used during the exploration and collection of seed sources, it is essential to record adequate information on each seed source, both the site and the trees (see, e.g., Appendix). Ideally, a set of forms for a species should convey the rationale for the collection strategy and indicate the pattern of environmental variation that has been sampled.

Natural Provenances and Land Races

People have been moving plants and plant seeds for thousands of years. Over a number of generations, a successful introduction adapts to the new site and may become physiologically or morphologically differentiated, both from the original source population and from other

populations of the same origin but introduced and adapted to different ecological sites. These are variously known as land races, naturalized provenances, or second-, third-, etc. generation, introduced populations. For example, the tentative distribution map of *Gliricidia sepium* shows a natural distribution area along the Pacific coast of Mexico and Central America, which is greatly exceeded by the extent of the introductions in the same region (Colombia and Venezuela northwards to Mexico, Cuba, and Florida) (Hughes 1987b).

When one moves seed within or near the natural range of a species, it is often difficult to know whether a particular population is natural, introduced, or both. This is particularly common for MPTs, which have been well-known and widely cultivated by generations of peasant farmers. Human interference in native gene pools takes distinct forms, which may affect seed-collection strategy:

- Active spread and cultivation outside the native range. For some species, this may lead to naturalization after a number of generations. This can involve (1) no selection (unlikely), (2) unconscious selection, e.g., vegetatively propagated land races of *Gliricidia* have almost undoubtedly been selected unintentionally for ease of propagation by stakes, or (3) deliberate selection or incipient domestication. Good examples are *Prosopis* (Felger 1977) and *Leucaena* (Zarate 1984). These selection pressures and gene-pool changes may have occurred over a long time. For example, *Leucaena esculenta* has been cultivated for over 3,000 years in the Tehuacan Valley in Mexico (Smith 1967).

- Passive changes through alteration of natural populations following extensive human disturbance and forest clearance. This has several effects: (1) loss of genetic resources as some populations are destroyed, (2) isolation of previously genetically linked populations, and (3) extensive spread of some aggressive colonizing species. Many MPTs fall into this category and have become dominant elements over large tracts of secondary and ruderal vegetation. This spread is often fast and may be accelerated along roads or domestic livestock routes. This greatly alters population structures. Large pure or mixed stands of species now occur that might have previously been restricted to natural disturbance sites (landslides, riverbanks, coasts). *Gliricidia* is a good example. It now covers vast tracts of mesic Central America and Mexico, but was probably only natural on freely drained, rocky sites as a sparse canopy tree in dry, deciduous tropical forests. Some of these new, large populations may have restricted parentage, which affects seed-collection strategy and interpretation of provenance-trial results.

C. Hughes

Gliricidia *densely colonizes extremely rocky slopes in Guatemala as a result of forest clearing.*

One can assume that, when a natural forest has established itself on a site and regenerated over a number of generations, the local seed source should be best adapted to the local site conditions. An important distinction must be made between a local seed source that is (1) natural and therefore (after generations of natural selection) well-adapted to the site and (2) of an introduced provenance on which local selection pressures have been operating only a short time (sometimes less than a full rotation). Such recently introduced sources are usually less adapted to the sites on which they are growing. After a number of generations, an introduced species or provenance grades into a naturalized one, and may be as well-adapted to local conditions as a truly indigenous one. Examples of species naturalized outside their natural range are fairly common, e.g., teak in Indonesia, *Casuarina* on tropical coasts, and ornamentals worldwide.

Neem (*Azadirachta indica* A. Juss.) is another species that has been used for ages, mentioned in ancient Sanskrit literature (Radwanski 1977). Its natural distribution is difficult to ascertain. Thus, some reference books restrict it to "the drier parts of Burma and India," while others add Pakistan, Sri Lanka, Thailand, Cambodia, Malaysia, or Indonesia. Troup (1921) considered neem in India indigenous only to a limited extent. During the reign of the Emperor Asoka in the third century B.C., extensive roadside plantings to provide shade for travellers were prescribed (Murthy 1980). Through the Buddhist missionaries he dispatched to neighboring countries (notably Burma and Sri Lanka), Asoka may well have encouraged international transfer of neem seed.

In Thailand, two taxa of *Azadirachta* are found. *A. indica* var. *siamensis* A. Juss is distributed widely throughout the country at altitudes below 200 meters. It has well-defined boundaries towards west and north, but extends into Cambodia, and possibly into Laos to the east. It extends south on the peninsula to about the ninth northern parallel. The densest populations occur on termite mounds and ridges in paddy fields. It occurs, though sparsely, in the dry dipterocarp or mixed deciduous forests, and it does not occur in the moist deciduous or evergreen forests. This variety is more robust than the typical variety found in India. It is unclear whether the occurrence in Burma is the *siamensis* variety or type.

E.B. Lauridsen

A. indica *var.* siamensis *growing in rice fields in Nakhon Sawan, Thailand (Khao Luang provenance, not planted)*

E.B. Lauridsen

A. indica *var.* siamensis *in dry dipterocarp forest in Kanchanaburi, Thailand (Ban Nong Hoi provenance)*

A second taxon is found in the southern peninsula from Malaysia and up to around the ninth northern parallel, where it grows to a large tree generally in villages and farmed areas. Its occurrence in the forest has not been verified, but the species is frequently confused with *Chukrasia velutina* Wt. & Arn. (syn. *Chickrassia fabularis* A. Juss; *Chukrasia fabularis* A. Juss), which occurs sporadically in the moist forests on the peninsula. The taxon has recently been verified as *A. excelsa* (Jack) Jacobs (syn. *Melia excelsa* Jack; *M. integrifolia* Merr.). Other than the above two taxa, the type occurs sporadically along the coast of the Gulf of Thailand, in temple yards and rarely in villages. It was introduced, probably at the beginning of this century, for its medicinal properties. The local name is Quinine, and a leaf extract is used as a cure for malaria.

The distribution of *Azadirachta indica* var. *siamensis* in Thailand has clearly been influenced by man. Most villagers interviewed during surveys in 1988-89 stated that neem normally establishes itself and is rarely planted. The species occurs sporadically in natural forests and is propagated rapidly when people clear the forest. Fruit bats are largely responsible for spreading the fruits. It is not known whether the species entered the forest

E.B. Lauridsen

Sixteen-year-old A. excelsa *planted in fruit orchard in Nakhon Si Thammarat, Thailand*

E.B. Lauridsen

One-year-old A. excelsa *planted along farm boundary in Nakhon Si Thammarat, Thailand*

from previously cultivated fields or originated in the forest. In any case, the spread seems to have been gradual, and may be considered similar to a truly natural process of extension of existing populations.

Man's contribution seems to have been to pave the way through forest clearing and land preparation, and to leave the naturally regenerated trees undisturbed once they appeared. It is thus probably justified to consider most existing neem populations as natural ones that have evolved relatively slowly. Recently, however, improved communications and large-scale, roadside plantings have caused the movement of neem seed over long distances. In these areas, the natural population may be mixed with introduced provenances of unknown origin.

Another species widely spread outside its natural range is *Melia azedarach*, commonly known as White Cedar, Persian Lilac, or Bead-Tree. The wild form, White Cedar, occurs as a forest tree up to 40 m tall, mainly in seasonal rainfall forests, from India and Nepal through Southeast Asia to Papua New Guinea, the Solomon Islands, and tropical Australia. The ancient, cultivated forms are considered either Chinese cultivars (China and Japan) or Indian cultivars (India, Iran, and Middle East) (Mabberley 1984). More recently, the Indian cultivar (Persian Lilac) has spread to Africa, Europe, and America. Mention is made of the Chinese cultivar in Chinese literature of 300 B.C. (Mabberley 1984), while Persian Lilac is mentioned in an inscription of the Assyrian king Assurnasirpal II at Nimrud dated at about 879 B.C. Such records confirm the antiquity of man's influence on spreading useful species.

Assumed land races within or adjoining the natural range should be sampled at the same time as natural provenances. As much information as possible should be recorded on the history of their introduction, especially on whether seed came from one, a few, or many parent trees; how ecologically distinct was the place of origin; how many generations have passed since the introduction; and (as for natural provenances) the degree of isolation from other stands.

In addition to genetic-base criterion (narrow if seed was introduced from one or a few mother trees to an isolated site, broad if seed came from many mother trees or the stand is open to unrestricted pollen invasion from neighboring stands), introductions may be characterized by degree of adaptation. Of the infinite possible number of gradations, some of the most distinctive examples are:

- a recent introduction from a different environment, likely to be ill-adapted to its present site but adaptable to any new site resembling its place of origin;

- successful over several generations with the gene pool now likely well-adapted to the new site but still retaining some genes that are "neutral" for the new site, possibly of selective advantage on sites similar to the place of origin; or

- fully naturalized as a result of adaptation and gene flow from neighboring stands over many generations. The naturalized seed source is indistinguishable from the natural one; as a source of genetic material, one is as valuable as the other.

Land races occurring outside the species' natural range, after previous introduction as an exotic, should be given special attention in the strategy of seed-source sampling. Many early introductions of MPTs were casual trials of what happened to be available. They sometimes lacked identification of the seed source, often from a narrow genetic base, sometimes a single tree (Hughes and Styles 1984). They may have been from a poor provenance or inbred. This view is supported by the poor showing in comparative trials of early introductions of *Gliricidia sepium* into Nigeria and the Philippines (Atta-Krah 1987; Bumatay, Escalada, and Buante 1987). The locally introduced seed source should always be included in trials as a sample of the seed available for plantation establishment. Only if its good performance has been demonstrated in local trials should it be considered for collection and distribution for international trials elsewhere.

Second-generation plantations from introduced seed have often shown superiority over the first generation of apparently the same origin. This has been ascribed to the possibility that:

- In natural forest of a species with limited seed dispersal, many neighboring young trees are likely to have arisen from the seedfall of a single mother tree and are half-sibs.

- When these trees mature and flower, a high proportion of the pollen reaching the female flowers will be from the nearby half-sib fathers. When seed is collected from them and dispatched for introduction to other countries, it will produce a first generation of reduced vigor because of inbreeding depression.

- If the seed collected is bulked and each bulk seedlot is constituted by a minimum of 25 trees at a minimum spacing of 100 m, genetic variability of the bulked seed will increase significantly over the seed from any one mother tree. This seed will give rise to a number of families; each individual family may be less vigorous due to inbreeding, but is not closely related to any other family.

- When the first introduced generation matures, much pollination will be between unrelated families. The increased outbreeding will confer heterotic vigor on the second generation. It can be expected to grow better than either its own parents, the first introduced generation, or any other first generation introduced from seeds collected in the same way from the same natural stands.

Increased vigor of the second generation in a new introduction, due to outbreeding, can be expected whatever the management regime. Management is often significantly more intensive in industrial plantations than in natural stands. For example, in a commercial plantation designed to produce sawlogs, the stocking per hectare is commonly reduced by maturity to about a quarter of the stocking when planted. In a seed production area, the fraction is about one tenth. The removal of the poorer phenotypes should increase genetic improvement in the next generation. Improvement through deliberate thinning is less likely in MPTs. Fuelwood plantations are usually managed on a short rotation, without thinning, using a clearfelling regime, while agroforestry row plantings are kept at close spacing. But natural selection can still be expected to eliminate some of the poorer-adapted genotypes in each generation.

Because exploration of genetic diversity in most MPTs is still at an early stage, most attention needs to concentrate on provenances within the natural range and within the ancient land races that are

often hard to distinguish from them. Seed collection from more recent land races, of which the history is better known (e.g., neem in Africa), may be considered where they adapt to site types differing from those of the natural provenances. As the most successful and versatile MPTS become established in new countries and on new sites, the potential contribution of these new land races to the global gene pool of the species will increase. When selection programs, breeding, and the creation of seed stands and orchards start to have an effect, the land race will, in turn, tend to be superseded by the genetically superior seed source.

Diversity versus Superiority

Tree improvement, in the broad sense, covers both the selection of populations (species, provenances, seed stands) and the selection and breeding of individual trees within populations. Selection/breeding of individuals involves identifying trees of a superior phenotype, testing their offspring in progeny trials to confirm the genetic superiority of the parents, and bringing together tested superior genotypes for seed production, to which both male and female parents contribute their superior genes. The economic benefits of this approach for industrial species are well-documented (Hollowell and Porterfield 1986, Stier 1986, Willan 1988, Hodge et al. 1989). There is every reason to expect no fewer benefits from individual selection in MPTs. Presently, no foresters or tree planters should be content to plant source-identified seed if they can obtain genetically improved seed of a well-adapted provenance.

Thus, selection for individual phenotypic and genotypic superiority is essential in the later stages of a tree improvement program. The case for selecting superior phenotypes (information on genotypic superiority is usually lacking) at the stage of investigating species/provenance in MPTS is much weaker. At issue is the extent to which phenotypic (or genetic) superiority in one area can be maintained in another. The same care is needed in matching a superior seed source to a planting site as in matching a locality-identified seed source. Naturally superior and man-improved exotic seed sources need to demonstrate their local adaptability no less than unimproved ones, and exotics comprise ecological rather than national foreigners.

No strict rule is used to choose between "best adapted" and "genetically superior" seed sources. Each case must be judged on its own merits. The hypothetical examples that follow illustrate the kinds of choices that have to be made.

(1) Country X has evidence that the seed source of *Eucalyptus camaldulensis* best adapted to its environment is a pronounced summer rainfall source, such as Petford. No improved seed sources of this provenance are available, but tested orchard seed is available of a pronounced winter rainfall source, such as Lake Albacutya, which has demonstrated in winter rainfall conditions a substantial genetic improvement over other such seed sources. Local adaptation should be preferred to an improved source of an unsuitable provenance. In fact, selection and breeding for improved performance under winter rainfall conditions is likely to have made this seed orchard seed even less well-adapted to Country X than the original, unimproved winter rainfall source. Country X should continue with unimproved Petford until it can develop its own seed production areas and seed orchards of this provenance, or obtain its seed from improved sources elsewhere, which have been developed under similar environmental conditions.

(2) Country X has selected a provenance well-adapted to local sites. It has not yet developed its own improved seed sources, but neighboring Country Y has available seed of the same provenance from orchards grown on sites virtually identical with the planting sites of Country X. Country X need not hesitate in using the seed orchard seed available from its neighbor. A similar example is using *Cupressus lusitanica* seed from the Elburgon (Kenya) seed production area on montane sites in Tanzania and Uganda.

(3) Country X is about to start a series of seed-source trials with *Pinus caribaea* but has learned that genetically improved seed from one source, Mountain Pine Ridge, is available from Queensland, Australia. Should it forego the provenance trials and proceed with a full-scale planting project using only improved Queensland seed? Country X should continue with the provenance trials but include the improved Queensland (and any other promising) land race with the seed sources from within the natural range. Only if the Queensland source proves its adaptability under Country X conditions should it be adopted for major planting schemes.

Generally, it is advisable to demonstrate the local adaptability of any seed source first and only later seek genetically superior individuals within the adapted population(s). A superior phenotype in natural forest may be superior because of a favorable microclimate. Even if it is genetically superior under conditions of the natural forest, genotype/environment interaction may prevent its offspring from showing phenotypic superiority on a new site.

Favoring diversity over superiority is limited, however. Seed cannot be collected from a randomly selected tree if it bears no seed. Common sense would deprecate the sampling of diseased, deformed, or suppressed trees even if they did bear seed. IUFRO has provided convenient guidelines for industrial species: "collect from not worse than dominant and co-dominant trees of average quality" (FAO 1969).

For MPTs, random sampling to collect the greatest possible genetic diversity is still preferred over selective sampling from a narrow range of "candidate plus trees." Recognizing multipurpose phenotypes with a combination of superior traits is often impossible. While visual assessment of stem straightness and diameter growth presents little difficulty to an experienced assessor, no instant methods measure efficiency in nitrogen-fixation or palatability and nutritional value of foliage. Thus, the best seed collection strategy is to sample over as wide a geographic area as possible, including sites at the environmental extremes, and switch the emphasis on studying patterns of genetic variation to the field evaluation phase where conditions are relatively controlled (Hughes 1987b). In this way, countries will judge superior adaptability in relation to local sites and superior end-use characteristics in relation to local needs.

Most seed collected within a given seed source is bulked to form a provenance seedlot; seeds from individual mother trees are not distinguishable. In some cases, a proportion of seed from individual trees may be kept separate to maintain parent tree identities within provenances. This has been done in recent collections of *Gliricidia sepium* (Hughes 1987b) and makes possible a series of early combined provenance/progeny trials. Since these trials need a more complex layout and more careful supervision than simple provenance trials (especially if conducted as alley-cropping trials), they are best undertaken by well-staffed institutes capable of sustaining a fundamental research project over a period of years. The results, however, will benefit many countries because the gain from every individual selection and breeding program is related to the level of genetic diversity within the population. The more variable the population, the greater the benefit from tree improvement.

For many MPTS, seed-collection operations will continue to emphasize species and provenances for some years. As countries identify from evaluation trials the provenances best suited to their various site types and establish seed stands or larger-scale plantings of these provenances, seed collection will progress from source-identified to genetically improved stands or seed orchards. Improved seed will become available from widely separated sources. At this time, similar dilemmas between local adaptation and genetic superiority may arise. Should scientists, for instance, prefer seed from their best phenotypes, selected at an intensity of 1 in 50 and not yet tested by progeny trials, or seed from a progeny-tested seed orchard in another country, where trees were selected at an intensity of 1 in 1,000, have shown 20 percent genetic superiority to standard unimproved seed sources, but are in an environment different from the proposed planting site? Each case should be judged on its own merits, based on: (1) similarity or dissimilarity of site environments, (2) genetic superiority and its relation to required end uses (superior wood production on site A is irrelevant to site B if the purpose of planting at B is foliage production), and (3) relative seed cost.

Generally, it is wise to ensure that at least two-thirds of seed used for operational planting should come from the appropriate silvicultural zone within the same country. If in doubt, one should choose local adaptation over non-local superiority. Ultimately, any country with substantial tree-planting programs will aim to develop its own land races well-adapted to local conditions and within them to select and breed superior individual genotypes. The bulk of all seed will be home-produced, although reproductive material of the best genotypes will be exchanged internationally for use in the appropriate environment.

Seed Collection for Conservation

Exploring the natural range of a species for provenance research often reveals that some

populations are seriously endangered through destruction of their habitat. Not only provenances, but some whole taxa of valuable MPTS are endangered. For *Leucaena*, the unnamed Guatemalan taxon has been reduced to a few hundred individuals (Hughes 1986). Where conservation *in situ* cannot be guaranteed, it may be necessary to collect seed to establish gene conservation stands elsewhere (Bouvarel 1970, Kemp 1976).

Collection strategy is similar to that for provenance trials, with the following exceptions:

- Total quantity of seed collected will usually be larger. The minimum area for a single conservation stand is commonly estimated at 10 ha per site, compared with about one-quarter ha per provenance per site in a provenance trial. If there is danger of imminent loss of the population, seed reserves should also be collected for conservation in controlled storage seed banks.

- To obtain the larger quantity of seed needed, it will usually be necessary to collect from more trees. This is desirable, in any case, to capture as much total genetic variation as possible. A minimum range of 50-100 trees has been estimated (Nikles 1974, Marshall and Brown 1974).

- Random sampling must be strictly enforced. Poorer-than-average trees should be included whenever selected by random sampling. The purpose is to capture the full range of genetic variation in the stand. The only restriction is the impossibility of collecting from trees that bear no seed.

- To increase genetic diversity, seed should be collected in a better-than-average year. A heavy seed year usually signifies that a high proportion of male parents have contributed pollen, and a high proportion of females contributed seeds.

Many MPTS are well-suited to *ex situ* conservation. They are commonly vigorous pioneer species, adapted to growing in communities of single or a few species. Many have hardcoated seeds and can therefore be conserved in refrigerated seed banks for decades.

Seed collection may also be a means of conserving genetic resources *in situ*. In parts of Central America, it is difficult (if not impossible) to conserve the few remnants of natural forest as a viable ecosystem. Yet, the value of some constituent species is well-appreciated by the inhabitants. These species could be conserved by being integrated into local farming systems by raising planting stock and providing seed. Several species, such as *Leucaena salvadorensis* and close relatives, could be conserved by this method (Hughes 1988).

Collection for Seed Research

Neem (*Azadirachta indica*) is an admirable MPT, although widespread use is limited by the short viability of seed. The same applies to most species of the equatorial forest. *Inga* is a large, neotropical leguminous genus of the lowland humid forest with great potential, but also severely limited by short seed viability (Little and Wadsworth 1964, NAS 1980). At the other environmental extreme, the arid-zone genera of *Acacia* and *Prosopis* suffer great losses from bruchid seed borers. Careful and prolonged seed research may help overcome these problems.

Close liaison is necessary between the seed collection team and the seed physiologist or entomologist who will carry out the research. Ideally, the latter should accompany the team into the field. Periodic collections may be needed in the same stand, ranging from immature fruits to the time of seed dispersal to observe the effects of timing on seed longevity or seed predation. It may also be necessary to compare seed-handling treatments at all stages between collection and the laboratory. This is a highly specialized operation requiring clear experimental prescriptions, close supervision, and time. It is best carried out as a distinct task, not combined with the more routine seed collections for species/provenances trials or *ex situ* conservation.

Planning and Collection

Day-to-day organization of MPT seed collections differs little from that prescribed for industrial species. General descriptions of tropical-forest seed collection include Kemp (1975, 1976), Turnbull (1975a, 1975b), Willan (1985), Doran et al. (1983), and Robbins et al. (1981).

1. Clear but flexible objectives. These are in terms of regions, species, purposes of collection (e.g., species trials, provenance trials, *ex situ* conservation). Since resources are seldom sufficient to attain all possible objectives, these should be stated in order of priority. If circumstances make it impossible to attempt the primary objective, the expedition will have been prepared to switch smoothly to the secondary objective. It is advisable to plan with provisional objectives and refine and strengthen them during the planning period as information is acquired.

2. Survey of published information. A literature search, supplemented by herbaria records, may provide data on the natural distribution and genetic or ecological variability of the target species, together with periodicity and season of flowering and fruiting. Information on communications is also needed to judge accessibility of the stands.

3. Information through correspondence. For international seed-collecting expeditions extending over several countries, close liaison must be established and maintained with local forest services. They may provide not only valuable, up-to-date information on ecology and phenology but also data on local regulations, entry permits, seed export, phytosanitation, and other administrative matters. Official information may be needed from customs, immigration, and phytosanitary authorities.

4. Field reconnaissance. For little-known MPTS, published information may be inadequate for immediate, full-scale seed collection. A full season of exploration is then required to prepare for efficient collection in subsequent years. Provided that a program is planned to continue over several years, exploration can be combined with seed collection each year. A new species or provenance of potential value discovered one year can be collected the next.

5. Timing seed collection. If possible, collections should be made in a prolific seed year. This may not be practicable in international seed-collecting programs of limited timespan. Fortunately, many MPTs bear good seed crops every year. Trained observers in the seed-collecting zones can give advance notice to the collection team leader on the crop size and its state of development. Advice on comparative ripening speed in different areas is particularly important to ensure an efficient order of successive collections. Ideally, each collection can then be timed to coincide with peak harvest in each area.

6. Preparation of equipment. Lists of standard seed-collecting equipment are available in the literature cited. Provision is needed for materials used in drying, field extraction, temporary storage, and transport, as well as for the climbing and gathering operation.

It is also important to plan what needs to be collected in addition to seed. For little-known species, good herbarium specimens are a must. More specialized collections, dependent on the proposed end use of the seed source, may include wood cores, foliage collections for nutrient analysis, extractives for chemical analysis, and rhizobial or mycorrhizal collections for inoculation. Specimens of insect pollinators and seed predators may also be valuable. Each would require additional, specialized equipment. Transport is a prerequisite for all successful seed collection, and advance arrangements for purchase or hire of vehicles are essential.

7. Staff recruitment and training. One or more team leaders; experienced climbers and seed collectors; drivers; and less skilled workers for ground collection, extraction, and handling of seeds will be required. Training of the leaders and climbers will be necessary. Time should be allowed for this every season if new staff are recruited (Robbins, Irimeicu, and Calderon 1981). For international

seed-collecting programs that last several years, foreign staff will need instruction in local language and customs. Some small MPTS in arid zones may not require climbing. Collectors may, however, still need a high degree of skill in the safe and speedy handling of thorny species.

8. Field records and labelling. Meticulous records about the site, stand, and seed collection at each site are essential. Equally important is good labelling to preserve the identity of every seedlot at all stages, from seed source to seed store and nursery. Appropriate labels and forms must be designed and printed well in advance. An example of a suitable collection record is shown in the Appendix. Particular attention should be paid to the preferred local uses of the seed sources collected and any evidence that the species could become a weed. A wider selection of seed forms used in various countries is given in Willan (1985). Photographs that show tree habit and stand type are a useful supplement to written descriptions.

9. Permits. Application for visas, health documents, and seed-collecting and export permits must be made well in advance. Although some may be issued after the arrival of the expedition in the host country, it is important to receive advance notification that no problems are anticipated.

10. Finalization of the collection program. For an international expedition, this can be done only after arrival in the host country. Several weeks should be allowed to consult with national cooperators, obtain any outstanding permits, recruit and train local collecting staff, and finalize transport arrangements.

11. Local liaison. Securing the goodwill of local communities is essential to successful seed collection. A national seed center collecting in its home country still needs the cooperation and local knowledge of district foresters, community leaders, and individuals knowledgeable about the forest. Advance information of intentions and consultation with the local experts can do much to secure this goodwill. For international expeditions, local liaison is even more important. Such expeditions can only succeed if staff from the local forest service are closely involved. In return, the cooperating service should have access to all documentation and a fair share of seed from the expedition.

12. Processing and transport. Arrangements for rapid movement of fruits from collection site to extractory often involve the advance organization of transport. Alternatively, arrangements may be needed for seed extraction close to the collection site. Staff responsible for transport, extraction, and cleaning must be told when to expect consignments so that they handle them with minimum delay. The success of an expedition depends on efficient transport and handling no less than on efficient collecting.

13. Information management. During any seed collection and distribution operation, much information is gathered on collection site characteristics, germplasm records, herbarium collections, seed physical quality, seed storage and stocks, seed distribution and field trial sites, designs, and compositions. This large volume of information requires careful data management.

Several computerized database systems have been developed covering some or all types of data involved. Good examples are the SISTEM database developed at the Oxford Forestry Institute, covering all aspects of seed collection, distribution, and trial information (Filer 1988) and the TREESEED system set up by CSIRO in Australia, covering seed-bank information handling (Wolf and Turnbull 1982). Other systems concentrating on trial network information include the IADSS developed under the Forestry/Fuelwood Research and Development (F/FRED) Project in Asia (Cady 1987), the MIRA system developed under the Tree Crops Production (Madelena) Project in Central America (Rose and Ugalde, in press), and the TREDAT system developed by CSIRO (Brown et al. 1987).

For well-known species that bear good seed crops every year, effective collecting expeditions can be carried out within a single season. For little-known species distributed over several countries, exploration and collection over a much longer period must be planned. Most MPTs fall into this category. Although exploration in the first year will yield little or no seed, it is still vital since it directly affects the efficiency of collection in subsequent years.

To the above operational period must be added a preliminary planning period. For international seed collections in several countries, at least one year should be allowed.

More than one sympatric species can be collected in the same year. The possibilities for this are increased if the peak seeding period varies among species. Often, the various stages of species exploration and collection will overlap without full synchronization. Thus, full-scale, rangewide provenance collections of such popular species as *Gliricidia sepium* or *Acacia aneura* can be combined with single- or few-provenance collections of lesser-known species from the same region. As more is learned about the latter, they can be investigated through rangewide provenance collections. The publicity and limitations of *Leucaena leucocephala* as an exotic in recent years have led scientists to realize not only the need to explore its full genetic diversity but also the potential of related *Leucaena* taxa (Hughes 1990).

Seed Storage and Distribution

Generally, the institute or organization responsible for collecting seed should be responsible for its distribution. A national seed center that collects or arranges seed collection within national boundaries is responsible for ensuring the users timely distribution, the right quantities, and satisfactory physiological condition. When seed is not distributed immediately, adequate storage conditions must be provided. Fortunately, most leguminous MPTs store well in ambient conditions, provided they are dried and kept so. More expensive, cold-storage facilities are required for some species if viability is to be maintained over a number of years. National seed centers with adequate staff, storage facilities, and funding can also supply seed to other countries. This is already done by the Division of Forest Research, CSIRO Canberra; the Direction des Semences Forestieres, Burkina Faso; and the seed centers in Honduras and Nicaragua.

A single agency (frequently with international or bilateral funding) that undertakes seed collection over the full range of a species should also distribute the seed and, at the same time, coordinate international provenance trials in which the seed is used. A common protocol can be suggested for trial methodology, which will facilitate the later comparison of results within and between countries. In this way, each country can benefit from information from internationally coordinated trials on the progress of species and provenances in which it is interested. Further, the coordinating agency may be able to contribute technically and financially to the subsequent evaluation in field measurements and extensive data processing that follow.

Good examples for industrial/fuelwood species are the international collections and trials of *Eucalyptus camaldulensis* (FAO/CSIRO), *Terminalia superba* (CTFT), tropical pines (OFI), and tropical hardwoods (DFSC) (Lacaze 1978, Corbasson and Souvannavong 1988; Gibson, Barnes, and Berrington 1983; Keiding, Wellendorf, and Lauridsen 1986; Lauridsen, Wellendorf, and Keiding 1987). The same approach has been used more recently for MPTs, e.g., *Gliricidia sepium* (OFI), arid zone MPTs (FAO), and Australian acacias (CSIRO/CTFT) (Hughes 1987a, Palmberg 1981, Thomson and Cole 1987).

The complexity and duration of extensive species and provenance seed collections, accompanied by full and meticulous documentation, should not be underestimated. The OFI *Gliricidia* collections included 30 provenances; 1,000 viable seeds of each provenance were distributed for each fuelwood woodlot trial and 300 for each alley-cropping trial (Hughes 1987a). The aim was to collect sufficient seed of each provenance for trial on 160 sites. Demand considerably exceeded supply. Some of

the seed was kept separate by mother trees to combine provenance/progeny trials. Maintaining identity of mother tree seedlots involved additional work at each seed-handling stage.

It is not surprising, therefore, that provenance collections of this type are costly. The *Gliricidia* collections, spread over three years, cost an estimated US$130,000, equivalent to about $250 per kg viable seeds, $50 per provenance per site, or $750 for an average 15-provenance woodlot trial. In Australia, collections of *Acacia aneura*, an erratic seeder, were expected to have an operational cost of $30,000 and were still incomplete after four years. Provenance collections of *Eucalyptus camaldulensis*, with detailed origin and germination data, were costed at $300-500 per kg. Costs for an overseas team collecting *Acacia mangium* in remote areas were estimated at $1,000 per kg (Turnbull 1984). An overseas team operating for a full year in Australia could cost close to $100,000 but, based on experience of the CTFT/CSIRO operations in 1973, could collect 1,500 seedlots in that period (Turnbull 1984).

It follows that scarce supplies of valuable seed, collected with much time and effort, must be used in the most efficient way. Nearly always, insufficient seed will prevent all countries from evaluating all provenances on all sites. Likewise, the organizations testing the provenances have limited resources. A few major research institutes may be able to test the full range of provenances within a species; other recipients need to select them.

Various factors may affect seed-collection and distribution strategies. Collectors of relatively unknown species take a global viewpoint. They assume that somewhere there may exist both an environmental and an end-use match for every variant found in the species they are investigating. Within the limits of available resources, they wish to sample all the variations they estimate as significant. Most recipient countries, on the other hand, are interested only in those species/provenances most likely to succeed on the planting sites available. They cannot afford to test probable failures. Out of 30 available sources, a country might test 6-12 on one site type and another 6-12 on a second site type.

At both the species and provenance levels, end uses are a major criterion for selection. Introducing an excellent fuelwood with unpalatable foliage is pointless if the primary purpose of planting is to provide fodder for stock. Information on end uses should be an important item in the species or provenance profile distributed when seeds are offered.

Another important criterion is the degree of apparent environmental similarity between seed source and planting site. Over the past half-century, experience from provenance trials and more haphazard plantings of exotics has, on the whole, demonstrated the adaptation of natural populations to their environments and, therefore, the importance of achieving a good environmental match between a natural seed source and the exotic planting site. Climatic matching can be expected as no less important for MPTs than for industrial species.

A major tool in matching seed source to planting site has been homoclime analysis, which is comparing climates to identify those closely similar, even though they may be physically distant. The recent development of computer programs has facilitated its application to finer comparisons of seed source or provenance with planting site. In Australia, the BIOCLIM and CLIMSIM programs have been developed to assist other countries to select Australian species and seed sources best suited to the climatic conditions of their planting sites.

The data required for each station consist of (1) monthly mean of daily maximum temperatures for each month of the year, (2) monthly mean of daily minimum temperatures for each month, and (3) precipitation for each month. From these 36 basic figures, 18 climatic indices are compiled for each location. It is possible to define the range of a native species and, from that, use homoclime analysis to predict regions in other continents where the species is likely to perform well. One study carried out on *Eucalyptus citriodora* (Booth 1985, Booth et al. 1988) indicated a satisfactory correlation between the degree of successful plantings in Africa and the degree of climatic similarity between the areas in Africa and of natural distribution in Australia.

In some cases, the species flourished in African climates outside the range of those in the natural Australian distribution, indicating that some provenances can adapt to new environments.

Evidence of such adaptation from more than one exotic site can be used to revise the original climatic profile of the species, based on natural distribution alone.

It is possible to reverse the procedure by first defining the climatic indices of the planting site and then identifying other locations with similar indices. This can suggest not simply a species trial but also one or more seed sources within the range of that species. Also, a location identified may have seed sources of more than one species to offer. The same location in Australia, for example, might provide seed of *Acacia* and *Casuarina* species, as well as *Eucalyptus*.

Within Australia, climatic indices have been estimated by interpolation techniques for 2,795 points on a half-degree grid. It is possible to compare these indices with those at a proposed planting site, e.g., in Africa, and grade the Australian locations according to their climatic similarity with the African site. A convenient grading method is to use the letters of the alphabet, where "A" indicates locations most similar to the planting site and "Z" those least similar. Zones of degrees of similarity can then be plotted on the map. Climatic estimates based on interpolation between existing meteorological stations work well in regions of gentle relief, such as much of interior Australia. They would be subject to considerable inaccuracy if applied in mountainous country, where rapid changes in elevation are accompanied by rapid changes in rainfall and temperature.

Although climatic matching is a valuable tool, provenances vary in their ability to adapt to different environments, as in the above example of *Eucalyptus citriodora*. *Gliricidia* occurs naturally in seasonally dry climates with 800-1500 mm annual rainfall, but grows successfully as an exotic in humid, non-seasonal areas where it sets no seed. Some caution is needed in interpreting early successes in conditions markedly different from those of the place of origin. Some species have shown great promise over a period of years, only to succumb later to pest or disease, e.g., *Pinus radiata* in East Africa or *Eucalyptus grandis* in India and Brazil.

Careful research therefore needs to assess how far a superior MPT provenance can adapt to new environments, such as a climate drier or colder than its natural range. Thus, genotype environment interaction, so important in the selection and breeding of individuals and families, is no less important at the provenance level. In this respect, it is important to distinguish between a variable species and an adaptable provenance. A single taxonomic species may occur over a wide range of environments, but it does not follow that any particular provenance within it can adapt to a major change of environment. For example, *Eucalyptus camaldulensis* grows under both winter and summer rainfall conditions. This does not imply that one of its winter rainfall provenances can adapt successfully to a summer rainfall climate or vice versa.

Climatic matching has generally proved more helpful than soil matching. Although soil characteristics may be critical for some species or provenances, they are more difficult to assess and interpret and more subject to small-scale variation than climatic factors. Frequently, soil interacts with climate, e.g., species growth may be the same on a free-draining sand with 1,000 mm rainfall as on a water-retentive loam with 750 mm.

The collecting institute should be able to give valuable advice on selection by environmental and end-use matching. This, however, depends on how explicit the seed users are in specifying their needs when they submit their requests. Turnbull (1984) provides a helpful list of ways the seed user can take advantage of the opportunity offered by the seed collector. Essential is precise information on:

- why the MPTs are to be grown,
- the environment(s) of the proposed planting site(s),
- whether separate mother tree seedlots are required for combined provenance and progeny trials, and
- numbers of plantable trees needed per provenance.

Equally important are such administrative details as the date by which the seed should be received and necessary import and phytosanitary documents.

The timing of seed distribution will often vary between countries. Some may not be able to organize evaluation trials as soon as the seed is collected. In addition, it is often not possible to

collect all seed sources in the same year. An international seed-collecting institute should therefore have access to seed-storage facilities of a high standard, both for deferred provenance trials and long-term conservation.

Since MPTs are so valuable for agroforestry, both foresters and agriculturalists are involved in their collection, evaluation, and use. In fact, most research in evaluation and genetic improvement of *Leucaena*, *Gliricidia*, and *Sesbania* has been carried out by agricultural researchers. While foresters deal with wild, outbreeding populations and speak of seedlots, provenances, families, and progeny, agronomists handle domesticated, inbreeding populations and speak of accessions, lines, cultivars, and composites.

Leucaena leucocephala, one of the most important MPTs, has a high degree of self-compatibility, but this is atypical. Foresters attach importance to exploring the wealth of natural variation that they find in most of their species. Agronomists emphasize pure lines and their artificial hybridization. Agricultural stations often maintain collections of many accessions, unreplicated across sites until a late stage. Foresters, because of the size of individual trees, must confine themselves to a restricted number of populations under testing and aim to replicate within and across sites at an early stage. The different approaches of the two disciplines can easily lead to misunderstanding. Mutual communication will be needed to achieve the fullest cooperation.

Institutes working in international seed collection for research purposes should be given as much freedom as possible. Relatively few institutes can tackle the needed exploration and collection. Cooperation between two international institutes can be fruitful, e.g., CTFT and CSIRO on Australian species or OFI and DFSC on Central American pines.

It is desirable to have one or more global information clearinghouses of recent and proposed activities in international seed collection, such as FAO's Panel of Experts on Forest Gene Resources, established in 1968. Most organizations concerned with international seed collection have a member on the Panel, whose recent sessions have increasingly emphasized the importance of MPTs. Between sessions, FAO's Forest Resources Development Branch acts as the clearinghouse and publishes *Forest Genetic Resources Information*. Two other information clearinghouses on MPTs are ICRAF for agroforestry species and NFTA for nitrogen-fixing species. Each has its specialized clientele that differ from each other's and those of FAO.

The aim is to ensure that everyone is aware of what others are doing. There is, however, no case for any central direction of who is to collect what, and still less for any central MPT seed bank controlling all seed storage and distribution.

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Appendix

Example of seed collection record (from OFI, Oxford)

Species: *Gliricidia sepium* (Jacq.) Walp. Site No.

Common Name: Madrecacao Ident No.: 15/84

Country: Guatemala **Department:** Zacapa

District: Gualan **Site:** Gualan

Latitude: 15°08'N **Altitude:** 150 m

Longitude: 89°20'W

Location:

The site is in the dry, eastern part of Guatemala in the lower valley of the Rio Motagua. The collection area lies on the north side of the river about 2 km downstream from the town of Gualan. Access is from the main road between Guatemala City and Puerto Barios 1.5 km east of Mayuelas at km 167. The best stands lie close to the river.

Climate:

The area lies in the marked rain shadow of the Sierra de las Minas and is one of the driest areas in the Central American isthmus, with a mean annual rainfall of 723 mm and a long and severe dry season (seven months receive less than 50 mm). Rainfall and temperature data are given for the station at Pasabien, some 30 km west of the collection site along the Motagua Valley.

Location of Meteorological Station: Pasabien, Zacapa.

Latitude: 15°02'N **Longitude:** 89°40'W **Altitude:** 480 m

Month	J	F	M	A	M	J	J	A	S	O	N	D
Mean Monthly Rainfall	1.4	0.5	4.6	22.0	127.2	147.7	105.7	100.5	143.3	8.2	16.4	6.3
Temperature °C												
Abs. Max.	37.5	38.2	40.2	40.7	41.0	37.5	37.0	38.2	37.5	37.5	37.0	37.0
Mean Max.	31.7	32.8	35.2	35.6	35.3	33.5	33.3	33.6	33.2	32.4	32.1	31.7
Mean	24.7	25.4	27.7	28.8	28.9	27.8	27.3	27.4	27.3	26.5	25.7	24.8
Mean Min.	17.5	17.7	19.8	21.2	22.0	22.1	21.3	21.2	21.4	20.7	19.5	17.9
Abs. Min.	9.5	10.8	12.2	10.0	16.3	19.0	16.5	16.5	17.0	14.5	13.5	11.5

Soils:

Soils are derived from alluvial material of volcanic origin. The soils are sandy, deep, and freely drained.

Vegetation:

The area has been largely cleared for grazing and little natural forest cover survives. Fires are common in the area. The original forest cover would have been a dry tropical forest and largely deciduous.

Associated Woody Species:

Guazama ulmifolia
Acacia collinsii
Lonchocarpus spp.
Leucaena diversifolia
Enterolobium cyclocarpum
Tecoma stans
Senna atomaria
Karwinskia calderoni
Acacia farnesiana
Jacquinia aurantiacea
Vitex spp.
Cordia alliodora
Pithecellobium dulce
Simarouba glauca
Ceiba pentandra
Calicophyllum candidissimum
Senna skinneri
Salix humboldtiana

Tree Characteristics:

Gliricidia sepium is abundant on the hills around Gualan, occurring as scattered individuals and small, pure stands. The stands at the collection site are fairly dense. Trees are mainly of coppice origin and multi-stemmed. Tree form is good with straight stems. Trees average 7-8 m in height.

The wood is used locally for posts, house construction, and firewood. Cattle browse the foliage and dry-pod shells.

Material Collected:

A large, bulk seed collection was made from about 80 trees. The pods had mainly opened at the time of collection, and most of the seed was collected from the ground below the trees. The large seed size and light color, combined with the heavily grazed ground vegetation, meant this was rapid and obviated the need for extraction and cleaning of the seed.

Collection Dates:

April 10-11, 1984

Herbarium Material:

C. E. Hughes 459 (leaves recently flushed, ripe pods)

Collector:

C.E. Hughes

Improvement Objectives for MPTs

Nancy Glover
Nitrogen Fixing Tree Association

Fast growth, environmental adaptability, and pest resistance are major improvement objectives for MPTs, as they are with industrial forestry species. The challenge to MPT breeders is to combine these objectives with improved quality for a multitude of desired products under diverse management conditions based on the needs of end users. It is possible to obtain improved products and, at the same time, maintain or broaden the genetic base for environmental adaptability and pest resistance (Zobel and Talbert 1984). One can develop disease resistance in either single-stemmed or multi-stemmed trees. The wood of drought-resistant trees can have either high or low specific gravity.

This paper focuses on improving MPTs for stress environments. Selection criteria and methods to improve pest resistance, drought resistance, and tolerance to mineral stress and acid soils are presented. Physiological responses in plants to stress environments that are likely adaptable to MPTs are reviewed. Improving product quality is discussed briefly.

Pest Resistance

Insects, nematodes, mites, parasitic plants and diseases caused by rust, fungi, bacteria, and viruses can decrease MPT yield. Numerous examples, from both temperate and tropical forestry, show large-scale pest damage. The shoot borer (*Hypsiphilla grandella*) in Latin America has prevented successful establishment of plantations of both mahogany (*Swietenia* spp.) and red cedar (*Cedrela* spp.) (De La Puente E. 1966). Extensive damage to Albizia trees caused by the vascular *Fusarium* wilt occurs throughout Iran and Russia (Toole and Hepting 1949). The leaf rust *Uredo sissoo* is a serious threat to *Dalbergia sissoo* plantings in India (Tewari, Joshi, and Singh 1988). Massive tree planting programs with *Pinus radiata* in Brazil, Zimbabwe, and East Central Africa have failed due to excessive damage caused by the rust *Dothistroma*; and the stem canker on *Cupressus* planted in Colombia, Kenya, and other areas is so severe that the quality wood products for which the plantations were established cannot be produced (Gibson 1972). The severe damage caused by the psyllid (*Heteropsylla cubana*) to *Leucaena leucocephala* in recent years brings the issue of pest management closer to advocates of MPT planting (NFTA 1986).

MPTs are often planted in areas with marginal site conditions, such as low soil fertility or rainfall, and stressed by frequent cutting or lopping, making the trees more susceptible to attack by pests. The various uses of MPTs also increase the ways in which losses may be incurred by pests. To reduce tropical deforestation, develop sustainable agricultural systems, and supply an increasing demand for fuelwood and animal feed, many MPT planting programs have been initiated based on introducing a single exotic species, with seed often from unknown sources or a small number of parents. This is especially insidious because exotics often grow well in a new environment, while pest-free in early years. Additionally, lack of information on pests of MPTs and rapid advances in the volume and speed of international transport increase the risks of introducing new pests, despite phytosanitary legislation and quarantine barriers.

No tree breeder expects to eliminate totally the losses due to pests. In some cases, losses may be reduced by silvicultural practices, biological control, chemical spraying, or a combination of these methods. Silvicultural control measures typically have been used in connection with diseases, and biological and chemical measures in connection with insects. Pest control strategies depend on valid estimates of the losses caused by destructive pests. The feasibility of pest management by genetic improvement must be weighed against the magnitude of potential losses and other control measures. For example, one concern to tree improvement efforts are insects that attacks seeds, cones, and flowers. These can harm natural regeneration and devastate seed orchards. Seed orchards, however, are generally

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small, and the use of systemic insecticides combined with management have proven effective.

Heritable resistance, either alone or combined with other measures, is a proven, effective method for pest control. Successful breeding programs for pest resistance have been developed, even when the cause of resistance is uncertain. Encouraging results in producing pest-resistant cultivars have been obtained from selection within species and from hybridizing closely related species. Intraspecific breeding programs have generally concentrated on identifying phenotypically superior, pest-resistant plus trees, collecting grafting material, establishing seed orchards for intercrossing, and testing their progeny. Pest-resistant cultivars have also been identified by provenance testing followed by plus-tree selection. Interspecific breeding programs for pest resistance have been successful for the genera *Alnus*, *Betula*, *Eucalyptus*, *Fraxinus*, *Leucaena*, *Pinus*, *Populus*, and *Quercus* (Bjorkman 1964, Brewbaker 1987).

Of the several important considerations in selecting pest-resistant trees, the most critical to success is selecting under heavy infestation of the pest. Poor results have been obtained when uninfected trees in infected stands were selected and considered resistant (Riker and Patton 1961). Forced attack in greenhouse conditions can give useful information about pest resistance if positive correlations with field conditions can be established. This has been done on a large scale for fusiform rust (Phelps 1977). Other important considerations include the age of the trees screened and silvicultural conditions.

Susceptibility to pest attack can change with tree age, making it essential to develop resistance effective throughout the life of the host. Trees that are periodically lopped for fodder or green-leaf production may be more susceptible to pest attack than unlopped trees, e.g., *Leucaena* (Glover 1988).

No simple protocol exists for designing MPT improvement programs for pest resistance. The approach depends on the type of pest; variability of host and pest; interactions between host, pest, and environment; and the time and cost of the improvement program. Over their life cycle, MPTs are likely susceptible to an array of pests, and improvement programs to resist many pests require time and money. At this stage, the wisest method to ensure protection against many major pests is to maintain genetic diversity. Populations without such diversity risk major losses. For many MPTs, time and money will be needed to collect seed from regions of origin to replenish genetic resources.

Environmental Adaptability

One of the most important MPT improvement efforts is to produce trees better suited to stress environments. MPTs are often grown in acid, sodic, or saline soils; areas with low rainfall; or cold sites. Much gain can be obtained for stress tolerance through provenance selection, which is usually the first approach followed after choosing species. However, improvement for stress tolerance is most successful when the physiological basis is known.

Breeders are accustomed to selecting for high yield, even though yield is inherited in a complex manner and is not under direct genetic control. The multitude of physiological and biochemical processes under genetic control determines yield. Yield as a selection criterion is aggravated when selection for yield is attempted under stress conditions. Results of agronomic studies for numerous crops have shown that selection for yield and yield components is most effective under nonstress environments because of greater genetic variance and heritability under these conditions (Blum 1988). The limitation of identifying genetic variance and heritability under stress is partly a direct result of the large environmental variance within stress environments.

Although breeding for wide adaptation (high mean yield, low genotype x environment interaction) may also provide for superior performance in stress environments, it is unlikely to arise from specific tolerances to all possible types of environmental stress. Rather, superior performance under stress is related to what may be called the "residual effect" of high yield. It is, however, not uncommon for genotypes with stress tolerance to have relatively low mean yields in nonstress conditions. Therefore, it is preferable to use specific physiological attributes for selection to stress environments rather than the genetically complex trait defined as yield. Of course, it is essential to measure yield to estimate performance under stress conditions.

Breeders and physiologists working together offer the best hope of deciding the most important physiological traits under genetic control. The combined knowledge of their two disciplines can help

plan experiments to understand better how MPTs adapt to stress environments.

Selection criteria for stress environments in MPT improvement programs involve 1) defining the physiological basis of resistance, 2) developing physiological selection criteria acceptable to breeders, 3) exploring genetic variability and heritability, and 4) incorporating desirable traits into improved varieties.

Drought Resistance

The physiology of drought resistance has been reviewed extensively by various authors (Blum 1988, Fischer and Turner 1978, Hale and Orcutt 1987, Paleg and Aspinall 1981, Turner and Kramer 1980, and Quisenberry 1982). Two important physiological processes that control drought resistance are 1) decreasing the rate of transpiration and 2) increasing the rate of water absorption.

Physiological traits that appear most useful for assessing drought resistance include stomatal control, stomatal number, cuticular resistance, leaf attributes, and root growth (Quisenberry 1982). Stomata exert critical control over water movement through plants. Stomatal frequency, size, and number are highly heritable and, therefore, subject to genetic manipulation (Miskin, Rasmusson, and Moss 1972). Although less is known of inheritance of stomatal behavior, it appears that the major mechanisms of water control in leaves could be changed in specific ways by breeders (Moss, Woolley, and Stone 1975). Such leaf-surface attributes as epicuticular wax load, heavy glaucousness, and dense pubescence reduce transpiration and are usually inherited in a relatively simple manner (Blum 1988). The density and extent of root development are positively correlated to drought resistance. Increased root growth increases the volume of stored soil moisture available, increasing drought resistance.

The field environment is highly desirable for selection work, provided a reasonable control is achieved. The natural semi-arid environment, toward which improved drought resistance is often directed, is not ideal for selection work. This low rainfall zone, typically 200 to 500 mm annually, is characterized by high annual variations in rainfall frequency and total amount. The conditions at planting may not be typical of the long-range rainfall pattern. If selection is undertaken at low rainfall sites (e.g., 100 mm annually), water stress conditions can be almost fully programmed and optimized by using irrigation. This allows the reproduction of stress conditions from one year to the next. While such a site may reside outside the tree's growing area, it allows a reasonable control over the moisture environment under field conditions. Irrigation in a dry area also allows for evaluation under a gradient of water stress conditions, including nonstress conditions.

Selecting for drought resistance should integrate several criteria into one selection index. The simplest method is visual scoring of wilting, leaf firing, leaf, senescence, leaf-surface attributes, growth, and perhaps plant phenology. Stomatal size, number, and conductance can also be assessed, but take more time and money to measure.

Mineral Stress

The most common approach to mineral stress is to change the soil to fit the needs of the plant. However, sufficient genetic variability for mineral responses exists within species to make selection and breeding a viable alternative strategy (Epstein and Jefferies 1964, Lauchli 1976). This strategy is particularly important for MPT improvement because soil amendments are often unavailable in areas where MPT plantings are recommended.

Genotypes resistant to mineral deficiency are often defined as "mineral efficient." Mineral efficiency may result from either a better ability to take up minerals or better efficiency in using minerals already available in plant tissues. Most improvements for mineral-efficient genotypes in agricultural plants address problems of mineral uptake rather than efficient use. Plants subjected to mineral stress adjust in three known parameters: 1) permeability of cellular membranes increase, resulting in greater mineral uptake, 2) chemical properties of the rhizosphere change, increasing the availability of the deficient mineral, and 3) root growth increases relative to shoot growth. The inherent potential differences in root size between genotypes can affect absorption of minerals, especially those of low mobility, such as phosphorous.

Mineral deficiencies are often expressed in easily recognized plant symptoms. MPT breeders involved in such work should be familiar with the spectrum of symptoms in a given MPTS for given mineral

deficiencies.[1] Deficiency symptoms are commonly employed in selecting for mineral-efficient genotypes, using a rating scale or plant scores (Wright and Ferrari 1976). While symptoms alone might suffice for selection, a combination of deficiency symptoms and yield is the most effective selection method.

Selection programs for tolerance to mineral deficiency should be performed under field conditions in well-defined mineral-deficient soils. Field sites must be chosen carefully, with spatial variability in mineral deficiency and site homogeneity major considerations. Many soils are deficient in more than one mineral, and these must be accounted for in any experimentation. Selection at a given site may also be affected by other problems specific to the soil at the site, such as microbial activity, pH, or interactions with other elements. The usefulness of selection in field experiments depends on the breeder's ability to define the problem soil and choose the most representative site for selection. When such conditions are met, field selection is far superior to controlled greenhouse or laboratory conditions. Controlled conditions using nutrient solutions, however, can be useful for resolving mechanisms of resistance. Field evaluations should involve split or factorial testing over stress and nonstress conditions. Such conditions can be attained by using a mineral-deficient soil and establishing a nonstress treatment with fertilizer or soil amendments. Genotypes can then also be evaluated by the yield ratio between stress and nonstress conditions, in addition to absolute yields.

Acid Soils

Aluminum toxicity and low soil calcium levels are major factors limiting plant growth in acid soils. Plants exhibit a wide range of tolerance to aluminum, both between and within species (Fageria, Baligar, and Wright 1988). Resistance to aluminum toxicity is generally due to an avoidance mechanism rather than a tolerance. Avoidance mechanisms include 1) increased pH around the roots, reducing aluminum solubility and uptake; 2) retention or binding of aluminum in the roots; or 3) accumulation of aluminum in older leaves (Hale and Orcutt 1987).

Roots are directly affected by aluminum toxicity and low soil calcium levels. In many plant species, growth is inhibited, and roots appear stubby, discolored, and lacking the finer root laterals. Inhibition of plant growth is generally not observed before root symptoms develop. Therefore, the time required before genotypes can be separated by root growth is relatively short. A direct reference to roots in selection for tolerance to aluminum toxicity and low soil calcium levels is a reasonable approach since the root is the immediate site of injury.

Three major approaches are used to create the proper selection pressure: 1) the problem soil under the natural field environment, 2) the problem soil in pots outside the field environment, and 3) nutrient cultures (Little 1988). Selection is best accomplished under a range of soil calcium and aluminum levels. This can be better approached in pots than in the field by the selection of proper soil type, which can be manipulated by soil acidification, liming, or the addition of aluminum. In general, agreement between results from screening experiments and field trials has been good (Little 1988). Root measurements are also easier to measure in pots than in the field. Oakes and Foy (1984) used a greenhouse setup to screen 148 *Leucaena* genotypes for aluminum tolerance using a soil with high aluminum saturation at pH 4.8. The nonstress control soil was limed to pH 6.6. Relative root yield (root yield at pH 4.8/root yield at pH 6.6) was used as an indicator of relative aluminum tolerance. Wolfe and Joslin (1989) studied root growth of *Gleditsia triancanthos* at varying levels of soil calcium and aluminum. The results indicated that the Ca:Al ratio was superior to Al or Ca alone as a predictor of growth in acid soils.

Desired Products and Characteristics

Implicit in the name MPT is the desire to obtain multiple products and services from a single tree species. Farmers plant MPTs for food, fuelwood, fodder, honey production, gum, construction materials, erosion control, living fences, improved soil fertility, and other useful products and services. Therefore, many characteristics must be assessed and incorporated into selection indices. Traditional forest mensuration of single stems is less important than biomass partitioning of coppiced or lopped stems, estimates of leaf production and fodder quality, fruit production, or environmental amelioration, including nitrogen fixation (Burley, Huxley, and Owino 1984).

[1] For general deficiency symptoms expressed in plants, see Sprague (1964).

Coupled with the desire to obtain multiple products are the many management options recommended. The variety of management options highlights the importance of management x genotype interactions as part of environment x genotype interactions. Ranking of performance by genotype may change depending on the type of management, as well as physical site characteristics. Tree morphology is also an important consideration in improvement programs. For example, branching and rooting patterns of MPTs can be important criteria when trees are grown in association with crops to reduce competition. Many MPTs are periodically lopped for fodder production or green leaf manure, requiring good coppice regrowth and high leaf:wood ratios, as well as good chemical composition.

MPT breeders are unlikely to be able to provide improved genotypes that combine more than two or three desirable products. More likely, individual improvement programs will need to be designed for different desired products. For example, selection of *Robinia pseudoacacia* cultivars in Hungary has resulted in three distinct groups based on end use: 1) production of logs suitable for saw milling, 2) production of poles and props, and 3) improvement of bee forage and decorative planting (Keresztesi 1988). Dual-purpose cultivars, for logs and beekeeping, have also been developed. In South Korea, a tetraploid *R. pseudoacacia* has been bred for fodder for pigs and broiler chicks. Its leaf weight is three times that of the common diploid and contains 1.4 times as much protein (Keresztesi 1988). It is impossible to list here all the possible combinations of desired products and tree characteristics for MPT improvement programs. The most important step is to identify desired products before improvement programs begin.

The ideotype or "ideal tree" concept has been proposed to provide a clear goal toward which MPT breeders can work (von Carlowitz 1986, Chuntanaparb and MacDicken, in press). Originally developed for agricultural crops by Donald (1968), this concept describes preferred or ideal morphological and physiological traits for producing desirable products from a given species. For example, Karki and Tigerstedt (1985) define a conifer tree ideotype for high-quality log production as having a straight stem with little taper, thin bark, slow growth, and small, 90-degree angled branches. Morphological, physiological, and phenological characteristics of an intensively managed, short-rotation poplar ideotype have been described in detail by Dickmann (1985). An alley-farming ideotype tree could be described as one that is easily established, tolerates regular coppicing, has a high leaf biomass yield, fast regrowth after coppicing, is deep rooting, nitrogen fixing, and provides such useful byproducts as fuelwood or staking material.[2]

General Comments

MPT improvements will progress fastest if selection work concentrates on a few important traits. Improved growth, environmental adaptability, and pest resistance will be the major objectives of MPT improvement programs. Product quality is more logically improved within the framework of better growth and greater hardiness.

Because MPT improvement is a long-term process, one of the most important considerations in an active, ongoing program is time. It may take years to obtain the information needed on the natural distribution, reproductive biology, and genetic variability and heritability of important traits of a given species before improvement programs can begin. National, regional, and international cooperation, as well as a commitment of resources and funds, are essential for rapid progress.

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[2] B.T. Kang, personal communication.

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Farmers' Perspective on Improvement Objectives for MPTs

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Tree improvement research has done little to enhance the production and use of MPTS on small farms. With the exception of *Leucaena leucocephala*, there are no other examples of successful identification and widespread adoption of improved MPTS for small-farm use. Success stories as striking as that of the self-pollinated *L. leucocephala*, where yield increases of well over 100% have been reported through simple selection, are unlikely to be as dramatic for other MPTS. Yet, the scope for improving many underexploited species is still considerable.

Despite the potential, research has done little to expedite MPT improvement. Most tree improvement programs rely on traditional criteria to guide selection and breeding. The ideal tree or ideotype for plantation forestry is one straight bole that is clear of heavy branching to 16 m. This goal is reasonable for mechanized sawmills and high-quality timber. However, small farmers have limited or no access to markets that require 8 m logs. More often their access is to small hand-powered or simple sawmills designed for short logs less than 3 m in length. Farmers also grow MPTS for a wide range of products, including timber, fodder, fuelwood, medicine, fruit, and other foods.

Traditional tree improvement objectives do not address farmers' needs for most non-timber products. Rarely included in traits for improvement are increased fodder, more appropriately sized fuelwood, or coppicing ability. For example, a major improvement objective for *Acacia auriculiformis* is to produce single-stemmed trees with long, clear boles. However, farmers growing *A. auriculiformis* in fuelwood deficit areas might be more interested in trees a low branching habit, multiple stems, and high coppicing ability.

Selecting Relevant Criteria

Choosing and improving species for small-farm use are complicated by MPTS being expected to fulfill many poorly defined functions (Chuntanaparb and MacDicken, in press). Non-timber traits for MPTS are seldom evaluated for improvement programs. It is crucial to define carefully the selection criteria for appropriate species and identify clearly the improvement objectives before programs begin. Well-defined improvement objectives for MPTS will also allow researchers to focus on species and varieties that most closely match farmer needs.

Improvement objectives are perhaps best described through ideotypes. The ideotype tree is defined broadly as a biological model expected to perform in a predictable manner within a defined environment (Dickmann 1985). Objectives described through ideotypes provide tree breeders the opportunity to define and examine a combination of desirable traits toward which they can work.

Farmers' Objectives

To determine MPTS ideotypes from the perspective of small farmers, a multilocation study was commissioned by the Forestry/Fuelwood Research and Development (F/FRED) Project.[1] The study's objective was to define and describe MPTS ideotypes desired by small-scale farmers in Asia. These ideotypes were to provide the basis for MPT improvement and provide research and development institutions information on species selection and improvement.

The major questions asked were:

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[1] Administered by Winrock International and funded by the U.S. Agency for International Development.

1. Do the traditional improvement objectives of straight bole and little branching provide a suitable definition for improved MPTS for small-farm use?

2. If not, can a more relevant set of ideotypes for MPTS improvement programs be defined?

Household surveys were conducted in 31 villages in 7 countries in tropical and subtropical Asia. In data collection and analysis, the countries were further divided into the subregions of South and Southeast Asia (see Table 1).

Table 1. Study Sites in Seven Countries in Tropical and Subtropical Asia

Subregions/Countries	Study Sites
South Asia	
Bangladesh	NW Bangladesh Belpukur, Rajshahi Samsadipur, Rajshahi
India	Haryana Sukhomajri, Ambala Maharashtra Kadus, Pune Sahajpur, Pune Satara, Pune Shindwane, Pune Shiradhon, Aurangabad Yavat, Pune Tamil Nadu Thennalur, Pudukottai Vadapalanji, Madurai
Nepal	Kaski Rakhi, Rakhi Panchayat Lekhnath, Lekhnath Kavre Kankre, Ugrachandi Tusal, Ugrachandi
Sri Lanka	Kandy Bambarabedda, Udadumbara Madugalla, Udadumbara
Southeast Asia	
Indonesia	West Java Karangasari, Padaherang, Ciamis Payangagung, Panumbangan, Ciamis
Philippines	Bauko Barangay, Bila Barangay, Guizadon Laguna Jose P. Laurel Juan Santiago Leyte San Isidro, Baybay San Miguel, San Isidro Mindoro Oriental Barangay Paiton, Nanjan Sitio Banilad Barangay, Dulangan 3
Thailand	Kalasin Ban Kam Kham, Nong Kung Si Ban Non Si Sawat, Nong Kung Si Chachoengsao KM 7, Sanamchaikhet Nongyang, Sanamchaikhet

Method

To identify appropriate ideotypes based on actual uses and preferences of small-scale, poor-farm households, a 10-step method was developed. The study built on the existing effort of an already established regional study on farm- and village-forestry land-use practices.[2]

Recommended methods for this study were divided into 10 steps:

1. A listing of priority species and such tree products as fuelwood, fodder, timber, and fruit was summarized for each household.

   This step used data from the regional study on farm- and village-forestry land-use practices. Researchers from India used the same format as the others to collect this data. Steps 2 through 7 below were conducted with the cooperation of five males and five females selected from the households participating in the regional study.

2. In discussions, the ten respondents in each village ranked products of each species.

3. Respondents were asked to describe the planting niches they preferred for these priority species, such as home gardens, field margins, intercropped with annual staple crops, etc.

4. Respondents were also asked to describe the characteristics they disliked about the priority species identified above.

5. Respondents were asked to identify in or near their community the top three individual trees for each priority species. They were asked why these trees were superior or preferred. Clearly labelled photographs were taken of each tree. Respondents were also asked to identify the source of the planting materials for these trees (e.g., neighbor, forestry department, private nursery, natural forest).

Lert Chuntanaparb

Preferred ideotype of the fast-growing MPT, Sesbania grandiflora, *in Thailand. Farmer-described ideotypes often included multiple stems, low branching, and heavy flower or fruit production.*

Lert Chuntanap

Preferred ideotype of a forest tree species, Shorea siamensis, *in Thailand. In general, ideotypes preferred by farmers for traditional, forest tree species differed little from those presently used by forest geneticists.*

[2] Conducted at all sites included in this study except those in India.

6. Respondents were asked to identify tree species that were used to provide the priority products listed in Step 1, but that were not as desirable and why.

7. A series of line drawings of the following tree parts was used to help informants describe the ideotypes they would like for each priority species (Fig. 1). The drawings included:

   - branching habit (e.g., many or few large branches, arrangement of branches [phylotaxy])
   - stem form (e.g., single stem, multi-stemmed, straight, crooked)
   - foliage characteristics (e.g., palatability, leaf size)

8. Information collected in Steps 2 through 7 was summarized after the second field visit. This synopsis provided the basis for the presentation made in Step 9.

9. The summaries were presented and discussed in group meetings with villagers. (At least one group meeting in each village was to be held with a women's group.) These meetings were conducted to reach a consensus on the ideotypes described by the sampled households. The line drawings in Step 7 were used as a basis for discussions.

   Step 9 was performed on a third site visit.

10. The researchers provided the study cooperators with summaries of up to six composite ideotypes that the villagers agreed on in Step 9. Study coordinators reviewed the composite ideotypes from which to abstract major generalizations about breeding characteristics for MPTS.

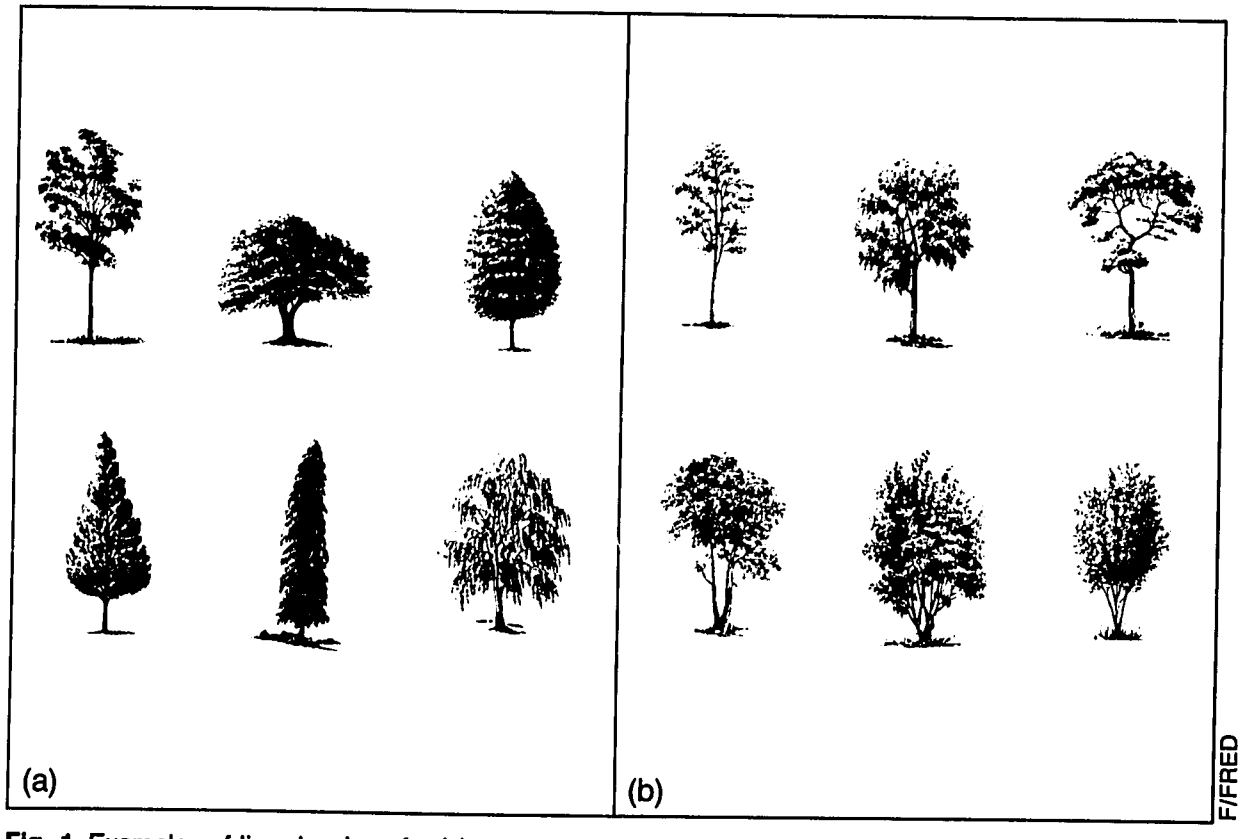

Fig. 1. Examples of line drawings for (a) canopy shape and (b) stem form.

Tree Uses and Ideotype Specifications

Species used and preferred by poor, small-scale farmers in the study communities have been broadly divided into three categories: 1) fruit and food tree species, 2) fast-growing MPTS on farms, and 3) forest tree species. The species, their uses, and the countries in which they are used are listed in Table 2. General ideotypes for each category are described briefly following the findings of Chuntanaparb and Ranganathan (1990) and Ranganathan (1990).

Table 2. Tree Use Practices by Small Farmers in Asia

Species	Countries	Uses*
Fruit and Food Species		
Achrus azpotta	Indonesia	Fruit, Minor timber
Artocarpus altilis	Sri Lanka	Fruit, Timber, Fuelwood
Artocarpus heterophylius	Bangladesh, Philippines, Sri Lanka, Indonesia	Fruit, Fuelwood, Fodder, Timber, Medicinal purposes
Cocos nucifera	Sri Lanka, India, Philippines	Fruit, Timber, Other minor uses
Coffea arabica	Philippines	Fruit, Fuelwood, Medicinal purposes, Mulch
Madhuca longifolia	Sri Lanka	Fruit, Timber, Fuelwood
Mangifera indica	Bangladesh, India, Sri Lanka, Philippines	Fruit, Fuelwood, Timber, Fodder
Parkia speciosa	Indonesia	Food, Fuelwood
Persea americana	Philippines	Fruit, Fuelwood, Timber, Medicinal purposes
Persea gratissima	Sri Lanka	Fruit, Fuelwood
Pithecellobium dulce	India	Fruit, Fodder, Fuelwood
Psidium guajava	Sri Lanka, Philippines	Fruit, Timber
Sesbania grandiflora	Thailand	Food, Soil conservation, Fuelwood
Syzgium cuminii	India	Fruit, Fuelwood, Timber
Tamarindus indica	Sri Lanka, India	Fruit, Fuelwood, Timber, Medicinal purposes, Fodder
Zizyphus mauritiana	India	Fruit, Fuelwood, Timber, Fodder
Fast-growing MPTS		
Acacia leucophloea	India	Fuelwood, Timber, Fodder
Acacia nilotica var. *cupressiformis*	India	Fuelwood, Fodder, Timber
Acacia nilotica var. *indica*	India	Timber, Fodder, Fuelwood, Tannin
Ailanthus excelsa	India	Mulch, Timber, Fuelwood
Albizia falcataria	Philippines	Fuelwood, Handicrafts

Table 2. Continued

Species	Countries	Uses*
Fast-growing MPTS (Continued)		
Albizia lebbek	India	Fuelwood, Timber, Fodder, Mulch
Albizia procera	Indonesia	Timber, Fuelwood, Fodder
Alnus maritima	Philippines	Fuelwood, Shade, Fencing, Mulch
Alnus nepalensis	Nepal	Fuelwood, Timber
Azadirachta indica	India, Thailand	Fuelwood, Fodder, Timber, Medicinal purposes, Mulch
Betula alnoides	Nepal	Fuelwood, Timber, Fodder
Borassus flabellifer	India	Timber, Fruit, Leaves (as construction material), Other minor uses
Carissa spinarum	India	Fuelwood, Fruit, Medicinal purposes
Ceiba pentandra	Thailand	Fuelwood, Silk-cotton
Dalbergia sissoo	India	Fuelwood, Timber, Soil conservation
Delonix elata	India	Mulch, Timber, Fuelwood
Eucalyptus camaldulensis	Philippines	Timber, Medicinal purposes
Gliricidia sepium	Sri Lanka, Philippines	Fuelwood, Mulch, Fodder, Timber, Food
Leucaena leucocephala	Thailand, Philippines, India	Fuelwood, Fodder, Mulch, Timber, Food, Windbreak, Shade
Maesopsis eminii	Indonesia	Timber, Fuelwood, Fodder
Melia azedarach	India	Fodder, Fuelwood, Timber
Morus serrata	India	Fuelwood, Fodder, Fruit, Handicrafts
Paraserianthes falcataria	Indonesia	Timber, Fuelwood, Fodder
Prosopis juliflora	India	Fuelwood, Fodder, Timber
Prunus cerasoides	Nepal	Fuelwood, Fodder, Timber
Sesbania sesban	India	Fodder, Fuelwood, Timber
Thespesia populnea	India	Mulch, Fodder, Timber, Fuelwood
Natural-Forest Tree Species		
Albizia amara	India	Timber, Fuelwood, Fodder
Cotylelobium melanoxylon	Thailand	Timber, Fuelwood
Dipterocarpus alatus	Thailand	Timber, Fuelwood
Dipterocarpus grandiflora	Philippines	Fuelwood, Timber

Table 2. Continued

Species	Countries	Uses*
Natural-Forest Tree Species (Continued)		
Dipterocarpus obtusifolia	Thailand	Fuelwood, Timber
Dipterocarpus tuberculata	Thailand	Fuelwood, Timber
Irvingia malayana	Thailand	Timber, Fuelwood
Phocebe sterculiodes	Philippines	Timber, Handicrafts
Pinus kesiya	Philippines	Timber, Fuelwood
Pterocarpus indica	Philippines	Timber, Fuelwood
Pterocarpus macrocarpa	Thailand	Timber, Fuelwood
Schima wallichii	Nepal	Timber, Fuelwood
Shorea obtusea	Thailand	Fuelwood, Timber
Shorea siamensis	Thailand	Fuelwood, Timber
Vitex parviflora	Philippines	Timber, Fuelwood

*Note: While all species have environmental uses, this list is restricted to farmers' intentional purposes.

Fruit and Food Tree Species

Fruit trees and other woody perennials are important sources of nutrition and income for rural households. The importance of coconut (*Cocos nucifera*) and mango (*Mangifera indica*) in rural economies is well-documented. Small farmers often plant a few fruit trees in their home gardens, but the situation is changing where farmers find fruit trees more remunerative. The study participants found a total of 15 multipurpose fruit/food trees being used by farmers in the study region. In addition to these major uses, all species have other such end uses as fodder, fuelwood, timber, and medicine.

Several generalizations across Asia can be made from the farmers' ideotype descriptions for these species. The major selection criteria for improvement are vigor, fruit yield and quality, early fruit set, and resistance to pests and disease. In addition, woody biomass is an important characteristic for farmers. Over 75% of all fruit and food species are used for fuelwood. In some cases, this is true even during the period when fruit yields are substantial (e.g., *Mangifera indica*, *Zizyphus mauritiana*, *Artocarpus heterophyllus*, *Coffea arabica*). Other species are used as fuelwood when fruit yield is on the decline. Over 50% of these species are used for timber when the tree no longer yields adequate quantities of fruit.

Farmers generally want the following traits for these fruit/food species:

1) a medium to large crown with many branches high on the stem;

2) single, straight, clear bole with no branches low on the stem;

3) deep tap root to withstand strong winds, bind the soil, and improve the infiltration capacity of the soil; and

4) vigorous regrowth after pruning or lopping of branches for fodder and fuelwood without reduced fruit yield.

While fruit is the major priority, selection criteria for improvement should amend traditional fruit-tree improvement methods to consider fuel and wood characteristics. For fruit trees also used for timber, stem form should be an important objective.

Fast-growing MPTS

While some may argue that all species in this category are not fast-growing, the classification is useful for trees growing on small farms. All trees are used in some combination for timber, furniture, handicrafts, toolmaking, fuelwood, and fodder. Farmers listed fuelwood as the major end use for only 8 of the 29 species grouped under this category. Fuelwood is listed as only one of many end uses for the other species.

A general ideotype description for these species is a tree with a large crown and many branches, straight stem (either single or multiple), with no low branching. A single long, straight stem is preferred if timber is an end use. The ability of the ideotype to vigorously resprout after harvest (coppicing, pollarding, or lopping) is also an important attribute from the farmer's perspective.

Leucaena leucocephala, *Sesbania sesban*, and *Prunus cerasoides* are the only species for which fodder is a major end use, although over 60% of the species in this category can be and are used for fodder. For the species from India, farmers report that 13 of the 17 can be used as fodder, but only four (*S. sesban*, *Prosopis juliflora*, *L. leucocephala*, and *Acacia nilotica*) are regularly used as fodder. Leaves have a competing use as mulch. *Prosopis* and *Acacia* pods are popular fodder but only in a few cases did farmers report that they harvested the pods regularly as fodder. Villagers in Sri Lanka use *Gliricidia sepium* as fodder, but it is not a major end use. Some of the sites in Thailand and the Philippines reported fodder as the major use of *L. leucocephala.*

The general ideotype description for fodder species is similar to that for fuelwood species, although many branches and dense foliage are also desired. Farmers want single or multiple stem(s) depending on the trees' other uses. Quick and prolific regrowth after lopping and shorter periods of deciduousness are also among the ideotype specifications expressed by farmers. For species with edible pods, farmers want trees to produce longer and fleshier pods.

The use of tree leaves as mulch in the study region was observed to be mainly for high-value crops like paddy and vegetables. Farmers in Thailand and the Philippines use *Leucaena* as a green manure. *Gliricidia sepium* is used in Sri Lanka and Thailand. *Delonix elata*, *Thespesis populnea*, *Albizia lebbek*, and *Ailanthus excelsa* are popular mulch species in parts of India. Ideotype specifications for mulch species are similar to those for fodder species.

Timber is the most important end use of fast-growing MPTS. Close to 80% of the 29 species in this category are used for timber. Some timber species have specific uses for which another species is substituted only if the one preferred is unavailable. Farmers have used stem form as part of their selection criteria to modify the species to their requirements. The most important characteristic of timber species is a long, straight bole with no branches up to a minimum height of about 3 m. Farmers are interested in improved wood characteristics such as durability, strength, resistance to termites and wood borers, and other properties desired by local timber markets.

Forest Tree Species

This ideotype was similar for natural forest species used for multiple purposes. Asian farmers who reside in or near remaining natural forests still use forest trees for timber and fuel. General selection criteria for this group of species were nearly identical for the timber uses of fast-growing MPTS.

Conclusions

MPTS ideotypes as described by farmers differ significantly from those commonly used as tree improvement objectives. For fruit and food species, additional emphasis is needed on such traits as stem form and branching to enhance further the quantity and value of timber. For example, multiple stems are not a constraint to fast-growing MPTS, but are rather desirable traits for many planting niches and end uses.

Some general ideotypes were common to all species irrespective of end uses:

1. Deep roots geotropically angled to allow the tree to withstand strong monsoon winds (Thailand, Indonesia, India) cyclones (Sri Lanka, India, Bangladesh), and typhoons (Philippines). Roots should

be able to bind the soil to prevent erosion on slope sites and increase the infiltration rates as well.

2. Reduced or complete absence of thorns.

3. Rapid growth. Farmers want fast, early growth to minimize the need to protect seedlings from grazing animals. In most cases, small farmers want fast growth for quick economic returns.

4. Vigor and resistance to insect pests and disease.

The definition of MPTS ideotypes for small-farm use is an essential step in tree improvement if this research is to benefit small farmers. The results of this study point to the need to redefine improvement objectives for MPTS. The diversity of farmer needs across villages, regions, and nations suggests that tree improvement professionals also need to consider conducting similar studies with their client end-users before beginning major improvement programs.

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Designing Experiments for MPT Genotype Evaluations

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Many types of experimental designs are available to breeders of multipurpose trees. Experiments must be properly planned and designed to obtain reliable results of the relative performance of the provenances or families tested. Such experiments may also function to estimate genetic variances and covariances or act as seed orchards. Some other functions are easier to accommodate within the experiment than others. Before beginning, it is important to define the experiment objectives exactly so that the design accommodates them.

Why Design Is Important

Why not make a plantation of each species, provenance, or family (hereafter referred to as "entries") and see which performs best? Performance depends not only on genes, but also on the environment in which they grow. The objective of designing field trials is to detect any differences between entries that are not due to chance.

Suppose we plant an experiment with five provenances, each making up a block (Fig. 1).

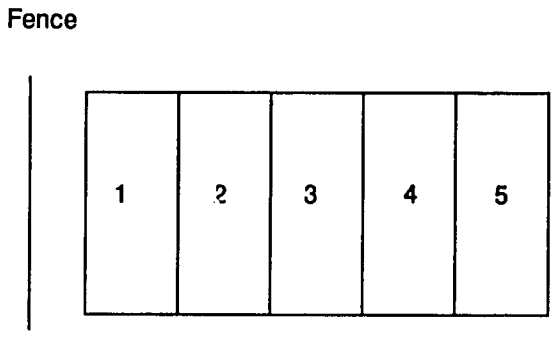

Fig. 1. Experimental blocks with 5 provenances

When we measure the experiment, we may find a gradient in growth from one end of the experiment to the other. Fig. 2 shows how plotting growth against distance from the fence would look.

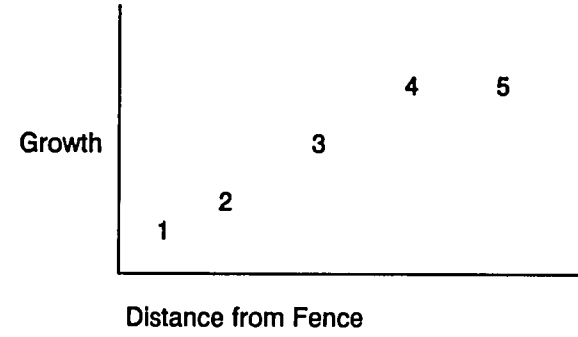

Fig. 2. Plotting growth against distance from fence

We could not be sure whether the larger trees in provenances 4 and 5 were taller because they were genetically superior to the other provenances in the trial or because of some environmental gradient that improved the site further from the fence.

This simple example shows that experiments must be designed to permit hypotheses about the species or provenances to be tested. It is usual to have a "null" hypothesis, i.e., no differences between entries. We reject this hypothesis (analogous to disproving a contention by finding a single counter-example) and accept an alternative hypothesis that the entries differ. In the above case, the genetic and environmental influences on growth are confounded and cannot be separated. This experiment will not provide any information about how these provenances are likely to perform elsewhere. Even if we reject the null hypothesis, the alternative hypothesis cannot separate the genetic and environmental effects.

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Arrangement of Blocks

It is clear that blocks should be arranged to take account of known environmental gradients. A possible design to include the gradient from left to right is shown in Fig. 3. Because each block (column) contains all five provenances, all five have an equal chance of growing on good and poor parts of the site. If there is still a gradient in growth with distance from the fence, this can be ascribed purely to a site or environmental effect. The mean values for each provenance taken over all blocks will represent each provenance's growth potential.

Replicate

Fence	1	2	3	4	5
1	1	1	1	1	1
2	2	2	2	2	2
3	3	3	3	3	3
4	4	4	4	4	4
5	5	5	5	5	5

Fig. 3. Blocks arranged to take account of left-to-right environmental gradient

Plot Layout

A well-designed experiment is usually defined as one in which the experimental error (that part of the variation due to unknown causes) is as small as possible. In few, if any, cases can all sources of environmental variation be identified in advance. In the above example, there may be a gradient from top to bottom as well as from left to right. In this case, the results would be invalid because the species' means would include the systematic environmental variation from the top to the bottom.

A better design would ensure that systematic differences from left to right and from top to bottom are experienced equally by all provenances (Fig. 4).

Fence

1	3	2	5	4
2	4	5	3	1
3	1	4	2	5
4	5	3	1	2
5	2	1	4	3

Fig. 4. Blocks arranged to take account of both left-to-right and top-to-bottom environmental gradients

Variation from top to bottom is accounted for by the differences between rows. Variation from left to right is accounted for by differences between columns.

One of many possible examples of such gradients is an experiment planted close to the sea. In this case, it is likely that the wind would carry salt, which could reduce tree growth. In addition, salt would more likely be deposited in the soil nearer the sea. A poorer growing environment is to be expected closer to the sea than further from it. Blocks should be arranged to take this into account.

If the experiment is to be planted on a hillside, it might be expected that the top of the hill is a poorer growing environment than the bottom. This could be caused by erosion of nutrients from the top to the bottom and by higher winds and greater exposure at the top. On the other hand, the presence of a stream at the bottom of the hill could indicate waterlogging of the soil after rain. There may even be watercourses that appear only after rain.

In general, it is preferable to place blocks at right angles to known environmental gradients (Fig. 8, p. 59). This minimizes variation within each block or replicate. If this is not done, variation within blocks that should be ascribable to genetic differences between provenances will, in fact, be caused by environmental factors.

The following two statistical techniques can help reduce the effects of such variation that cannot be determined in advance:

- Randomization. Entries should be assigned to plots within blocks or replicates at random so that environmental effects within blocks randomly affect entries under test. This can be done either from tables of random permutations (Fisher and Yates 1963, Cochran and Cox 1957, or Green 1968) or by generating pseudorandom numbers in a computer. One assumption of the analysis of variance is that the residual variation is normally distributed and that the errors are uncorrelated. If entry 1 were always planted next to entry 2, for example, the random environmental effects would tend to be similar on both entries and the errors would be correlated. Proper randomization leads to these entries appearing next to each other with a known probability dependent only on the number of entries in the trial.

- Replication. Plots of each provenance or family under test should be replicated at each experiment site. This means that several plots of each entry should be planted at each site. Plots are usually grouped into block replications, i.e., each block contains one plot of each entry. Blocks are then arranged as above to take account of some of the environmental variation. Without replication, we cannot estimate genotype x site interactions free of variation within each site. The standard errors of differences between entry means from each site decreases as the square root of the numbers of replications increases, so the increase in precision from three to four replications is greater than that from 19 to 20 replications. The optimum number of replications depends on the inherent variability of the entries and the budget allocation for the experiment. In any case, it should not be less than four (except for some lattices).

  One rule of thumb for obtaining the number of replications is that the residual degrees of freedom in the analysis of variance should be 10 or more (Burley and Wood 1976). If the level of variability in the test material is known in advance, the required number of replicates $(r) = t^2 \times range)/8 \times LSD^2)$, where t is Student's "t" for the appropriate degrees of freedom and *LSD* is the Least Significant Difference between entry means (Burley and Wood 1976). Other approaches are given in Cochran and Cox (1957).

Plot Size

Plot size is a function of the number of trees in the plot and the space occupied by each tree. Each site has its own features, and no single design or layout is preferable for all conditions. In general, smaller plots are preferable to larger ones because they lead to more environmentally uniform blocks (Fig. 5). It is important to minimize environmental variation within blocks.

On the other hand, smaller plots have competition effects between adjacent plots that are larger in relation to competition within plots; i.e.,

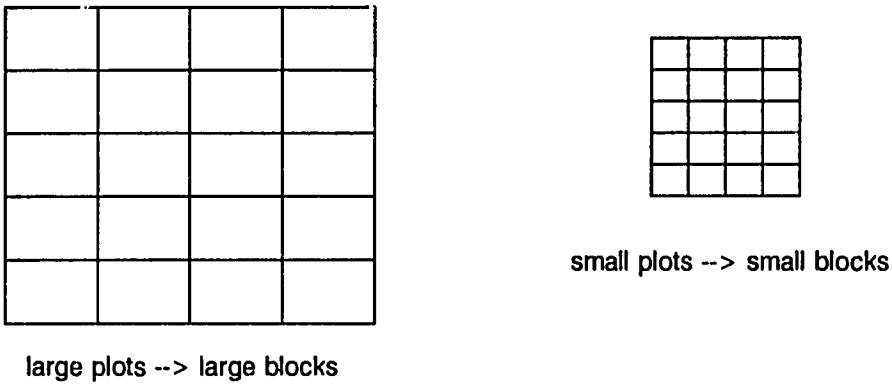

Fig. 5. Larger plots create larger blocks, which are less uniform environmentally than smaller ones.

they have greater length of boundary in relation to plot area. If competition between plots is likely to be large, the plots should tend to be larger (Fig. 6). This is likely the case for species trials and some provenance trials, particularly long-term ones. Large plots also demonstrate such differences more readily to the eye.

Two kinds of inter-tree competition are (1) with like trees (same plot) and (2) with unlike trees (adjacent plots). The smaller the plot area, the smaller the component due to competition with like trees. Competition with unlike trees is more heterogeneous because there are four unlike adjacent plots. It is preferable to minimize this competition component.

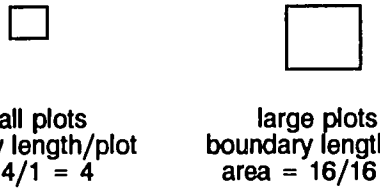

Fig. 6. Comparison of boundary length/plot area ratio of small and large plots

If competition between adjacent plots is large, the outer row of large plots can be ignored for analytical purposes. The larger the plots, the more efficient this procedure becomes. If competition between adjacent plots is small and differences between entries small, plots can be small and the number of replicates large. Many designs are available to help cope with these problems. The main criterion in choosing an experimental design is its ability to minimize unexplainable variation--the experimental error. This must be done, of course, within the constraints of available land and money, as well as the amount and level of skilled labor.

Types of Design

Completely Randomized Design (CRD)

Replications that do not form discrete blocks but are randomized throughout the whole experimental area are "wholly randomized" (Fig. 7). The analysis has terms representing differences between entries, between plots, and within plots. Differences between plots contain environmental variation within the experimental site, as well as interactions between entries and this environmental variation. This design is suitable only for particularly uniform sites. On more normal sites, it does not discriminate between entries as efficiently as do other designs.

Randomized Complete Blocks (RCB)

The RCB design is most commonly used in forestry experiments (Fig. 4, p. 56). Once the

2	2	5	2	1
4	1	4	1	3
3	5	3	5	3
5	1	2	4	2
5	4	1	3	4

Fig. 7. Completely randomized design of 5 entries with 5 replicates

number of replications (which, in this case, form blocks) has been decided, entries are allocated to plots at random within each block. Because each block contains one plot of every entry, blocks are said to be "complete." RCBs are slightly more difficult to arrange and analyze than completely randomized designs. However, they do permit some consideration of variation across the experimental site (Fig. 8).

In Fig. 8, the RCB design has restricted the allocation of entries to the 5 x 5 array of available spaces so that each of the five entries appears once in each column. Each column forms a discrete block in this case. Allocation of entries within each block must be at random for this to be an RCB design. As discussed earlier, blocks should be laid out at right angles to known sources of variation, such as slope. If there are no known sources of environmental variation, blocks should be as compact as possible (i.e., square) so they are as environmentally homogeneous as possible.

The analysis of variance of RCB designs has terms for differences between entries, differences between replicates, and interaction between entries and blocks, as well as the residual or error term. Interaction between entries and blocks may be due to "preferences" of entries for the environmental conditions within particular blocks. Or it may be due to environmental heterogeneity within blocks. In either case, it represents variable performance of entries in different blocks.

If the number of entries is large, block size is also generally large (Fig. 5, p. 58). The larger the blocks, the more likely is environmental heterogeneity within blocks. This is particularly likely when plots are large. As a rule of thumb, when there are more than 20 entries, some other design should be used, especially when the site varies considerably.

Replicate

1	2	3	4	5
1	2	1	3	2
4	1	5	4	5
2	5	4	2	4
3	4	3	1	3
5	3	2	5	1

<--| direction of site gradient e.g., slope

Fig. 8. Randomized complete blocks with 5 entries in 5 complete block replications

Latin Squares

While RCBs effectively take account of known environmental variation in one direction, variation in two dimensions may occur, such as a slope in one direction and aspect variation as the slope goes around a hill. It is possible to arrange the experiment to take both gradients into account. In a Latin Square (Fig. 9), entries are present exactly once in each row and each column of the layout.

		Column				
		1	2	3	4	5
	1	1	5	2	3	4
	2	5	3	4	2	1
Row	3	4	2	5	1	3
	4	2	1	3	4	5
	5	3	4	1	5	2

Fig. 9. Latin Square with 5 entries

Variation in one direction is estimated by the differences between rows and in the other between columns. Latin squares are not used widely in forestry because there are other ways of taking two environmental gradients into account that require less land. If there are more than five or six entries, other designs are easier to lay out on the ground.

Incomplete Block Designs

Incomplete block designs are used to compare large numbers of entries (i.e., more than 20), but can also be used for smaller numbers. Entries are planted in groups or blocks that are smaller than a complete replication. Each group of plots forms an incomplete block. Many incomplete block designs are described by Cochran and Cox (1957).

Where incomplete blocks can form a discrete replication, the design is "resolvable." Resolvable designs can be analyzed as RCBs, if necessary. This is a great advantage if computing facilities are limited, if the trial has been damaged, or if it is more efficient to do so. Some designs are not resolvable (Fig. 10). In this case, the incomplete blocks cannot be grouped into discrete replications. Non-resolvable designs are not recommended as the analysis options are too limited.

Block						
1	2	3	4	5	6	7
1	2	3	4	5	6	7
2	3	4	5	6	7	1
4	5	6	7	1	2	3

Fig. 10. Balanced Incomplete Block (BIB) design of 7 entries in 7 blocks with 3 replications

Lattices

This class of incomplete block designs is probably the most useful for forestry experiments because it is available for large numbers of entries and relatively few replications. Lattices make best use of limited land and can take many kinds of environmental heterogeneity into account. Although analysis is considerably more complicated than for randomized blocks, the availability of both small computers and programs to analyze lattices makes this a small consideration. Standard errors of differences of means (SED) are almost always smaller for lattice designs than for RCBs of the same size. For this reason, experiments can usually be somewhat smaller for lattices than for RCBs yet achieve the same precision. In the few cases where SEDs are not smaller for lattices, the experiment can be analyzed as a RCB because lattices are resolvable.

Lattices are balanced when the pairwise comparisons between entries are of equal precision. This is ensured by entries occurring in the same incomplete block with each of the other entries the same number of times.

For square lattices, the number of entries is an exact square (i.e., k^2). There are square lattices for 9, 16, 25, 26, 49, 64, 81, 100, 121, 144, etc., although only those for 9, 16, 25, 49, 64, 81, 121, etc. can be balanced. The numbers of replicates required for balance in these cases is $(k + 1)$. Lattices with fewer replicates are "partially balanced" and the analysis more complex.

Computer programs are available to analyze both balanced and partially balanced lattices with equal facility (SASS 1987). An example of a 3 x 3 balanced square lattice is given in Fig. 11. Rectangular lattices have $k \times (k + 1)$ entries (i.e., 12, 20, 30, 42, 56, 72, 90, etc.) (Fig. 12). For cubic lattices, the number of entries is a cube rather than a square, i.e., 27, 64, 125, 343, 512, 729, etc. entries. There are successful provenance trials with 64 entries of *Eucalyptus regnans* (Eldridge 1972) and 216 entries *E. obliqua* (Brown et al. 1976).

	Replicate 1			Replicate 2			Replicate 3			Replicate 4		
Block 1	1	2	3	1	4	7	1	5	9	1	8	6
Block 2	4	5	6	2	5	8	7	2	6	4	2	9
Block 3	7	8	9	3	6	9	4	8	3	7	5	3

Fig. 11. Balanced square lattice with 9 entries and 4 replicates
Source: Cochran and Cox 1957, p. 428

	Replicate 1			Replicate 2			Replicate 3		
Block 1	1	2	3	4	7	10	6	8	12
Block 2	4	5	6	1	8	11	2	9	10
Block 3	7	8	9	2	5	12	2	4	11
Block 4	10	11	12	3	6	9	1	5	7

Fig. 12. Rectangular lattice of 12 entries in 3 replicates
Source: Cochran and Cox 1957, p. 435

A new class of lattices, termed generalized lattices, has been developed (Patterson and Williams 1976, John 1987). These designs, which include alpha-designs, do not have $k \times k$ entries as in square lattices or $k \times (k + 1)$ as in rectangular lattices, but have $k \times s$ entries., where s is any integer (Fig. 13). It is even possible to have incomplete blocks of different sizes, so s does not have to be an integer.[1] Computer programs are now available for use on IBM compatibles and perhaps others to generate and analyze alpha-designs (SASS 1987, Robinson 1987).[2]

	Replicate 1			Replicate 2			Replicate 3			Replicate 4		
Block 1	10	15	13	14	13	12	13	7	5	2	7	3
Block 2	12	9	7	3	5	1	2	9	14	13	1	8
Block 3	6	2	1	9	8	4	6	10	8	12	6	4
Block 4	8	14	3	7	15	6	4	3	15	10	9	5
Block 5	5	4	11	11	2	10	11	1	12	11	14	15

Fig. 13. Example of alpha-design (a generalized lattice) with 15 entries in 4 replicates (generated using the computer program ALPHAGEN on an IBM-compatible PC)

[1] E.R. Williams, personal communication.

[2] Data from such alpha-designs may be analyzed using the programs ALPHANAL or REML, available from the Scottish Agricultural Statistical Service, University of Edinburgh, James Clerk Maxwell Building, The King's Buildings, Mayfield Road, Edinburgh, EH9 3JZ, Scotland. REML will be available in the next version of the general statistical package GENSTAT (GENSTAT 5 Committee 1987).

Neighbor Designs

New methods of analysis are becoming available in which adjustments to plot means are based on the adjacent plot rather than on the incomplete block to which the plot belongs. One approach is to take the difference between the means of adjacent plots, called "first differences," and then fit an ARIMA 101 time series model to the data. This is used in the computer program SAFE (Spatial Analysis of Field Experiments) available from the Agricultural Research Institute at Wagga Wagga in Australia. The program has been used successfully for agricultural experiments on cereal crops, but at present requires a strictly rectangular field layout for block replicates, precluding many, if not most, forestry experiments. Other approaches are analogous, e.g., Williams (1986). Programs can probably analyze almost any field design, from completely randomized designs to generalized lattices, but design principles are involved to maximize efficiency (Wild and Williams, 1987).

Plot Arrangement

In well-designed experiments, the unexplained variation (usually within plots) is small. The source of most such unexplained variation is environmental heterogeneity. Causes include soil variability, variability in planting technique, pests and diseases, and physical damage by game. These effects may be minimized by arranging plots so that blocks are as compact as possible, containing environmental differences in those between blocks. Environmental variation within blocks should be minimized, but should be shared by all the plots in the block (Fisher 1971). Where this is not done, the differences between plots are partly caused by environmental differences within blocks and appear in the analysis of variance as entry x block interactions.

Single-tree Plots

Designs discussed apply equally to plots of any size and shape, from 100-tree to single-tree plots. Some genetics experiments seek to minimize the effects of such common environments as common litters in animals or multiple-tree plots in trees. Progeny tests are sometimes used as seed orchards for which single-tree plots minimize inbreeding between adjacent trees. In such cases, single-tree plots are indicated. The loss of single trees clearly leads to the loss of whole plots involving a cost in terms of accuracy and interpretation. In addition, the means of multiple-tree plots are more likely normally distributed (an assumption of the analysis of variance) than observations from single-tree plots. Although many computer programs can handle missing trees or plots either by estimating missing values, which inflates estimates of entry effects, or by ignoring them (as in General Linear Model programs), missing plots should be avoided as far as possible.

Non-contiguous Plots

So far, we have considered only contiguous plots in which multiple-tree or single-tree plots are arranged in blocks of some sort. When using RCBs, the trees comprising each plot can be arranged at random throughout the block rather than in contiguous plots. Libby and Cockerham (1980) proposed this arrangement to overcome the problem of how to handle mortality in single-tree plots, which causes analysis problems. The mean of a 10-tree plot is little different in precision from the mean of a 9-tree plot with one tree missing. The main problem with non-contiguous plots is that the component of variation for block x entry interaction is mostly the same as the intra-plot error (Matheson 1990). They are both caused by environmental heterogeneity within replicates although some true interaction may occur. There is, therefore, no interpretable statistical test for the significance of the variability within replications.

Nested Entries

So far, entries have been treated as if they had a single level, i.e., species, provenances, or families. It is perfectly feasible to combine species and provenance trials so that a single experiment tests not only for species differences, but also for differences between provenances. One compelling argument contends that species cannot be represented by a single provenance, and bulking seed to represent a species begs questions about how the bulking should be carried out. It is also possible to combine provenance and progeny trials and examine the significance of genetic variation at different hierarchical levels within a species. Provenances may differ significantly with essentially no genetic heterogeneity at the family level. Alternatively, families may vary so much

within provenances that small differences between provenances are difficult to detect. This can profoundly affect the way seed-sampling strategy is designed.

Such experiments can be designed in one of three ways. In all three, entries are classified according to the hierarchical levels represented. For a provenance/progeny trial, entries are families, with 5 or 10 families per provenance, not necessarily the same number of families for every provenance.

In the first design, families may be physically grouped together into provenance main plots in each block, forming sub-plots within the main plots. In the second design, families may be allocated to plots at random in each block, regardless of provenance. In general, it is better not to have provenance main plots because the families within provenances experience less environmental variation (because they are physically together) than the provenances. This means that the provenance variance will contain a level of environmental variation not experienced by families. Entries are better allocated at random so that the variance between them can be partitioned into a component due to variance between provenances and another within provenances (i.e., families). The third design maximizes the precision of particular comparisons (e.g, families within provenances) in incomplete block designs by ensuring they appear together in an incomplete block.

Genotype x Environment Interactions

Large genotype x environment interactions can mean that the best entries for one environment are not best for another. Deciding whether to breed for separate environments depends on the level of interaction and its effect on ranking entries.

Forestry environments are rarely defined sufficiently to repeat them. This is less true for glasshouse or controlled environment studies than for field trials, even fertilizer trials. There is a fundamental dichotomy in models used in the analysis of variance--the difference between fixed and random effects. Fixed environments are under the control of the experimenter and are repeatable (without error). For example, the effects of alpine and coastal environments are fixed if the sites were chosen to represent one or the other environment. A particular site is either alpine or coastal, known without error. On the other hand, many experiments are grown on sites not chosen to represent environments, but a sample of all possible sites. Site effects in this case are random. Entries representing a random effect are assumed to be a random sample of all such possible entries; inferences are made about the whole population, not just the sample. Entries representing a fixed effect by themselves represent the whole population about which inferences are made.

This dichotomy bears on the utility of interactions between genotypes (in this case, genotypes are genetic entities with a degree of repeatability, i.e., clones, families, provenances, or species) and sites (Wright 1976). Where sites are well-defined, they are repeatable and the interactions with known genotypes are also repeatable. Where sites are chosen essentially at random and are not well-defined, interactions are unpredictable and can lead to choosing an inferior genotype for planting at a particular site.

Management of experiments planted on several sites can create a problem, especially where the sites are owned by different organizations and perhaps are located in different countries. One is tempted to permit the application of "local standard" silviculture on each site, resulting in different silviculture on each site. Where this is done haphazardly, it is a random effect and is totally confounded with differences between sites.

Experiments that examine management x genotype interactions within and between environments are particularly important for MPTs. MPTs are managed in many distinct ways, compared with industrial forestry plantations. For example, MPTs managed for fuelwood, animal feed, or green manure may be periodically pruned or pollarded. Using this type of management, the results in the ranking of performance between genotypes may or may not differ from those of an experiment in which MPTs are not pruned or pollarded. To be useful, interactions between silviculture and genotypes must become a designed part of the experiment (Fig. 14). Environments should be well-defined and repeatable for the interactions to be useful (Matheson and Cotterill, in press).

In reality, many more families and treatments are likely than those shown in Fig. 14. The treatments

Environment 1

Block 1		Block 2	
trt1 fam1	trt2 fam2	trt2 fam1	trt1 fam2
trt2 fam3	trt1 fam3	trt2 fam3	trt1 fam1
trt1 fam2	trt2 fam1	trt1 fam3	trt2 fam2

Environment 2

Block 1		Block 2	
trt2 fam1	trt2 fam3	trt2 fam3	trt2 fam2
trt1 fam3	trt2 fam2	trt2 fam1	trt1 fam3
trt1 fam2	trt1 fam1	trt1 fam1	trt1 fam2

Fig. 14. Combining 2 silvicultural treatments (trt) into a progeny test of 3 familles (fam)

may combine site preparation, cutting regime, or cut versus noncut trees. It is also quite possible that the family growing best in treatment 1 does not grow best in treatment 2. The results from environments 1 and 2 may also differ.

Some calculations can be made even when the environments are random. Falconer (1952, 1960) proposed that the concept of genetic correlation between two characters (Hazel 1943) be extended to include the genetic correlation between the same character in two environments. This genetic correlation is approximately the correlation between family means *(r(xy))* divided by a pooled estimate of the heritabilities of the character at each site (Burdon 1977):

$$rG(xy) = \frac{r(xy)}{\sqrt{[(h^2(x) \cdot h^2(y)]}}$$

This genetic correlation allows us to estimate how much gain we can make at one (random) site y by making selections at another (random) site x for the same character. The correlated response (CR) to selection is:

$$CR = i \cdot h(x) \cdot h(y) \cdot rG(xy) \cdot \sigma Py$$

where *i* is the intensity of selection and σPy the phenotypic standard deviation at site y.

Genotype x environment interactions reduce the precision of selection by increasing the phenotypic variance for a given level of genetic variance. Heritability, the proportion of phenotypic variance transmitted to the next generation, is therefore smaller in the presence of genotype x environment interaction (all other sources of variation remaining the same). The presence of genotype x environment interaction therefore diminishes potential gain.

If genotype x environment interactions would substantially diminish potential gain, the breeding strategy should be designed to minimize its effects. This could be by dividing the plantation area into breeding zones based on patterns of genotype x environment interactions. Characterization of the zones must be based on experiments in which zones are treated as fixed effects, i.e., repeatable. If the loss of potential gain is small, it can be safely ignored provided the sites on which this conclusion are based truly represent a random sample of all potential sites.

It is possible to estimate the magnitude of the loss of potential gain (C) through genotype x environment interaction (Matheson and Raymond 1984, 1986). This is 1 - ratio of phenotypic standard deviations:

$$C_{\text{Individual tree selection}} = 1 - \sqrt{\left[\frac{(V_f + V_e)}{(V_f + V_{fs} + V_e)}\right]}$$

where V_f, V_{fs}, and V_e are the family, family x site, and error variance components, respectively. Alternative formulations for family and provenance selection are given in Matheson and Raymond (1984, 1986).

The above calculations of C presume that experiments have been carried out to estimate the variance components. In the above case, this means that a replicated progeny trial of a number of families has been planted in each of several environments.

Levels of C greater than about 0.05 (5%) are generally considered unimportant. This means that losses from about 20 to 19 % are acceptable. Managers must decide what level of loss is acceptable before deciding to split up plantation areas into separate breeding zones.

Age:Age Correlations

Correlations between performance aspects in young and older trees are sometimes called "juvenile-mature correlations." In this context, the terms usually denote levels of sexual maturity. Such correlations between young and old trees, however, have more to do with age. "Age:age correlations" is thus preferred (Lambeth 1980).

Genetic tests are designed to test the performance of one entry against others. They may also be used to estimate genetic parameters from components of variance and covariance. When performance has been assessed, selections are made either for inclusion in breeding programs or to form plantations (via seed orchards, clone plantations, and the like). It is important to know the appropriate time for assessment and how the measured traits relate to those at harvest (since assessments are usually made long before final harvest).

Traits that either do not change throughout the tree's life or are relevant for later performance are termed *non-developing*. These traits can be measured early and include apical dominance, resistance to pest attack, frost resistance of seedlings, and germinability of seeds.

Traits that change greatly throughout a tree's life are termed *developing* and are usually assessed at some significant point in a rotation. Examples are height, diameter, crown form, stem straightness, branch thickness, and wood density. Rankings for growth rates are usually considered to change little after about 10 to 12 years for *Pinus radiata* and measurements taken at this age are considered good indicators of performance at rotation. Stem straightness, however, cannot be measured very early or close to rotation age. Early kinks in stems are frequently obscured by later growth, although they reduce wood quality of the inner core.

For some traits, direct measurement on living trees is not possible, e.g., pulp quality, timber strength, wood density, and combustibility. We estimate these through indicator traits, such as the density of a core sample, a pilodyn measurement, or a torsiometer reading. The relationship between desired and indicator traits is not perfect, and we expect that selection for the indicator trait will not be as effective as direct selection for the main trait. The CR to selection in trait y following selection in trait x was given above when discussing selection at one site for gain at another.

If two traits are measured on the same trees, the genetic correlation (r_{Gxy}) is calculated from the genetic covariance component (COV_{Gxy}) in an analysis of covariance (or analysis of cross-products) divided by the square root of the product of the two genetic variance components (Falconer 1981):

$$r_{Gxy} = COV_{Gxy}/\sigma_{Gx} \cdot \sigma_{Gy}$$

If we consider only developing traits, early and later measurements may be considered two separate traits for the purposes of selection. We would select on the early measurement x, hoping for a response in the later trait y. The closer x is to y in time, the closer the two traits will be correlated and the closer will be the response to selection for y on y.

The other way to calculate genetic correlations of related trees is to divide the correlation of family means by the pooled estimate of the analogous heritabilities (Burdon 1977) (see formula in section above, "Genotype x Environment Interactions"). Using this relationship, it is possible to calculate genetic corelationships between young seedlings

grown perhaps in greenhouses and much older trees of the same families growing in field trials.

Conclusion

Our ability to detect differences between entries is maximized when the unexplained variation is minimized. Unexplained variation is usually caused by environmental variation not considered in the design. Known environmental variation should be taken into account by blocking, whereas unknown environmental variation should be taken into account by making blocks as small as possible (whether complete or not). Designs described in this paper follow these principles, compromising them at different levels depending on the other experimental constraints.

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Breeding Strategies for MPTs

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Genetic improvement of a species implies that it has been altered to increase its usefulness to people. It also implies the permanence of being inherited from one generation to the next. Natural genetic changes through mutation, natural selection, and recombination enhance the transmission of genes to the next generation through survival, fecundity, etc. and rarely have direct economic benefit. Breeders intervene in the natural process, altering the criteria that determine which genes are transmitted to the next generation. The population then gradually changes in that direction.

Background

MPTs have been grown successfully by people for hundreds, if not thousands, of years. Why is it now necessary to intervene in such a successful process? The pressures of an increasingly greater human population mean we must use more efficiently the land on which MPTs are grown. This requires maximizing long-term yield of useful products while minimizing environmental damage. For example, trees that fix nitrogen require less environmental input than those that do not to yield such desirable products as wood, fodder, and medicine.

Historically, people replaced less productive species with more productive ones. They then found that some provenances of these new species were more productive than others. We now know that even greater yields are possible by breeding from the best trees from superior provenances and that the return from such breeding is much greater than the cost.

Critical to a successful breeding program are:

- people to do the work (with adequate documentation),
- good choice of base material,
- development and execution of a plan based on a breeding strategy, and
- an appropriate budget.

Because tree breeding is a long-term business, the workers involved at the beginning of a program are frequently not those involved later. Therefore, adequate planning and documentation are essential to success.

Choice of base material is also critical. Some programs began with a poor choice of species or provenance and, in many others, the initial sample of germplasm was much too limited. Two examples are the Queensland pine program, where slash pine has been replaced largely by Caribbean pine, and *Eucalyptus grandis* programs in several African countries where Coffs Harbor provenance grows much faster than early introductions.

The plan to be carried out has an underlying breeding strategy, which, together with logistical and biological constraints or opportunities, governs the way the plan is realized. The purpose of this paper is to show how to develop a breeding strategy, present criteria that determine the choice of one strategy over another, and to examine some existing programs for multipurpose tree species.

Long- and Short-Term Objectives

The evolution of most species has resulted from a compromise between fitness to survive and reproduce in the immediate environment and flexibility to accommodate environmental changes over generations. Trees, as well as other species, must maximize their fitness to reproduce in the current generation and therefore aim to vary as little as possible from the best adapted. Any genetic variation in fitness tends to reduce the fitness of the population as a whole. On the other hand, environmental conditions never remain constant, so the definition of greatest fitness changes from generation to generation. For example, cool, moist conditions at one time may give way to hot, dry conditions at another. It is to the species' advantage to be able to adapt to changing conditions, not only on an individual level, but also on a population level where the species evolves gradually as the environment changes. Long-term flexibility must not be sacrificed for immediate gain.

Breeding and selection programs imitate natural systems. It may be possible to select the best individual tree and to clone it. A population composed of such a clone would grow well provided environmental conditions did not change, for example, through a new pest or disease. In such a case, further genetic gain would not be possible in succeeding generations, and selection criteria, such as including wood properties, could not be changed. A breeding program is a trade-off between such long- and short-term objectives as maintaining as much genetic variability as possible while sacrificing the least short-term gain.

Basic Concepts

A list of books was suggested by Eldridge (1986) to help in understanding tree breeding and forest genetics. For breeding, he suggested Allard (1960), Brewbaker (1964), or Simmonds (1979), particularly the sections on breeding outcrossed plants and omitting the sections on inbreeding and chromosomes. For forestry programs, Zobel and Talbert (1984) and Wright (1976) are practical texts and Namkoong, Kang, and Brouard (1988) is more advanced. For a deeper understanding of genetic principles underlying breeding, Falconer (1981), Namkoong (1979), and Becker (1985) are suitable, provided the reader has an adequate understanding of statistics. A useful book on experiment design and variance component estimation is Hicks (1973).

Genotype versus Phenotype

The appearance of a tree, its height or diameter, etc. results from the genes that it carries and from the environment in which it grows. Even if a tree carries genes conferring fast growth, it will grow slowly in poor soil. The genetic complement of a tree is termed its *genotype*, while its appearance is termed the *phenotype*. Phenotype results from the action of both genotype and environment. Thus, Phenotype (P) = Genotype (G) + Environment (E).

In terms of variance (or variability), the observed phenotypic variance (V_P) is composed of genetic variance (V_G), environmental variance (V_E) and their interaction (V_{GE}). Thus, $V_P = V_G + V_E + V_{GE}$.

Genetic variance is made up of two parts: an additive part (V_A), due to average effects of genes, and a non-additive part (V_{NA}), due to such deviations from additivity as dominance. Thus, $V_G = V_A + V_{NA}$.

Recurrent selection depends on the accumulation of many favorable genes in the breeding population, each acting independently (additive effects). Superiority of individuals based on favorable interactions between genes (non-additive effects) breaks down each generation as random assortment and recombination occur. For this reason, most recurrent selection programs can use only the additive part of the genetic variance. To take advantage of non-additive effects, favorable genetic combinations need to be identifiable and capable of being captured vegetatively without undergoing sexual reproduction during which the combinations break down. Recurrent selection in the breeding population can be combined with vegetative propagation as a "packaging" technique.

Heritability

Heritability (h^2) is the proportion of the phenotypic variance due to the additive effects of genes: $h^2 = V_A/V_P$. The amount of genetic gain will be high if the genetic variability in the breeding population is high relative to the variability caused by environmental variation. In other words, genetic gain is high when heritability is high. For constant selection intensity, gain may be increased in two ways: (1) by increasing V_A or (2) by decreasing V_P. We can do nothing about the magnitude of V_A for a particular population, but we can reduce V_P by reducing the environmental variance (V_E). This means that, for efficient selection, progeny tests should be planted on uniform sites and designed to minimize residual variation.

Inbreeding versus Outcrossing

When mating occurs between relatives, the offspring are inbred to an extent depending on the degree of relatedness of the parents. There is good evidence that inbred trees grow more slowly, have more crooked stems, and die earlier than outcrossed trees. Inbreeding effects can, however, be removed in a single generation of outcrossing. This means that the progeny of a cross between two unrelated but inbred parents will be completely outcrossed and grow much better than the parents.

Controlling inbreeding is an important part of tree breeding but can be difficult to achieve. Inbreeding will occur whenever the effective population size becomes too small. For many crop plants, it is easy to maintain large breeding populations. But for trees, it is more difficult and expensive.

Expected Gains

It is difficult to quantify the gain to be made either from replacing one species or provenance with another without knowledge of the consistency of the performance of species and provenances. However, it is possible to calculate the gain expected through breeding once basic information has been obtained on the genetics of the traits under consideration.

Selection Pressure. Selection pressure can be expressed in two ways. The difference between the mean of the selected group and the original population (selection differential = s) is conveniently expressed as multiples (selection intensity = i) of the phenotypic standard deviation (σP). Thus, $s = i \cdot \sigma P$.

The relationship between the fraction of the population selected and the selection intensity is exponential (Table 1). The effort required to further increase selection intensity becomes unrealistic because of this exponential effect and because site heterogeneity increases as soon as more than a few hundred trees are considered. This increases the environmental variance and reduces heritability.

Complex traits, e.g., growth rate and pulp yield, combine simpler traits. It may be better to define the components of complex traits and deal with them separately or by index selection. For example, pulp yield of a plantation depends on survival, stem volume, and wood density. Considering multiple traits has implications particularly for multipurpose trees because of the selection differential applicable to any single trait.

The superiority of selected trees over the average diminishes for each additional trait included (Table 2). only a small selection differential can be applied to each trait if several traits are being selected at once. Therefore, selection is usually concentrated on only a few traits.

Table 1. Relation between selection intensity (i) and number of trees (N) observed before making a selection.*

i	N
1.0	4
2.0	41
3.0	739
4.0	31,540
5.0	3,588,000

*See Falconer (1981) for more detail.

Table 2. Superiorty in units of σP of selected trees over all trees for numbers of traits*

No. Traits	No. Trees Scanned per Selection	Superiority of Selected Tree per trait	total
1	1,000	3.29	3.29
2	32	2.15	4.30
3	10	1.65	4.94
4	6	1.35	5.38
5	4	1.14	5.72

*From Matheson and Brown (1983) after Wright (1976).

The total gain rises as the number of traits increases, if they are equally valuable (Table 2). If the first traits are the most valuable, the value of the overall gain decreases as less valuable traits are added. Index selection with adequate economic weights can be used to maximize the value of the genetic gain (Cotterill, Dean, and Jackson 1990).

Response to Selection. The genetic gain or response to selection in a trait depends on the intensity of selection and the heritability of the trait: response $= s \cdot h^2 = i \cdot h^2 \cdot \sigma_P$. (Fig. 1.) After intercrossing selected trees, large response to selection is achieved by high heritability and high selection differential (or selection intensity).

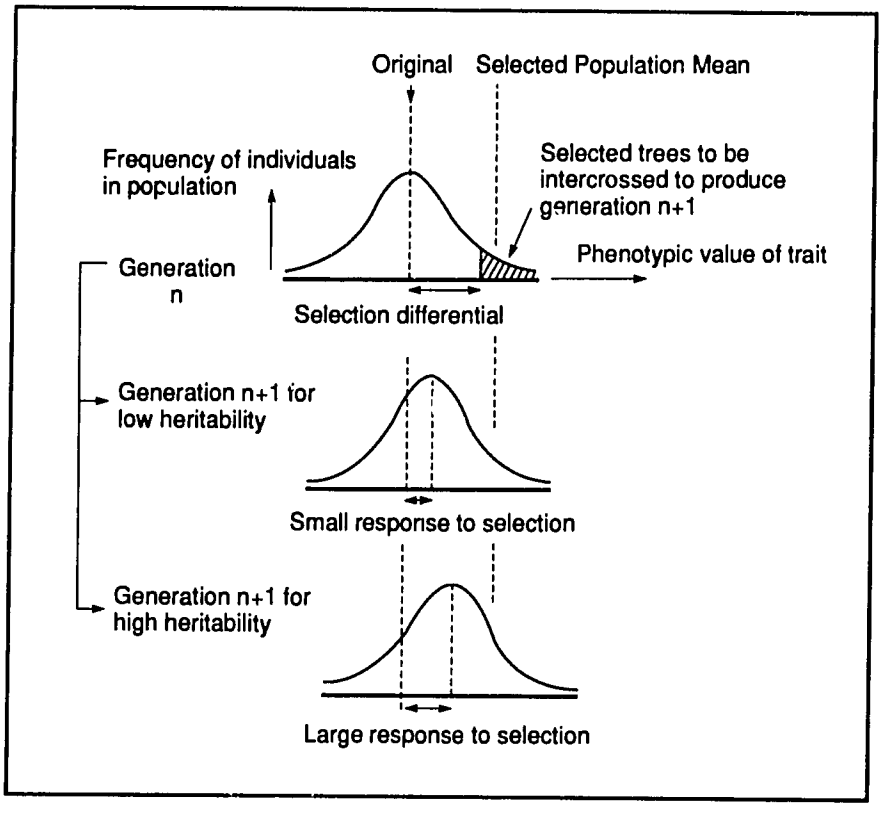


Fig. 1. Response to selection for selection differentials and heritabilities

Breeding Strategy

A breeding strategy governs the way a breeding program is carried out. The strategy aims to maximize opportunities offered by a species (such as the capacity for vegetative propagation) and to minimize the effects of constraints (such as the inability to make controlled pollinations). The strategy must aim to maximize long-term genetic gain and minimize the effects of inbreeding. The careful choice of the base population to start selection is therefore very important. Long-term genetic gain should provide adequately for changes in selection criteria through conservation of genetic resources.

Because many criteria determine which strategy to use, no single one is appropriate for all cases. Some programs are well-endowed and have a large plantation base, thereby justifying an expensive and perhaps complex strategy. Less well-endowed programs may be able to afford only a relatively simple strategy. Whatever the circumstances, the gains to be made from each strategy should be estimated (Shelbourne 1969, Cotterill 1986).

The purpose of breeding trees or any other crop is to increase productivity, including quality, by modifying the gene pool of the planting stock. This may be done by increasing pest resistance, palatability of leaves for fodder production, or stem size for wood production. The principles are the same whatever the selection criteria.

Recurrent Selection

Breeding is an ongoing process with benefits that accumulate over successive generations of the activity cycle shown in Fig. 2.

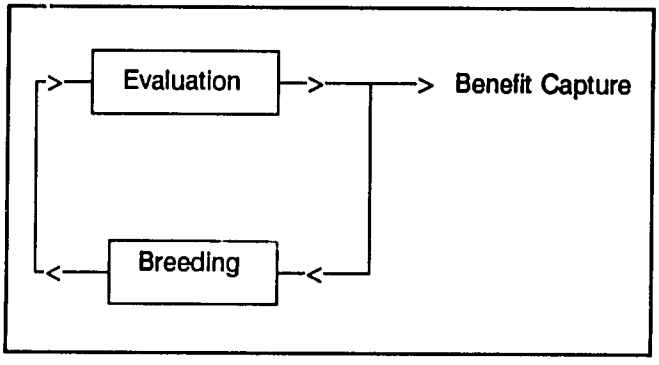


Fig. 2. Activity cycle for breeding

The generalized scheme in Fig. 2 is termed *recurrent* because it continues over generations. The evaluation process aims to isolate individuals with the most favorable genes. These individuals are bred together, allowing the favorable genes to recombine so that new individuals arise carrying even more favorable genes. The benefits are captured each generation for use in plantings.

Random assortment and recombination of genes each generation mean that selection can lead to the average of a breeding population, eventually exceeding the entire range of the original population. It also means that clonal programs must be backed up by a breeding program to provide new gene combinations for clonal propagation.

Tree breeding programs are generally one form or another of recurrent selection. Most of the differences between programs lie in the method of regenerating the breeding population and in the "packaging" for plantings. Selection and regeneration in the breeding population must be carried out in a way that minimizes the long-term effects of inbreeding, keeps the effective population size large, yet maximizes progress in desired traits. Although relatively simple at first, progress can become quite difficult in small breeding populations without becoming subject to inbreeding. This is because select trees will eventually be related to each other to some degree.

Components of a Breeding Strategy

The breeding population must be built from an adequate base population, perhaps from several provenances of the desired species. However, the constitution of the initial breeding population depends on the species, its biology, and the program's objectives. The breeding population is the stock of genes that is being developed, reorganized and improved from one generation to the next. Each generation the breeding population needs to be regenerated and improvements must be transferred from it to plantations.

The most important component of any breeding strategy is an adequate set of objectives. Writing down a breeding plan is a good way to clarify them. If long-term objectives are sought, then adequate conservation of genetic resources must be built into the program. Selection criteria must be defined clearly at the start, even though they may change later.

In addition to adequately-defined objectives, a worthwhile breeding strategy requires at least the following components (Fig. 3 and Libby 1973):

- **A breeding population.** This is essentially the population under improvement, derived from the base population.
- **Methods of selecting superior material.** This includes the progeny tests in which selection is carried out, measurement techniques, and selection technology (e.g., selection indices).
- **A method of regenerating and upgrading the breeding population.** This can be by open- or controlled-pollination.
- **A method of transferring material from the breeding population to the planting site,** e.g., a seed orchard, nursery cuttings, or tissue culture laboratory.

Breeding strategies also succeed by:

- Avoiding establishing plantings of inbred trees (in outcrossing species);
- Having the potential to incorporate new material into the breeding population from other

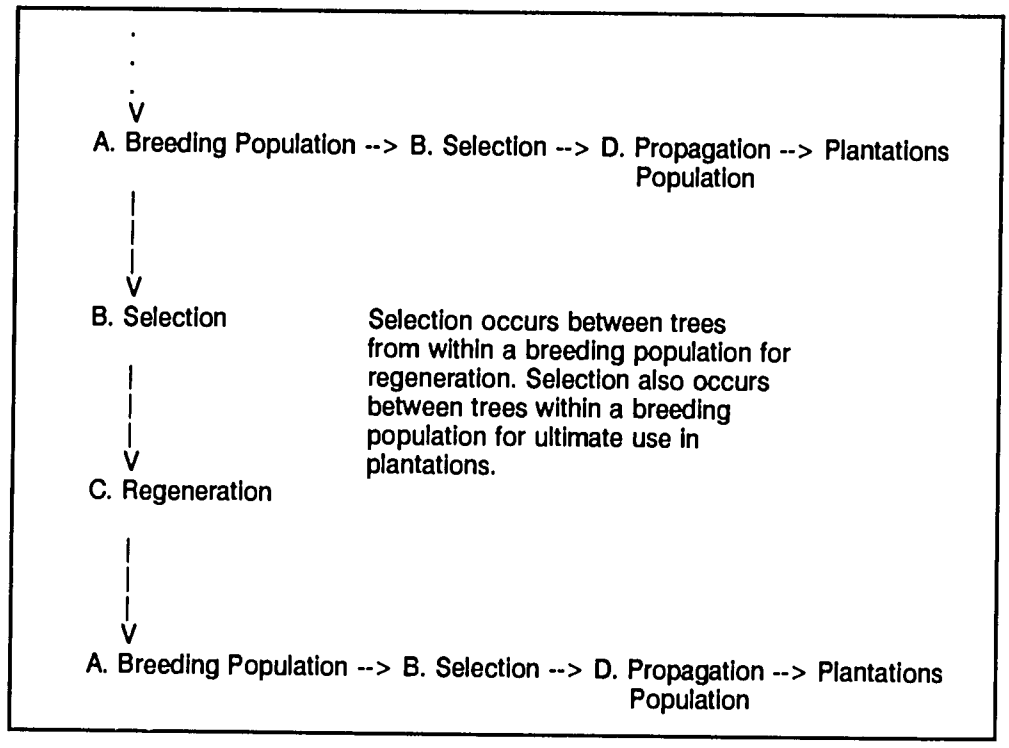


Fig. 3. Outline of breeding strategy

sources, and therefore maximizing gain per unit time;

- Having suitable facilities and equipment, sufficient skilled labor and long-term funds; and

- Conserving genetic resources for future selection.

Structure and Regeneration of Breeding Population

The breeding population is the population under improvement. Under recurrent selection, improvements in the breeding population are "packaged" for transfer to planting sites as the benefits of breeding. The breeding population may be in one place, e.g., as a breeding arboretum, or may be scattered, e.g., selections in progeny tests. It may be physically in one place but subdivided conceptually into multiple populations or sublines. The breeding population is an integral, planned part of the breeding program. Its physical structure depends on the breeding strategy as a whole and how it is to be regenerated. Its function may also be combined with other functions, as in Breeding Seedling Orchards (BSO) (see section below, "Multiple Populations," p. 76, and Barnes 1986).

In many mainstream forest tree improvement programs, the breeding population is regenerated through controlled pollination. This is an expensive process because of the amount of skilled labor and time required. For MPTS, mating may well be by open pollination since lower levels of investment may mean that less skilled labor is available. The process of mating trees in the breeding population, combined with selection, determines the level of genetic change taking place in the breeding population.

Open-pollinated regeneration of breeding populations means that trees are left to cross with adjacent trees in an uncontrolled manner. If adjacent trees are not already part of the breeding population, their genes will be incorporated anyway. For open pollination, therefore, the breeding population should form one physical unit, isolated from contamination. Without this, the genetic gain is halved as selection only involves seed parents. Open pollination provides approximately half-sib families of trees with unknown numbers of unidentified relatives in every other family. Open-pollinated families are also inbred to an unknown degree, but can provide quick and easy, although perhaps inaccurate, estimates of additive variance and covariance.

Controlled pollination can be carried out in almost any number of patterns of any level of complexity. Some crossing patterns are best for estimating genetic parameters such as additive and non-additive variances and covariances (Fig. 4). Others are best at providing material for further selection. For example, random, single pair crosses provide many unrelated families for further selection but provide estimates only of total genetic variance (both additive and non-additive). On the other hand, diallels (all possible combinations of crosses) and partial diallels (a subset of all possible crosses) provide excellent estimates of many genetic parameters but relatively few unrelated families for reselection. The North Carolina Design 2 crossing pattern (NC 2), a factorial crossing pattern in which a number of males are crossed with a different set of females, provides somewhat more unrelated families than diallels but at the expense of some genetic parameters.

Propagation Population

In many cases, propagation between the breeding population and the planting site is via open-pollinated seed orchards in which superior trees breed together to produce seed. Seedling seed orchards, or dual-purpose seed orchards, are usually produced from seedlings in multiple-tree plots (Libby 1976). Selection (one purpose) reduces trees to one per plot before seed production (second purpose). Clonal (or single-purpose) seed orchards are produced either from grafts or from cuttings of superior trees. Trees are usually arranged in single-tree plots to minimize inbreeding and no thinning is based on tree performance in the seed orchard. There can be some culling of inferior clones as a whole from the orchard.

Propagation need not be by seed orchards. In species like *Pinus radiata*, it is possible to produce much seed (perhaps 100 per cone) by controlled pollination of particular superior crosses. The young seedlings of each family can be propagated further by vegetative means (termed *family amplification*). This method has the advantage of using some non-additive variation caused by particularly favorable gene combinations and uses half of the additive variation (the other half lies within families). Other species, like *Gmelina arborea*, produce few seeds per controlled pollination (between one and two per flower), and so have little capacity to produce many individuals per family. For such species, it may be necessary to use tissue culture for the initial amplification. Alternatively, superior individuals can be clonally propagated either by cuttings or tissue culture, thus making use of all genetic variation. Plantations established using clones that are identified and tested before propagation are said to involve

4 x 4 Diallel

Male Parent	Female Parent 1	2	3	4
1	x	x	x	x
2	x	x	x	x
3	x	x	x	x
4	x	x	x	x

4 x 4 Partial Diallel

Male Parent	Female Parent 1	2	3	4
1		x		x
2			x	
3	x			x
4	x	x	x	

4 x 4 NC 2

Male Parent	Female Parent 1	2	3	4
5	x	x	x	x
6	x	x	x	x
7	x	x	x	x
8	x	x	x	x

4 x 4 Random Pair Crosses

Male Parent	Female Parent 1	2	3	4
5	x			
6		x		
7			x	
8				x

Fig. 4. Comparison of controlled pollination patterns

clonal forestry. Time is lost by the necessity of clonal testing for this option, although it may not be a problem for fast-growing species.

Simple Strategies

Breeding strategies involving mass-selection are usually simple programs whose prime object is to provide an assured seed source rather than to make much genetic improvement. Mass-selection is the simplest method of selecting trees from stands with regard only to phenotype and not pedigree or genotype.

Example Mass-Selection 1. MS1. The simplest mass-selection strategy selects trees in plantations and collects seed from them for plantings. Genetic gain for this strategy would be low because selection is based on phenotype where heritability is low, i.e., in plantations without environmental control. In addition, selection is based only on the female parent, the male parent being uncontrolled. Plantation areas selected and managed for seed production are called Seed-Production Areas (SPAs) and may well be an important first step in MPTS breeding programs, to provide an assured seed supply with low but nevertheless desirable genetic gain.

Example Mass-Selection 1. MS2. In Fig. 3, p. 72, a mass-selection strategy would select trees in plantations, propagate into seed orchards, and collect seed for plantings. This has the advantage of selecting both male and female parents and would yield greater gains than the MS1 strategy. However, the original selections would not be very accurate since the heritability in plantations is very low (due to high environmental variation rather than low genetic variation). So it is probably not worth the extra effort and time lost in preparing the seed orchard (unless an assured seed supply independent of plantations is an important criterion).

The first selections from plantations or from a natural stand for inclusion in a breeding program are by mass-selection. Since the selections have been made from populations in which heritability is low, it is preferable to test selections in progeny tests before including them in a breeding program.

More Complex Strategies

Example Recurrent Selection 1. RS1. (Fig. 5). This strategy separates the seed production functions

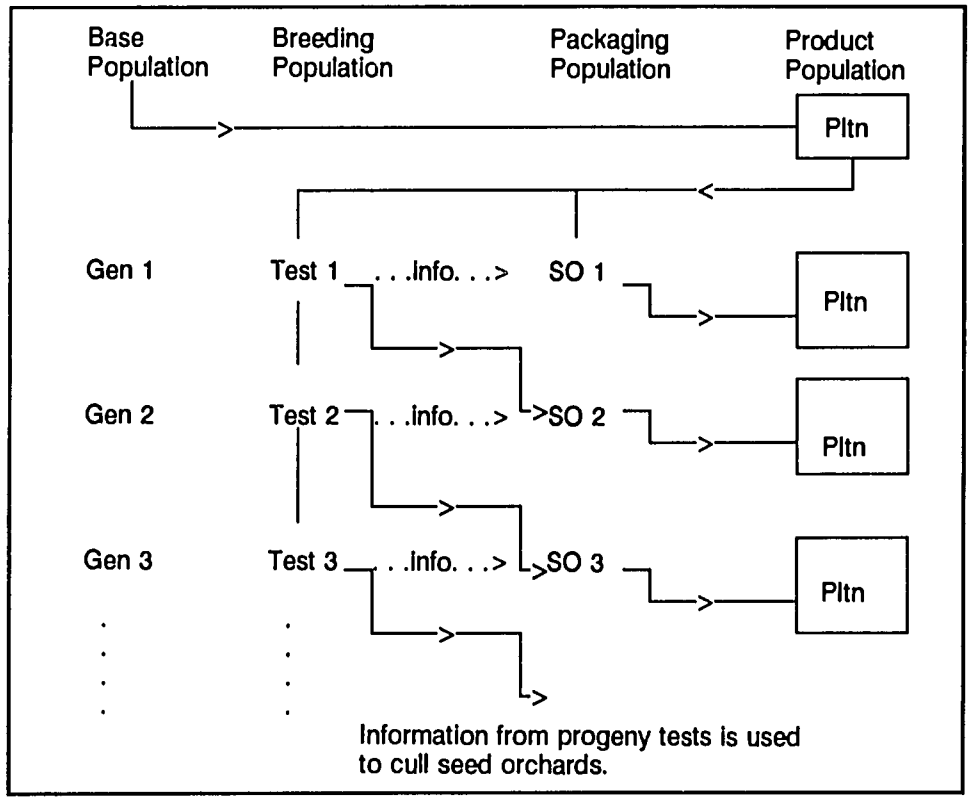


Fig. 5. Recurrent Selection Strategy (RS1) in which breeding population is substantially larger than and separate from the seed-orchard population (after Libby 1973).

from the breeding population. Here, the breeding population is the progeny tests rather than the seed orchards. In RS1, trees are selected in the progeny tests for regeneration of the breeding population. A smaller number are selected for the seed orchard or "packaging" population. Information from progeny tests is used to cull seed orchards. In this case, the breeding population is undivided and, unless it is kept large, inbreeding will eventually become appreciable.

Example Recurrent Selection 2. RS2. This is another strategy in which the seed production and breeding populations are kept separate. In this case, the breeding population is divided into strictly separated sublines (Fig. 6).

In RS2, the sublines are regenerated separately to keep them genetically isolated from one another (Fig. 6). Inbreeding is permitted to build up within sublines but, provided only one or few selections per subline are included in the seed orchard, the seeds collected from the seed orchard will not be inbred. The regeneration process can be either simple or complex, depending on resources available. Several programs have adopted the disconnected diallel pollination design, one for each subline, but these are complex and demanding of labor. Polycrossing (controlled pollination with a pollen mix) or open pollination are much simpler options, but involve loss of pedigree information. This does not matter greatly because inbreeding need not be controlled within sublines. If the number of parents in each subline is relatively large (30 or more), regeneration crossing could be by pair crossing within lines.

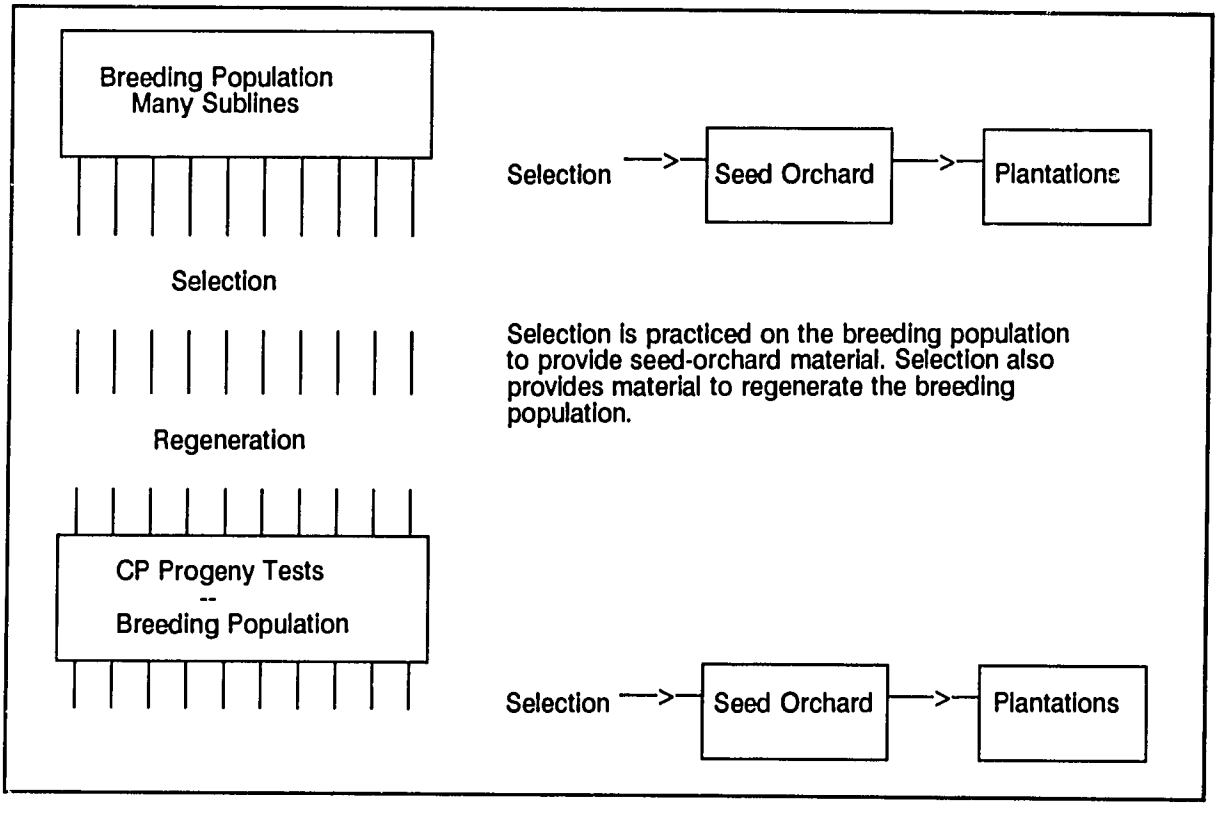


Fig. 6. Strategy in which breeding population is divided into sublines to avoid inbreeding (after Matheson and Brown [1983]).

Example Recurrent Selection 3. RS3. A new strategy adapted from successful animal breeding programs is nucleus breeding (Cotterill et al. 1990). This also involves recurrent selection among genetic recombinants over a number of generations. It aims to concentrate breeding, i.e., controlled-pollination, effort on the very best genetic material (Fig. 7).

Each generation, a number of the best trees in the main population are transferred to the nucleus population, and a number of the lowest-ranking trees in the nucleus population are transferred back to the main population. This is intended to ensure that the nucleus does not become too inbred and provides for the infusion of new trees not only from the main population but also from elsewhere. Regeneration within the main population could be by any of the controlled-pollination methods as in RS2. Regeneration of the main population would be by open pollination, which is simple and much cheaper. The essence of this strategy is that it concentrates effort and expense on the best trees.

Seed orchards could be composed of selections from the nucleus population, superior families could be mass-propagated vegetatively, or the best individuals in the nucleus population could be cloned for plantings.

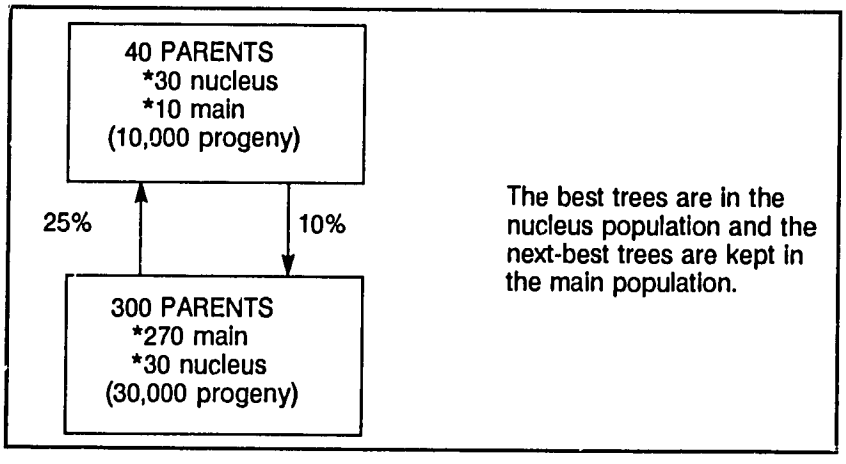


Fig. 7. Nucleus breeding strategy (RS3)
Source: Cotterill et al. (1990)

Multiple Populations

This strategy, like subline breeding, has a subdivided breeding population. The subline strategy involves many, narrowly-based sublines whereas the multiple-population strategy involves fewer, more broadly-based populations. Sublines are crossed together to yield planting stock, whereas in the multiple-population strategy planting stock is derived from each population. The objective of multiple-population breeding is to select for different gene complexes between each of the populations by imposing selection and breeding within each (Namkoong, Barnes, and Burley 1980). Sublining, however, is carried out primarily to combat inbreeding depression whereas multiple-population breeding has additional objectives, such as providing the potential to develop different selection criteria in different populations. It is also potentially much simpler to operate than sublines, partly because there can be as many, or more, sublines as entries in the seed orchard, whereas there need be only a few of the multiple populations. Populations can be crossed to make use of particularly favorable gene combinations.

There is probably some point between programs with few, broadly-based sublines and those with many, fairly narrowly-based populations where the distinction between subline and multiple-population strategies is unclear.

Populations should generally be made up of, say, 50 selections with the intention of minimizing inbreeding. As inbreeding inevitably builds up, it can be removed entirely by crossing between two populations to reestablish them. Maintenance of populations can be complex or simple. It is possible to imagine a complex case in which each population is divided into sublines and maintained by disconnected half-diallels.

The best examples of multiple-population breeding to date are the Zimbabwe programs for several species, including many pines and eucalypts (Barnes 1984, 1986). In the Zimbabwean programs, breeding, testing, selection, and seed production all occur within the same stand--the BSO. The BSO is thinned selectively and progressively on the basis of genetic information until only the seed producers remain (Barnes 1988). Pedigree control within BSOs can be complete (via controlled pollinations) for intensive programs on valuable species to very little (via open-pollinated mass-selection) for simple programs on peripheral species.

Hybrid Breeding

Hybrid vigor, or heterosis (Gowen 1952), is observed when hybrid offspring perform better (however measured) than the parents. Heterosis frequently breaks down in the second generation (F_2) whose variance is frequently extremely high. If apparent heterosis in the first (F_1) generation is caused by release from the inbreeding frequently found in natural populations then the F_2 will generally perform less reliably than the F_1. However, genetic recombination, which is the major source of novel genetic combinations, can only be expressed in the F_2 generation. When combining single-gene traits, one from each species, the F_1 generation will be genetically uniform and heterozygous. Genetic segregation, permitting recombination of alleles at different loci into new combinations not found in the original parents is manifest in the F_2. There is some scope for research on the nature of the heterosis. Intra- and inter-specific hybrids should be compared to test whether hybrid vigor is caused by increased heterozygosity or by release from inbreeding.

Within Species

In the sublining strategy RS2, growth rates of outcrossed trees from the seed orchard of inbred trees will be fully restored compared with their inbred parents. If inbreeding depression is caused by increased homozygosity, i.e., particular genes from both father and mother being the same, then the opposite of inbreeding depression should occur if heterozygosity is increased. Hybrids between inbred parents have been shown to exhibit hybrid vigor in maize (Allard 1960). Crossing provenances may have two advantages: release from inbreeding and combining complementary traits (particularly in the second generation following recombination). Crossing between populations in the multiple-population strategy is designed to achieve the same end. Hybridization is also a way to introduce new genetic material when pollen of the desired trees is available and seed is not.

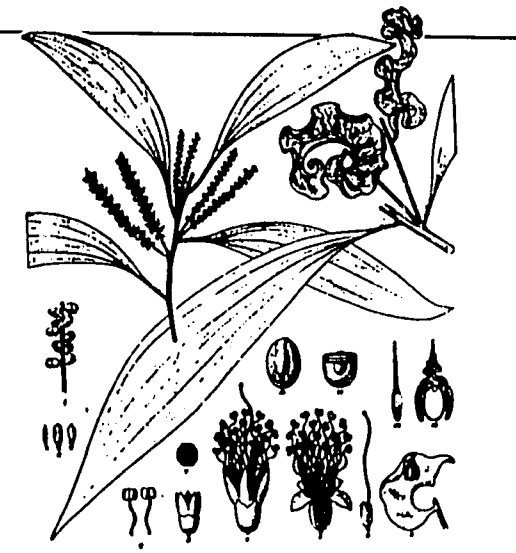
Between Species

In several cases, inter-specific hybrids have shown great promise. Examples are the hybrid eucalypt program in the Congo (Delwaulle 1985), the slash x Caribbean pine program in Queensland, Australia (Nikles and Robinson 1990), and the hybrid *Leucaena* program in Hawaii, where desirable features in one species complement those in another and combine favorably in the hybrid (see section below). However, such cases are the exception rather than the rule. Wide crosses are more likely to fail than succeed as shown for eucalypts by Griffin, Burgess, and Wolf (1988). It should be well-established that neither pure species is appropriate before embarking on an expensive and time-consuming inter-specific hybrid breeding program.

Existing MPT Breeding Programs

MPTS breeding has only been in progress for about a decade. Better developed programs are now setting up good base populations from provenances of known variability as a starting point for selection and breeding. Plans are being developed for each species but only one (*Acacia mearnsii* in China) has adopted a formal, long-term breeding strategy or a detailed, written breeding plan although some others are about to do so. This section details their present status.

Acacias at Sabah Softwoods



Acacia mangium grows naturally in northern Queensland, southern Papua New Guinea (PNG), and the Indonesian provinces of Irian Jaya and Maluku (Doran and Skelton 1982, Turnbull 1986). Leaves of *A. mangium* can be used for fodder and its wood is heavy and hard, making it a good fuelwood (NAS 1983). In Sabah, its wood is chipped and used for pulp. Basic density of the wood is 420 kg/m^3, higher than many other tropical plantation species (Turnbull 1986).

Its introduction to Sabah in 1973 came from a single tree at Mission Beach in Queensland, Australia. Plantations in Sabah have been established from this very limited seed source initially by collecting seed from plantations (mass-selection) managed as seed stands. Growth rates by the third generation were only half those of the first (Sim 1984). Later plantations were derived from a seedling seed orchard made up of families from five Australian provenances and the seed stand. A new collection from throughout the Australian and PNG range was undertaken by CSIRO in 1989. Some evidence indicates that the species is predominantly outcrossing although genetic variation at allozyme loci is extremely little (Moran, Muona, and Bell 1989a).

Jaffirin Lapongan

The A. mangium/A. auriculiformis *hybrid has slender branchlets and large phyllodes, often approaching the size of* A. manigum.

Nancy Glover

This provenance trial of A. mangium *will help in selecting the best seed source for reforesting degraded pasturelands in Puriscal, Costa Rica.*

U.T. Ongleo

Three-month-old A. mangium *in F/FRED-supported field trials in Ratchburi, Thailand*

About one third of plantation trees in peninsular Malaysia is subject to heart rot (Gavinlertvatana, Matheson, and Eng 1987) and some work is being done to identify the causal organism (Lee 1986). No provenance trials are yet old enough to conclude firmly about intra-specific variation, but data from existing and new trials involving collections made in 1988 by CSIRO will be available in a few years.

Acacia auriculiformis has a similar distribution to *A. mangium* with the addition of the northern part of Northern Territory in Australia. It was introduced to Sabah, as well as to other parts of Southeast Asia many years ago, and sources of introductions are unknown. Its mating system is predominantly outcrossing (Moran, Muona, and Bell 1989b).

Many trees in Sabah have been identified as inter-specific hybrids between *A. mangium* and *A. auriculiformis* by the shape of the phyllodes, color of the flowers, as well as shape of seed pods. Such trees show the straighter stem form of the *A. mangium* parent and do not appear susceptible to heart rot. Putative hybrids have appeared among young trees planted in new provenance trials of *A. auriculiformis* near Darwin (Northern Territory, Australia), suggesting that hybridization also occurs within the natural distribution of the species, as well as outside the natural range of both species in Sabah.

Breeding programs for both species and the hybrid at Sabah Softwoods are currently under review.

NAS

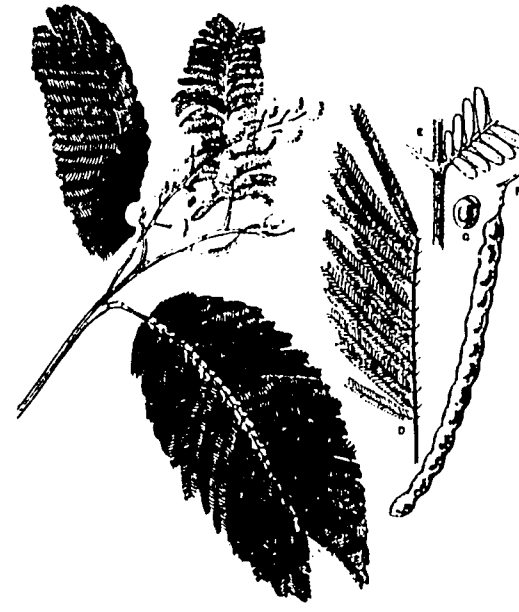
Flowering A. auriculiformis

C.B. Briscoe

Three-year-old, pruned A. mangium *at Kiarabandung, West Java, Indonesia*

Acacia mearnsii in China

Acacia mearnsii is a fast-growing, nitrogen-fixing temperate tree with a natural range from south of Sydney, NSW through southern and eastern Victoria to southeastern South Australia. It has been grown in China since the early 1950s with introductions from Indonesia and later from many places including Kenya (where the species was named), Europe, and Australia. The origin of the seed currently used in plantation ostensibly is unknown and is sometimes even another species.



A. mearnsii is grown commercially for the tannin in its bark, for fuelwood, charcoal, construction and for pulp. About 10,000 ha have been established in 10 Chinese provinces with an annual plantation rate currently of about 3,300 ha. The breeding program proposed by ACIAR was intended to overcome the problems associated with present poor-quality seed of unknown ultimate origin (Raymond 1987).

A. mearnsii, *coast of New South Wales, Australia*

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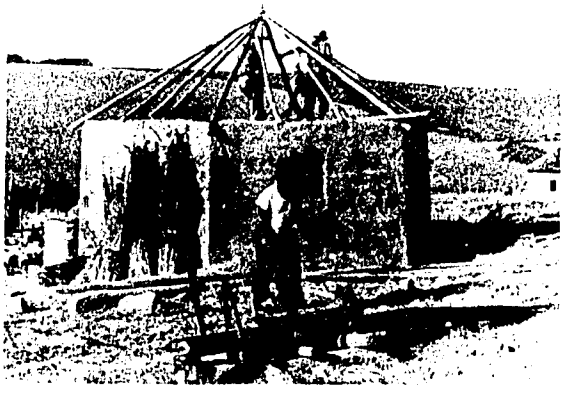
African women bearing headloads of A. mearnsii



NAS

A. mearnsii *poles for roofing a rustic hut*

The breeding strategy was essentially simple given the impracticability of controlled-pollinations or vegetative propagation. It is based on progeny trials that are converted into seedling seed orchards by being thinned twice. The progeny test consists of over 160 open-pollinated families taken from many provenances. The first thinning essentially removes the poorest trees in each family plus a few of the poorest families. Seed is then collected for the next progeny test/seedling seed orchard. The second thinning converts the progeny test into a seedling seed orchard and only the best trees are retained to produce high-quality seed for plantation use.

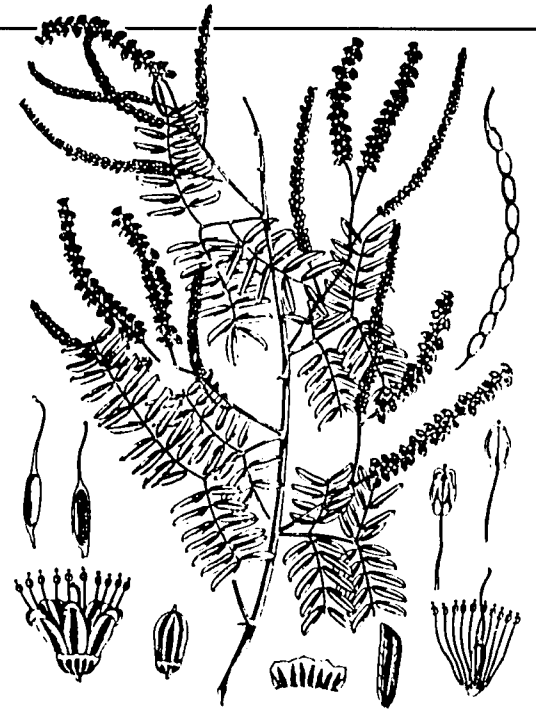
The progeny tests will be established as balanced incomplete block designs to make best use of limited material and to account for as much environmental variation as possible. Single-tree plots will be used on the assumption that they will provide estimates of individual performance in competition with different genotypes. Unless survival is high, the use of single-tree plots will add to the complications of analysis. However, it does allow all the best trees to be retained; in multiple-tree plots, only one tree can remain per plot in the seedling seed orchard and the next best trees must be removed even if they are much better than trees in other plots of the same family.

The strategy has been well-documented by Raymond (1987), and a work plan up to year 8 has been devised. A strategy beyond the first generation has been anticipated. It is an excellent example of how plans for MPTS can be prepared.

Prosopis in Haiti

Prosopis, an outcrossing, leguminous American genus, grows from the southern United States to central South America. Several species are aggressive weeds that are hardy and resist heavy grazing, e.g., *P. glandulosa, P. ruscifolia,* and *P. juliflora* (NAS 1979); others are less aggressive. It has been introduced to Sahelian Africa and the Indian subcontinent. *Prosopis* pods are used as fodder for domestic animals, and the wood is valuable for fuel.

Several species form part of the Haitian program: *P. alba, P. chilensi P. glandulosa, P. juliflora,* and *P. pallida.* The program's objective is to improve growth, reduce thorns, improve pods for use as fodder, and increase browse resistance. Collections were made in Haiti, Peru, California, and Texas and grown in a field trial in Haiti. Collections were chosen to represent geographic regions. In Haiti, individual trees were selected that exhibited desirable features.



Peter Felker

Thornless P. alba, *only nine months after transplanting from seedlings*

NAS

Prosopis *spp. produce excellent-quality pods used for animal feed.*

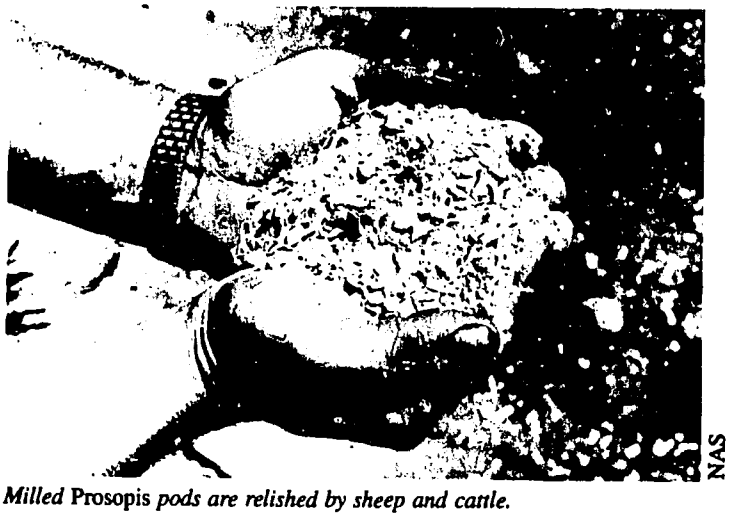
A field trial of the seedlots forming the collections was planted in 1987 in four randomized complete blocks of plots consisting of five trees per plot.[1] Not all seedlots were present in all replicates, so statistical analysis was carried out by fitting a general linear model. Highly significant differences between seedlots were found for height, stem form, and number of main stems per tree assessed nine months after planting. The 11 fastest-growing seedlots came from Peru, the putative Vavilov center (center of genetic diversity) for the genus. Collections from large trees in Haiti did not produce the largest Haitian progeny, indicating that, as for other species, phenotypic selection in uneven-aged stands growing in diverse conditions is rarely effective.

The program intends to select superior individuals in the field trial and, by air-layering, propagate cuttings in greenhouses. This strategy should be more effective than selection in native stands as the field trial is more environmentally uniform.

The program is recent and no selection has yet been practiced for pod characters. However, Peruvian *Prosopis* collections were made from trees whose pods are suitable for use.

So far, no breeding is being carried out for this genus. Material is being provided from trees selected in a relatively uniform environment for propagation as clones for plantation purposes. Future breeding may involve seed orchards to which *Prosopis* is particularly suited because it is self-incompatible.

[1] P. Felker, personal communication.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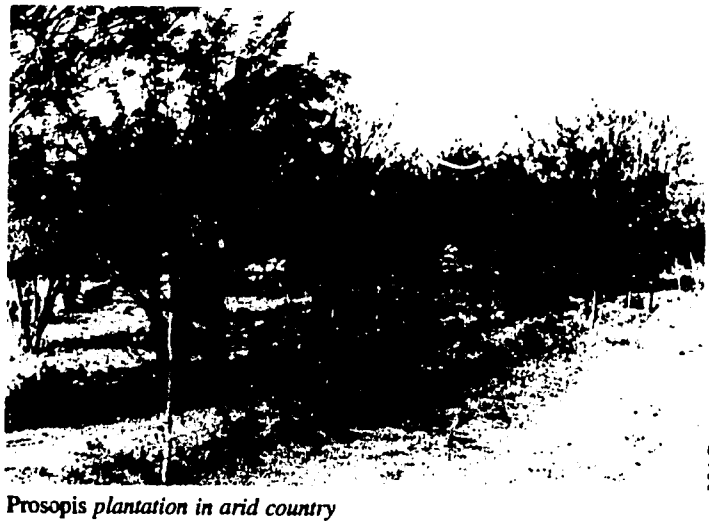
Milled Prosopis *pods are relished by sheep and cattle.*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Prosopis *plantation in arid country*

Gliricidia at ILCA

Gliricidia sepium is a native legume of Mexico and Central America that plays an important role on farms in the tropics. It is used for fuelwood, poles, living fences, shade for crops, green manure, and fodder. It has been introduced into northern South America, the Caribbean, Africa, South and Southeast Asia, and Australia. It is naturally propagated by seeds although it has traditionally been propagated by cuttings.

Collaborative research on *G. sepium* improvement was initiated in 1982 by ILCA and CATIE (Sumberg 1985). A collection of 49 provenances throughout Costa Rica was made in 1983. Subsequent provenance collections were made by the Oxford Forestry Institute (Hughes 1987), NFTA (Glover and Brewbaker 1984), CATIE (Chang and Martinez 1985), and ViSCA (Bumatay, Escalada, and Buante 1987).

Trials of the Costa Rican provenances collected in 1983 were established at CATIE in Costa Rica, the International Livestock Centre for Africa (ILCA) in Nigeria, and at the University of Hawaii (Atta-Krah and Sumberg 1988, Atta-Krah 1990, Glover 1987).

The ILCA trial was designed to test provenances for growth in an alley-farming system at a spacing of 3 x .5 m, interplanted initially with grass and later with cowpea. The CATIE and University of Hawaii trials were planted at a spacing of 2 x 1 m and managed as fuelwood plantations.

J. Stewart

A living fence of G. sepium *strung with barbed wire separates two adjoining fields in Honduras.*

R. Gonzales

Planted as a living fence, G. sepium *is periodically lopped for fuelwood and also provides support for pepper vines.*

At ILCA in Nigeria, there were large differences between provenances for post-pruning vigor and coppice regrowth, which were strongly correlated. Four provenances were identified as consistently superior for coppice regrowth yield in Nigeria, three of which were also identified as superior in Costa Rica and Hawaii, although managed quite differently. This indicates that management x provenance interactions are not likely to be important.

The four superior provenances were combined by planting in a seed orchard arranged as a Latin Square to promote random mating. It was hoped that the seeds would result largely from outcrossing and would represent a broader genetic base than cuttings of each provenance. Although this is probable, some inbreeding is likely, leading to lower growth rates than would be achieved if crosses were made by controlled pollination.

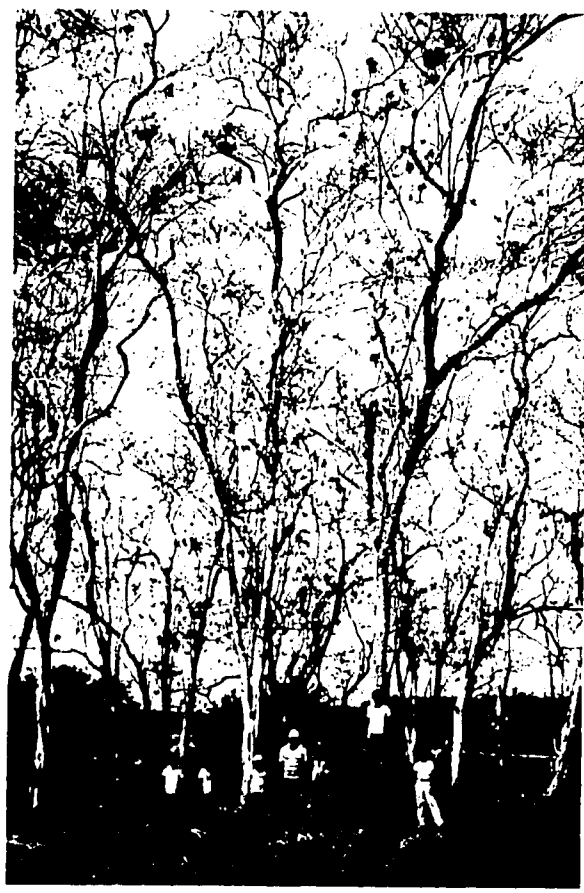
The seeds obtained from the seed orchard were compared with OFI collections in three trials and proved better than the 1984-collected provenances at Ibadan. The OFI provenance collections were planted in network trials in several countries in West Africa in 1986. Considerable variability found in growth performance between sites of the seed-orchard seedlot suggests that seedlot x environment interactions may be important in this species. Comparisons of this sort

B. Seibert

G. sepium, *commonly called "mother of cacao," is planted for shade in cacao plantations.*

present problems between provenances derived from collections in the wild and naturalized provenances (or land races). Any apparent superiority of naturalized sources may be due to release from neighborhood inbreeding still present in the natural provenances.

So far, *Gliricidia* improvement is at an early stage. The availability of vegetative propagation makes improvement of the species interesting. When vegetative means are used for propagating desirable genotypes, more genetic gain from selecting in the breeding population is captured in the resulting plantation. Results are better than for seed propagation of whole families or vegetative amplification of whole families under three conditions:



C. Hughes

G. sepium *trees in a native stand in Central America average 12 m in height with stem diameters up to 50 cm.*

F.C. Byrnes

G. sepium *is used as fodder in the Philippines.*

1. Clonal propagules must resemble their seed-based progenitors. Some evidence in eucalypts indicates that clones do not always resemble half-sib seedling progeny of the same trees (Kageyama and Kikuti 1990). This means that when clonal plantations are the objective, genotypes should be tested as clones.

2. Clonal repeatability must be high, i.e., ramets of a clone must resemble each other. This means that genetic variance (both additive and non-additive) must form a large part of the total variance.

3. Non-additive variance should also be high relative to additive variance. If not, selecting particular individuals in desirable families is to no advantage. Such selection takes time and effort that would be better used in turning over generations in the breeding population and recombining genes so that favorable genes can accumulate and be selected.

Calliandra at CATIE

Calliandra calothyrsus Meissn is a Central American legume, occurring from southern Mexico to Suriname. It was introduced to Indonesia in 1936 and now occupies more than 30,000 ha in Java (NAS 1979). Trees grow quickly and, in addition to providing fuelwood over many coppice rotations, suppress *Imperata* grass in Indonesia. *Calliandra* is not extensively used in tree planting programs in Central America although it has been used as a shade tree for coffee.

Provenance collections were made in Costa Rica and Guatemala and grown in three field trials in Costa Rica with an Indonesian collection (originally from Guatemala). On a Pacific site with a five-month dry season, a Costa Rican provenance grew best over two years, whereas the Indonesian-derived provenance grew best on an Atlantic site where the dry season was only one month. This suggests that provenance x site interactions may be important, particularly where length of dry season is a major feature of the climatic differences between sites (Matheson and Cotterill, in press). No differences were detected between provenances for wood density, calorific value, or ash content. However, stem form differed considerably, trees from Indonesia being taller and with fewer, although larger, stems per tree.

N. Glover

C. calothyrsus *is a multi-stemmed shrub that grows four to six meters in height.*

No further genetic improvement work has been done beyond these initial provenance trials. However, the species flowers early (less than one year from seed), and seed matures two months after pollination.[2] Prospects for rapid turnover of generations are good. The indications from the Indonesian provenance are that this short generation interval has led to a considerable divergence from its base population in Guatemala. Because *C. calothyrsus* can be propagated by large cuttings (NAS 1979), prospects for a clonal program must be good. However, seed production is abundant and early, so clonal propagation may not be worthwhile as a breeding-strategy tool. By the time clonal trials could be established, the next improved generation would be ready for testing. Perhaps the best strategy for this species would be an open-pollinated program, with progeny tests carried out carefully and thinned heavily before each seed collection for the next generation.

[2] J. Campos, personal communication.

C. calothyrsus *at 39 months, coppiced at four months (Badulla, Sri Lanka)*

C.B. Briscoe

C. calothyrsus *growing along the roadside in Java, Indonesia*

R. Van Den Beldt

Paulownia at the Chinese Academy of Forestry

Species in this genus grow in Japan and widely in China where its light wood is used to build houses, aircraft, ships, and other vehicles. The wood is also used for musical instruments, packing cases, and is promising for pulp and paper. Although not a nitrogen-fixing tree, leaves are high in nitrogen and are used as fodder and green manure. *Paulownia* has been planted on over one million ha of farmland in China where it grows successfully in intercropping systems, particularly in the north-central plain area (CAF 1986).

Paulownia can be propagated either by seed or vegetatively by various forms of cuttings. Flowering occurs in the spring when trees are from two years old (*P. tomentosa* and *P. kawakamii*) to five or six years old (*P. fortunei* and *P. catalpifolia*). Pollination is by insects, and fruit are harvested in autumn. Inter-specific hybrids are viable, easy to obtain, and morphologically diverse (CAF 1986).

The breeding program is centered on the observation that certain hybrid offspring of *P. tomentosa* and *P. fortunei* surpass their parents in height growth. The planned program for *Paulownia* improvement is shown in Fig. 8.

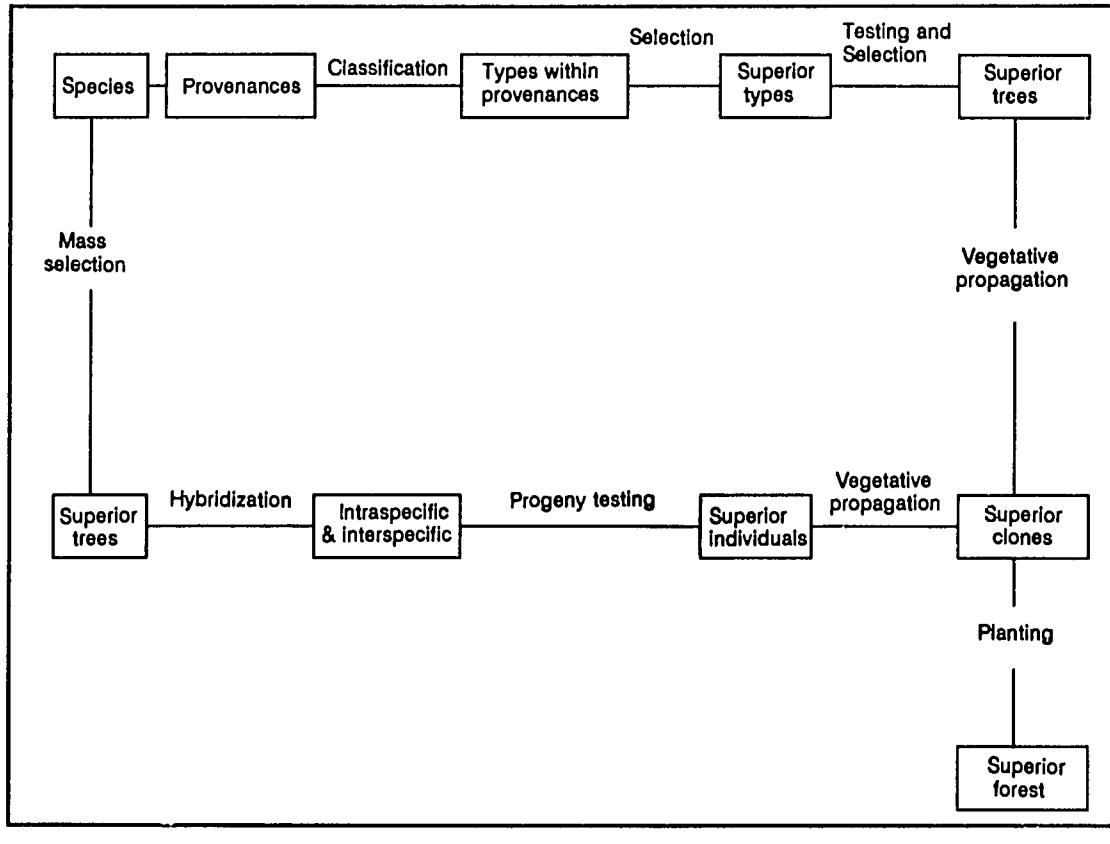


Fig 8. *Paulownia* plan from the Chinese Academy of Forestry

Two sources of material for plantations are (1) vegetative propagules of trees selected and tested from appropriate provenances without crossing and (2) inter- and intra-specific hybrids that are tested and propagated. It is unclear whether progeny testing of hybrids means that selected superior individuals are F_1 or F_2. Earlier comments in this paper on heterosis and hybrid breeding are relevant here.

K.G. MacDicken

Paulownia *is intercropped with wheat in Henan Province, People's Republic of China.*

K.G. MacDicken

Zhu Zhaohua of the Chinese Academy of Forestry meets with provincial and local government researchers and administrators at a Paulownia *intercropping experiment.*

The breeding program in China is not recurrent. Once the superior forest is planted, further progress is not possible without further breeding, e.g., by mass-selection and crossing among superior trees (Fig. 8). An effective hybrid strategy, provided hybrid vigor is caused by increased heterozygosity and not release form inbreeding, would be to use reciprocal recurrent selection. In this strategy, both parent species would be improved as independent lines, with each generation undergoing selection and regeneration. Trees to be propagated vegetatively would be produced by hybridizing the two lines each generation, with the hybrids being tested clonally before production (Fig. 9).

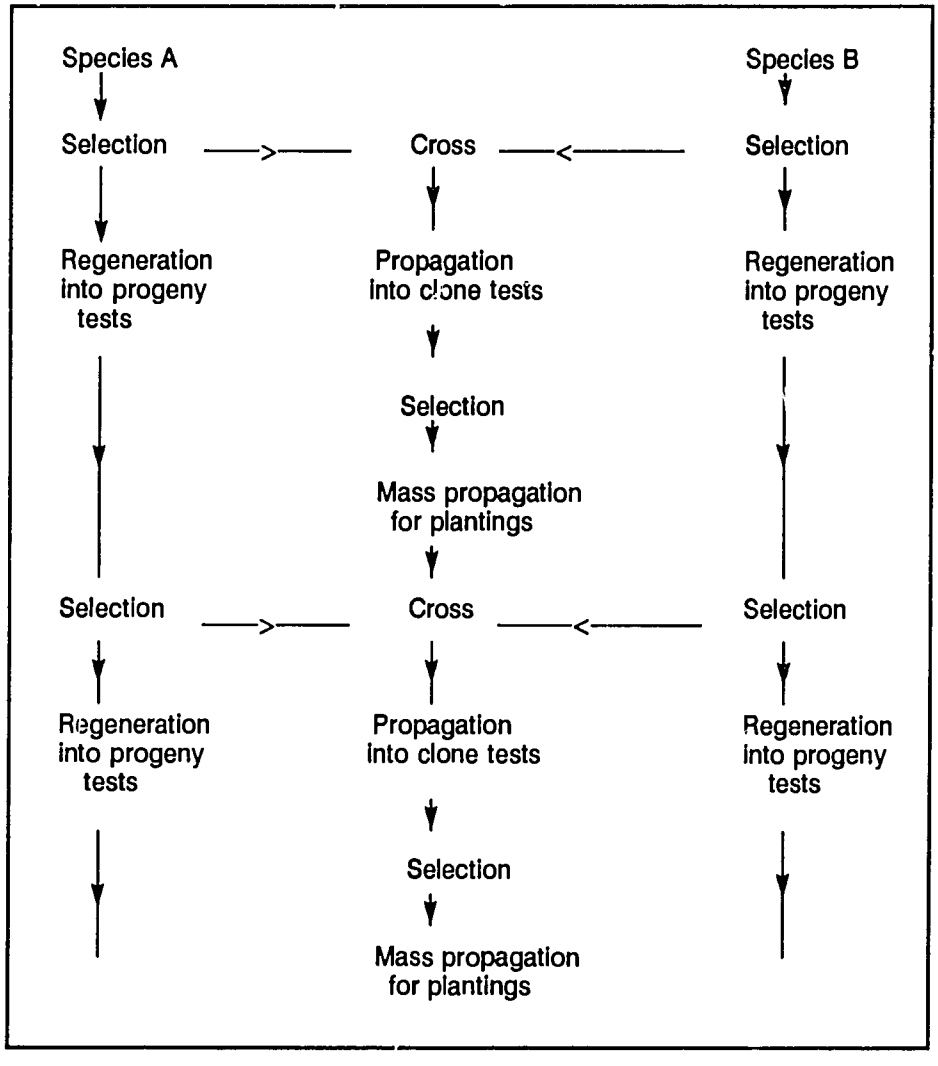


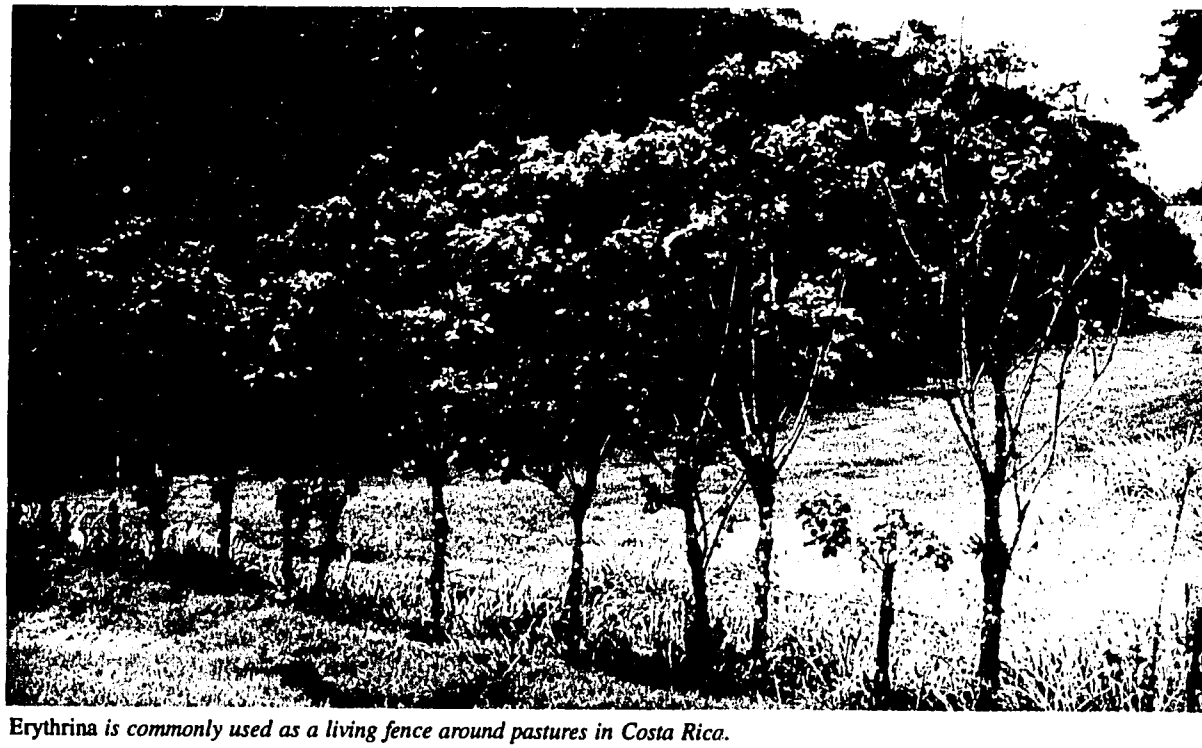
Fig. 9. Reciprocal recurrent selection strategy for clonal plantings of hybrids

Erythrina at CATIE

This leguminous genus is widespread in North and South America, Australia, Africa, and Asia. Some species are used in association with agricultural crops either for shade or support. The leaves and cooked seeds of others species are used for food, and many species provide living fences (NAS 1979).

Erythrina trees are bird-pollinated, and seeds are germinated easily. They can also be propagated by long stem cuttings. At CATIE in Costa Rica, an arboretum collection contains 28 species and a clonal archive of commonly used species (*E. berteroana, E. lanceolata, E. cohleata, E. costaricensis, E. poeppigiana,* and *E. fusca*).[3] A clonal trial has been established, testing 11 clones of each of the four most common species. Traits being assessed are height, diameter, number of shoots, length and diameter of stems, and quantity and quality of biomass. So far, the program's objectives are to maintain and evaluate a broad genetic base of material, determine the best material to use, determine how to propagate it for agroforestry, and provide a primary source of superior material for mass propagation.

[3] E. Viquez, personal communication.



N. Glover

Erythrina *is commonly used as a living fence around pastures in Costa Rica.*

Like *Paulownia, Erythrina* hybrids are easy to produce and may exhibit vigor (NAS 1979). Without evidence for hybrid vigor, however, it would seem more appropriate to improve pure species first and test hybrids later, establishing a reciprocal recurrent selection scheme as for *Paulownia* if justified. *Erythrina* is a good candidate for a program based on family amplification. Control-pollinated families could be produced and tested, and superior families could then be "amplified" by vegetative propagation. If non-additive variation for desired traits is substantial, a clonal forestry program based on identified and tested clones may be warranted. The extra gains would have to be significant to warrant the extra expense.

N. Glover

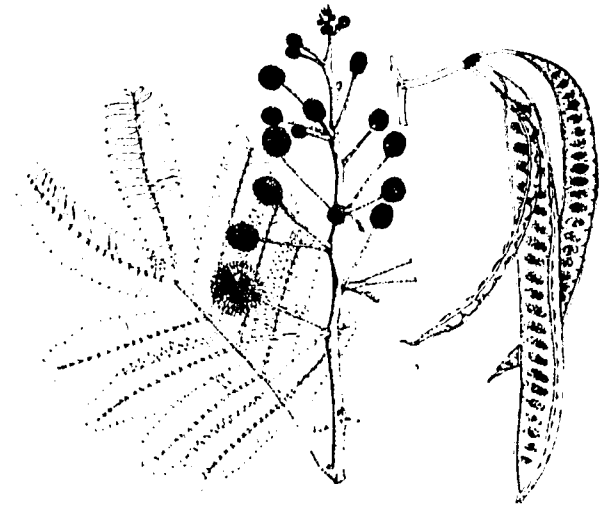
E. poeppigiana, *used as a shade tree in coffee plantations, is maintained at four to six meters in height by lopping branches twice or several times annually.*

N. Glover

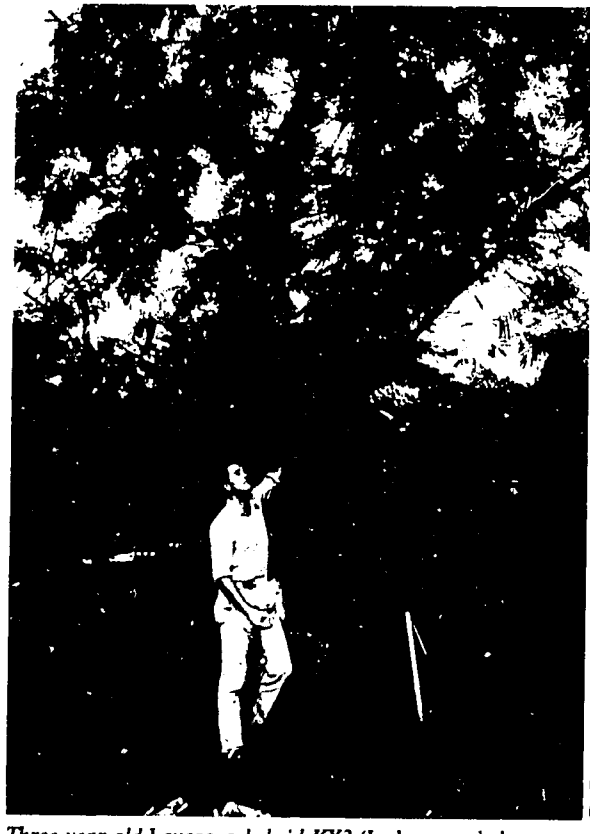
Erythrina *flowers, highly prized for their flavor, provide an additional source of income for farmers.*

Leucaena in Hawaii

Leucaena is a nitrogen-fixing genus native to North and South America from Ecuador to Texas (Brewbaker 1987a). *L. leucocephala*, the most widely used of the 13 species, is a self-pollinating polyploid grown for wood, fodder, green manure, and many other uses. The first plantings were of a shrubby variety, but new ones have been introduced, particularly arboreal or "giant" Salvador types, which occur naturally in Guatemala and southern Mexico. Its greatest drawback in recent years is the damage caused by the *Leucaena* psyllid (*Heteropsylla cubana*). However, the potential for *Leucaena* as a multipurpose tree is so great that it is worth investing in a program to identify psyllid-resistant material rather than abandon the species altogether.



Breeding *L. leucocephala* has been impeded by polyploidy and self-fertility. Genetic variation in the progeny of self-pollinating mother trees is low because outcrossing is low (about two percent) (Brewbaker 1983). In the past, improved varieties have generally been derived directly from collections in the wild in Central America. Current breeding efforts are concentrated on producing inter-specific hybrids (Brewbaker 1987b). *L. leucocephala* has been crossed successfully with all other species, except *L. greggi*. Over 50 species hybrids are now being studied in Hawaii for growth, tree form, psyllid resistance, cold tolerance, seedlessness, and fodder quality. High resistance to psyllids occurs in Hybrid KX1 (*L. pallida* x *L. diversifolia*) and Hybrid KX2 (*L. pallida* x *L. leucocephala*) and their reciprocals

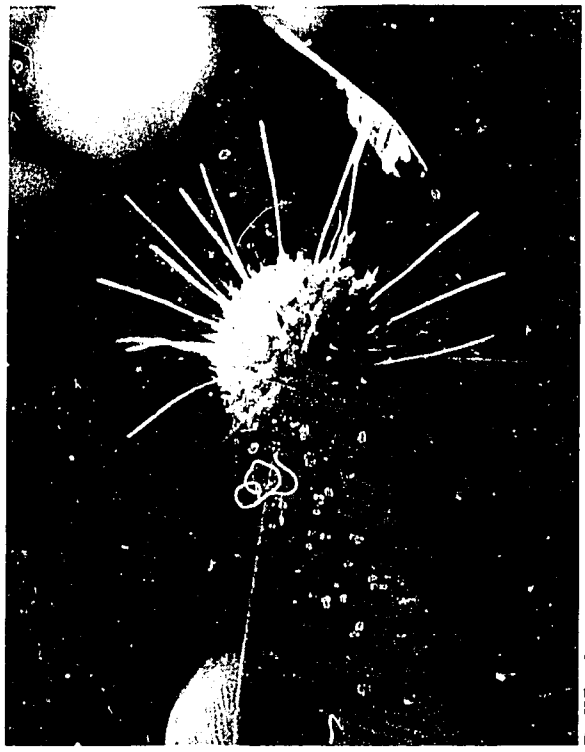


C. Sorensson

Three-year-old Leucaena *hybrid KX3* (L. leucocephala × L. diversifolia)

D. Withington

Leucaena *species and hybrids are being evaluated for psyllid resistance in the NFTA International Psyllid Trial Network.*



R. Wheeler

Hand pollination of emasculated Leucaena *flowers has resulted in over 50 species hybrids under evaluation in Hawaii.*

(Glover 1988). Although resistance of Hybrid KX3 (*L. leucocephala* x *L. diversifolia*) depends greatly on the choice of parents, much future improvement is expected to be based on this high-yielding hybrid. Three-way crosses of these and other species expand the options for breeding among seed-fertile leucaenas (Brewbaker, Sorensson, and Wheeler 1990).

Hybrids between *L. leucocephala* and other species may well be promising, but it will take many generations of selfing to become sufficiently genetically stable to release for plantings propagated by seed. Gavinlertvatana, Matheson, and Eng (1987) proposed a hypothetical scheme involving vegetative propagation via tissue culture (Fig. 10).

K.G. MacDicken

L. leucocephala *used as a windbreak in Burma*

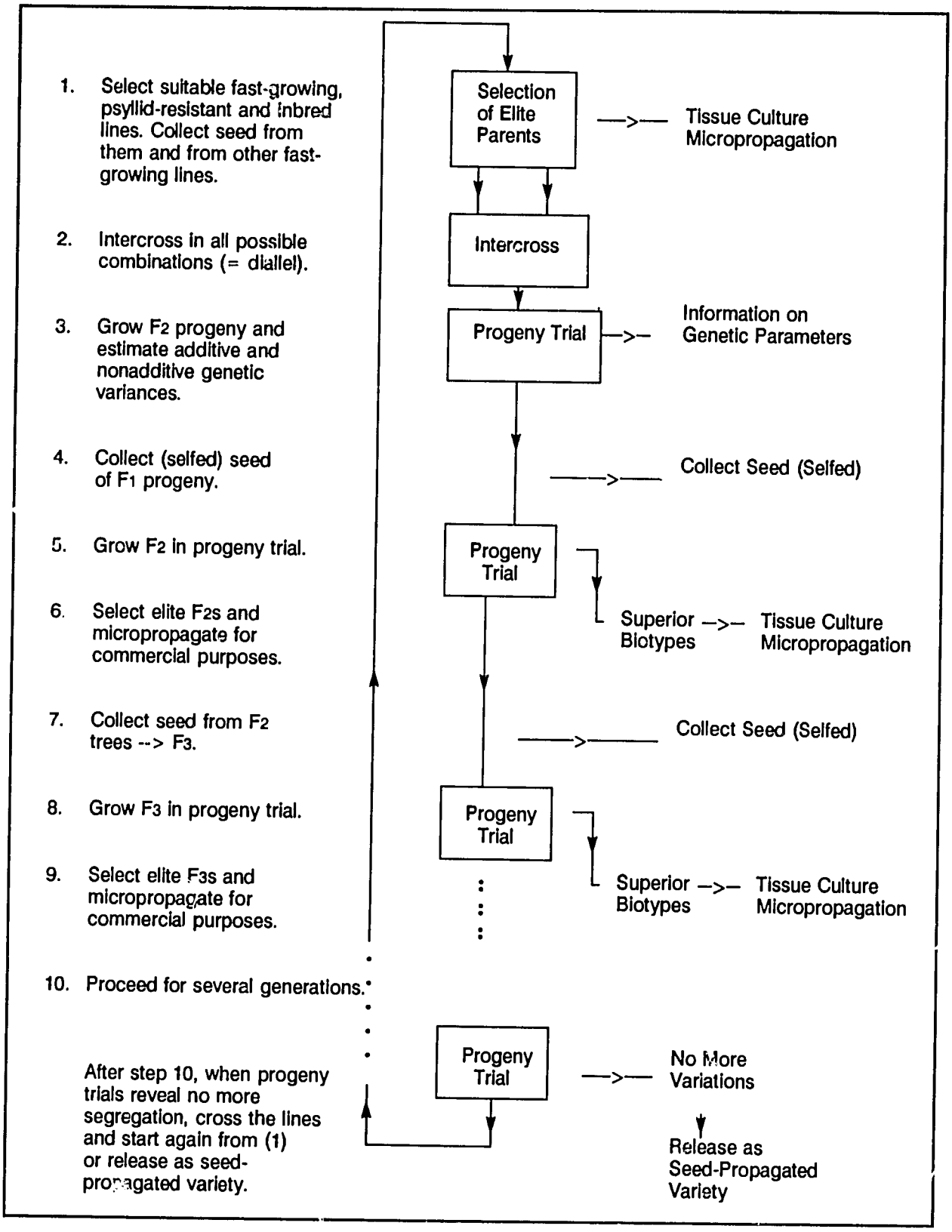


Fig. 10. Breeding scheme for fertile hybrids involving vegetative propagation by micropropagation

Species other than *L. leucocephala* also show promise, but have rather different biology. They are outcrossing, and most have fewer chromosomes and less growth potential than *L. leucocephala*. New collections have been made in Central America, Mexico, and northern South America and some promising new taxa are available for testing, broadening the scope for further improvement (Hughes 1990). Self-incompatible leucaenas are probably best improved by fairly standard programs of recurrent selection.

Because *Leucaena* has so many diverse uses, it is unlikely that a single species, variety, or hybrid will satisfy them all. Hughes (1990) recommends a multiple-population breeding strategy in which populations are constructed from different provenances and improved for various selection criteria. This is appropriate for self-incompatible species, but not for *L. leucocephala*.

NAS

Common uses of Leucaena *include forage for fodder (left) and fuelwood for cooking (right).*

General Comments on MPTS Strategy

Breeding strategies for MPTS are at an early stage of development. Few well-established breeding plans are in place, although ideas exist that will lead to them. Strategies outlined in this paper are only a framework for building a working plan that must consider the constraints and opportunities of particular programs.

Some programs have abundant labor and land but little capital or professional expertise. Such programs can afford to carry out controlled pollinations and plant progeny tests, but will have some difficulty designing breeding plans and analyzing and interpreting experiments.

Other programs may have little labor or land available, but have strong professional expertise. These will probably rely on cooperating with programs that have such resources available. Networking is an excellent way to provide professional expertise coupled with land and labor.

No program will succeed without a well thought-out breeding plan. Control of inbreeding while achieving rapid genetic change is not a simple process. It requires careful study of the issues raised in this paper and of the traits under consideration, bearing in mind that including too many traits reduces the effectiveness of selection in the others. The multiple-population approach allows for mutually-exclusive selection alternatives in different populations of the same species, but not in the same population. Single-population breeding allows for many breeding objectives, so long as they are not mutually exclusive. Progress in a single trait may be low if too many are included.

Any breeding plan must compromise between what is possible and what is desirable. The challenge is to make the compromise work.

Acknowledgements

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Seed Orchard Management[1]

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When seed orchards for forest trees were first established, one of their functions was to provide reliable seed sources for reforestation. That role is still vital in reforestation programs, and equally important for MPT plantings. Techniques for establishing and deriving maximum benefit from seed orchards are largely based on the economies of such collections. However, seed orchards are also established to make genetic management of forests possible. Hence, the management of seed orchards and the genetic management of breeding populations become confounded. This paper considers how seed orchards can affect forest management via seed supply and the genetic structure of managed forests.

Seed Supply

Whether seeds or seedlings, a reliable seed source is needed for MPT planting programs. Seeds need not be collected from selected individual trees or stands that have a permanent designation. The seed collector can thereby be given the *de facto* power of deciding the genetic composition of the forests planted from those seeds. Obviously, selection of parent trees or stands for heritable traits can influence the characteristics of the next generation. Through careful selection, gains can be obtained and seeds supplied without much investment in what are called "seed production areas" (Nikles 1984) and *in situ* breeding or conservation stands. In these areas, the benefits of selection can be obtained with stand treatment methods that do not require any greater efforts than do random collections. Using this time-honored breeding method, termed *mass selection*, gains can accumulate if reselections are confined to stands generated by such selection in the previous generation.

Several problems can limit the utility of such a minimal program. Seed production may be low and unreliable, the possibilities of site management for seed production may be poor, or the control of parentage of the forests planted from the seed may be weak or non-existent. Hence, the seed yield may be poor, immediate gain may be reduced, and future gains imperiled. The effects of managing natural stands on the genetic quality of seeds are poorly understood. Relatives may be located in clusters and, especially for dioecious species, sex ratios and effective gamete production may involve poorly-known and complex mechanisms. In addition, for some important forest trees, reproduction from root suckers generates clonal clumps of genetically identical stems (Palmberg 1985).

When non-indigenous species or provenances provide greater gains or economic productivity than do local sources, problems associated with achieving gains become more complex. Practicality dictates the use of seed orchards to achieve the best possible gains and to ensure reliable seed quantities.

For temperate-zone conifers of industrial importance, even moderate-sized seed orchards are often preferred over seed stands. Planting programs must be large enough to justify the expenses of seed orchards. However, ordinary planting of as little as 2,400 ha per year can suffice. For special plantings as subsets of larger planting programs, as few as 400 ha per year can justify a seed orchard program. The actual areas and number of ramets needed to supply this seed can range widely depending on the reproductive system. For *Platanus*, the area can be as small as 0.4 ha (Zobel and Talbert 1984). For temperate-zone conifers, 1 ha of orchard can supply seeds for an annual planting of 10 to 100 ha of forest (Barrett 1985a, Quijada 1985) or even several hundred hectares in the southeastern U.S.; it might be expected to do so for 30 years or more.

The translation of production needs into orchard size also depends on such factors as variation in seed production due to age, soil, or climate and the percentage to be planted from those seeds. Some organizations may wish to plant only a portion of their forests with improved seeds, while others may have sale or trade options available for surplus seeds.

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Since pollen parentage must also be managed and optimizing pollen production often requires inputs that differ somewhat from those for optimum female gamete production, the spacing of ramets and the arrangement of ortets are subject to different constraints for optimum gamete production, sexuality among clones, and types and levels of inbreeding. In addition, decisions on the total size of orchards, thinning regime, and design of breeding-block units within orchards and border or isolation areas around them require more than optimizing input functions for total seed production (see, e.g., Barrett 1985b, Zobel and Talbert 1984).

Orchard design also differs according to whether the trees are ramets of some set of ortets or are seedlings of some set of families. Limiting consideration to a single generation of breeding, the concept of using seedlings instead of vegetative propagules for seed production was advanced not only for convenience, but also to select seedlings to generate more gain. The relative ease, earliness, and efficiency of seed production between the two propagation methods then became confounded with earliness and effectiveness of selection with materials from the parental or progeny generation. The relative advantages of these methods have been explored in some detail (see, e.g., Nikles et al. 1984; Namkoong, Snyder, and Stonecypher 1966). While the method chosen is still controversial, the resolution is often dictated more by the practicality of managing graftings versus seedlings than by any deeper genetic issues.

Regardless of the clonal or seedling nature of orchard trees, their spacing, or the location and design of borders, most orchards are arranged to facilitate interbreeding intended among genotypes. A breeding block or breeding-management unit can then often be defined as the set of genotypes intended to intermate that usually contains one individual of each of the intermating genotypes. In this paper, a breeding block is defined as the set of unrelated and often, but not necessarily, contiguously arranged ramets or seedlings expected to intermate. Orchards may contain as many breeding blocks as necessary to produce desired amounts of seed. Each breeding block within an orchard may have the same or different arrangements of ramets or families and may have the same or different sets of genotypes or families. For a set of 50 clones or families, at a spacing of 10 x 10 m, a breeding block will occupy about 0.5 ha. Even for a small planting program of 5,000 ha/year, a minimum of 20 breeding blocks may be needed in a highly productive seed orchard (e.g., North Carolina State University-Industry Cooperative Tree Improvement Program 1988).

Genetic Management

Since a major reason for managing seed orchards is to control the genetic makeup of the seeds produced, breeding objectives must be considered in addition to seed-production efficiency. Disproportionate thinning of clones or culling of ramets can alter the genotypic composition, and management of breeding blocks can affect the interpopulational structure of the trees produced.

Perhaps the simplest situation in tree breeding is one in which all of the naturally occurring variation in a species can be captured and used within a single population, and breeding for future changes is not needed or desired. In this rare case, the breeder presumes that all possible gains are already contained in the initial collection of genotypes, and the geneticist is presumably free to concentrate on other species. The only need for constructing replicated breeding blocks is to ensure that ramets of different genotypes are well-interspersed, that the same sets of parents are used in all breeding blocks, and that enough breeding blocks are created to satisfy seed needs. Blocks do not have to be physically contiguous. For reasons of safety or site quality or to isolate ramets, the seed orchard might be composed of physically separated blocks.

Genotypes in the orchard can also be grouped reproductively not by physical separation of ramets but by pollination control. This might occur through bagging or other means of strict pollen control, or more loosely by properly timed, supplemental mass pollination. By the timely application of large doses of pollen from one small set of males to a particular set of receptive females, reasonably high proportions of the chosen mating types can be expected (Bridgwater, Bramlett, and Mathews 1987; Blush 1987). By designating a particular set of such groups, a mating design is produced. Such techniques are more expensive than open and uncontrolled pollination, but they are cheaper than other means of parental control, such as building seed orchards in various locations. They can preserve as much as 50 percent of the potential gain from methods that avoid pollen contamination (Friedman 1981). The additional gain can be obtained merely

by ensuring the proper choice of a male parent for a specific female parent.

Such mating control affords more sophisticated breeding than simply allowing parents to contribute to the gene pool according to their fecundity and other accidents of mating success. Certain males can dominate the pollen pool, and certain clones are particularly well-timed and fecund to dominate the seed pool. Hence, parental representation in the progeny is highly uneven and not particularly representative of those one would choose for performance. Hence, if any parental control is desired and can be managed by physically separated breeding units, the opportunities for controlling the effective population size and structure of the breeding population are open. The particular intermating patterns chosen for sets of genotypes normally have little effect on total cost. That is, if a system of controlled pollination is used, total cost is affected little by which parents are mated and which are not. This choice can, of course, vastly affect the structure of the progeny generation.

The effective size of the breeding population is affected by the mating design. If only a few individuals contribute almost all the pollen and only a few contribute most of the seeds, the population sample of the genes of even many potential parents is small and probably unrepresentative. In addition, immediate inbreeding problems may arise if the male and female gametes are from the same parents. Because of the deleterious effects that inbreeding can have on growth and the loss of some useful genes and gene combinations caused by sampling few parents, geneticists often set lower limits to the effective population size than can be permitted in a breeding population. One such expression is the "inbreeding effective number." Where the frequency of a genotype *(i)* in the gamete pool is f_i, the effective number is $1/\Sigma f_i^2$ (Kang and Namkoong 1988).

If that limit is accepted as a constraint on managing the population genetically, it may still be possible to use seeds from only a small subset of the orchard parents for forest planting or for a source of clonal material. In the latter case, as few as one cross of high value or a single clone of outstanding merit might be expanded for production purposes. Generally, there are other reasons, such as fear of epidemics or of genetically avoidable catastrophies that may require more than such minimal numbers of parents or ortets. Even so, preliminary analyses suggest that a single generation of trees may not require more than 20 parents in the parental generation to buffer genetic disasters (Roberds and Namkoong, in review).

In crossing to create the next breeding generation (which is distinct from providing seeds for reforestation), the tree breeder must maintain genetic variation and population size. To maximize gain from selection under these constraints, the breeder may select just those parents that have an estimated or observed breeding value above a minimum truncation point and eliminate all others from the breeding pool that form the next generation. Within the set of chosen parents, an equal contribution of each parent to the gametic pool will provide the maximum gain for a fixed, effective population size, or conversely, will give the maximum effective population size for a given level of genetic gain (Kang and Namkoong 1988). Thus, almost any scheme that increases the contribution of a portion of the parental pool at the expense of any other diminishes the effective population size.

Compensating for loss in population size by increasing the number of parents included in truncation selection diminishes gain to less than that from the original system of truncation selection with equal gametic contribution (Nanson 1986). It is possible to arrange some mating systems with unequal contributions to be better than truncation selection with equal contributions (Kang, in press), but such decisions cannot be made without careful analysis of the joint effects of mating pattern on effective population size and generational gain. For breeding purposes, the choice of partial diallel, factorial, or other design for the multiple crossing of parents little affects the generated gain as long as each parent contributes equally to the next generation. This rule stems from the requirement for equal representation of parents in the gametic pool. As long as each parent contributes the same number of gametes to the next breeding generation, the maximum gain for the given population size (and vice versa) in truncation selection is achieved.

An easy method to achieve equal representation is through a circular half-sib system (see Fig. 1). In this example of five parents (A-E), parent A is mated to parent B, which is mated to parent C, etc., without repeat of parental indentity until the last parent (E) is mated to the first (A). In this scheme, every parent contributes the same number of gametes to the next generation. If the total number of parents is kept

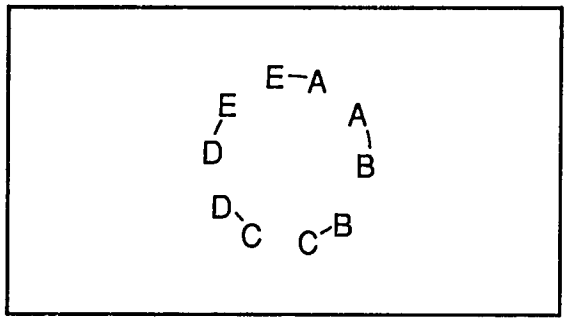

Fig. 1. Circular half-sib mating design with 5 parents

constant from one generation to the next, only the highest ranking individual from each family can parent in any cross in the next generation. Further, once the selection scheme has arrived at the desired number of parents, only within-family selection is pursued within any breeding population. This does not imply, however, that multiple crosses per parental genotype are not useful for other such purposes as testing or parameter estimation. For example, if the orchard is composed of plus trees and some genotypes are to be culled after their progeny have been tested, multiple crosses are often desirable to estimate accurately the parental breeding value. However, for breeding purposes, multiple crosses per parent will not be needed, and family selection will no longer be practiced.

A question naturally arises as to whether every breeding block in the collective orchard must be treated alike or include the same set of genotypes. If some mating control is affordable, only small differences in operating cost are likely if the parental selections were the same for each breeding block or if the same clones were maintained in each breeding block. With a few tens or hundreds of breeding blocks needed for even a small planting program, changing the genotypic composition of some blocks or of every tenth block should not increase orchard management costs. For example, if progeny testing over the range of sites to be planted indicates that different sets of genotypes will provide maximum gain for two subdivisions of the species range, then, with no additional cost, half the breeding blocks may be culled for one set of parental genotypes and the other half for an alternate set. If the species range is large and the seed demand large enough to warrant the construction of many breeding blocks, opportunities are increased for subdividing breeding blocks to contain different genotypic mixtures.

One way that breeding blocks are created *de facto* is by the arbitrary subdivision of seed-orchard zones according to presumed planting zones that match presumed zones of adaptability. This approach may follow from an assumption that seed orchards must be located within a planting zone or that different seed orchards must be constructed if a species' range is subdivided into adaptability zones. While multiple seed orchards may be desirable for seed production or managerial reasons, for breeding purposes, the basic unit of operation is the breeding block. Since breeding blocks can be physically separate or contiguous as required for seed and pollen production and can be composed of different genotypes, their physical location may be independent of the zones in which their seeds are planted. The ensemble of breeding blocks may be considered as one seed orchard program whether the blocks are physically contiguous or not. Therefore, the subdivision of a species into planting zones that may require the construction of different breeding populations is as easy to manage genetically as considering only one breeding population that requires multiple breeding blocks containing identical genotypes.

The seed orchard manager and tree breeder must therefore consider the seed needs for national or regional planting programs and subdivide into as many sets of breeding blocks as required for multiple breeding populations. When planting regions are wide enough or the species being bred sensitive enough, there can be optimum zonation schemes requiring multiple populations to maximize genetic gain (Roberds et al., in press).

Since data are usually meager at the beginning of breeding programs, most current programs formed breeding zones based on experience and intuition and adjusted zone sizes according to the degree of environmental heterogeneity. In the southeastern U.S., the North Carolina State University-Industry Cooperative Tree Improvement Program has approximately eight geographic zones that include larger areas per zone than the Inland Empire Tree Improvement Cooperative program in the northwestern U.S. (Fins 1981). In Sweden, many relatively fine zonations are constructed so that selection for growth and survival can be relatively fine-tuned (Eriksson et al. 1980). Some theoretical derivations for optimum zonations are based on various criteria (Raymond and Namkoong, in press).

Since the number of breeding blocks is finite and a minimum planting area can justify a breeding operation, it is not possible to breed for maximum growth and yield or fitness at every point in the environmental domain.

Two ways to optimize zones are: (1) set a minimum amount of loss below the theoretical maximum that will be tolerated and (2) maximize the total gain that can be achieved over the entire planting range (Raymond and Namkoong, in press). By the first method, a breeding population is chosen that gives at least the minimum gain allowed in every planting site and is at least as good as the minimum over as wide a span of environments as possible. At the point where the first provenance or population can no longer sustain the minimum performance, a second one is chosen that does so over as wide a subsequent range as possible, and so on (Raymond and Lindgren, in press). This method ensures that no point in the environmental domain has a population with less than some minimum possible value.

The second method calculates the value of planting one best population, then calculates the value of choosing the best pair of populations (which probably does not include the single best population), then calculates the best three (which probably differ from either of the best two), etc., until the marginal value of adding another population is less than the marginal cost of further subdividing the planting area. By this method, the planting value integrated over the total range is maximized but does not ensure that any minimum level of gain will be attained at individual planting sites (Roberds and Namkoong 1989). In such ways, an ideal set of breeding blocks can be developed, and the total ensemble of seed produced from the collection of breeding blocks can satisfy gain and cost objectives.

The populations that may have originally been available for constructing the breeding blocks may come from any source, but will often be simplest to obtain from collections of provenance tests. If they are samples of natural populations, then the breeding blocks are replicates of any natural population subdivisions that may exist. In such cases, the breeder may wish to maintain those natural subdivisions. By selection and controlled mating, the populations can be further diversified into smaller units or homogenized into larger interbreeding gene pools.

For some local breeding programs, enough seeds may be obtained from a few breeding blocks and the selection objectives, environments, and genotype-by-environment interactions simple enough that only a single set of parental genotypes is needed. In such cases, the few breeding blocks can efficiently be composed of replicates of the same composition. To avoid inbreeding depression and to permit enough genetic variation in the next few generations, only a few tens of genotypes need be included in the breeding population. However, for programs of larger scope and those committed to developing breeding populations of use to future generations (where selection objectives may differ and where environments may shift unpredictably), the genes contained in such small samples may be insufficient. Larger parental genotypic sampling is needed, and the problem of how to include different adaptabilities and a larger gene pool without diluting present gain becomes critical.

However, these objectives can be considered as extensions of the adaptability problem considered above, where present geographic range was accommodated by subdividing breeding blocks, and undiluted gain could be attained within breeding blocks. In this case, wider selection objectives can be included by creating other breeding blocks. If they are of little-known value, they may be replicated only once or a few times, not to generate seeds for forest plantations but to generate alternate breeding populations. In a regional set of programs or in a cooperative venture across local or national boundaries, the alternate populations created in each seed orchard may be linked to each other; in fact, the main population of one orchard may become the alternate population of another.

Geographic adaptability need not be the only basis on which multiple populations are constructed. The concept of multiple-population breeding is not new (Namkoong et al. 1979), and selection criteria can be economic as well as environmental. In Japan, for example, breeding zones are constructed for trait objectives, as well as for climatic zones and for insect and disease problem zones for *Cryptomeria* (Ohba 1984). The seed orchard manager and geneticist can simplify the genetic structure by assuming that the same selection criterion exists for the entire planting region and simply repeat the same clones of seedling families in each of the breeding blocks in the collective orchard.

Alternatively, as many breeding populations as blocks can be created, and the distinctions between orchard manager, tree breeder, and creative geneticist become blurred. The mix of seed populations delivered to the forest manager may be used in pure population blocks within planting blocks, population blocks contiguous within planting blocks, or they may be mixed before planting. Planning and coordination between planting and development of the genetic structure in seed orchards would be needed to create an effective partnership in the general forest plan.

Sequences of Generations

When the structure of one generation of breeding populations is decided, the transition to the next generation and the structure of those populations must be considered. If the breeding objective is to create further diversity, it is reasonable to assume that any initial diversity will increase when selections are made from the progeny of the first generations' breeding blocks. At its most extreme, conservation for diversity may be included in an *ex-situ* captive breeding program, and extremely different types can be selected in subsequent generations. For commercial forest production, the original environmental and trait adaptabilities might be refined or shifted according to the predicted needs. Least disruptive are changes in adaptabilities that only increase yield, resistance, or other trait performance level. These directions may often be decided with little disruption to the management of seed orchards, but the pace of change might be different in some breeding blocks because earlier selections may be required for some zones. Hence, more disparity among breeding blocks can be expected in the future.

The substitution of materials can then be made on a block-by-block basis, or can be more gradually introduced as the performance of candidate parental genotypes rises or as various traits or adaptabilities are introduced. If the selection-objective changes are large or if they introduce intergenerational relatives, such as progeny of parents that remain in the orchard, gradual change may not be possible. Whole-block substitutions would be needed.

Various schemes have been proposed for gradual change by substituting single clones, as their breeding value is proven to exceed any previously used clone (Nanson 1986). Such "evolving seed orchards" allow a continual upgrading of value to occur. Similarly, instead of a clone-by-clone replacement, Libby (1964) has suggested that, since most orchards are arranged in rows, it would be operationally convenient to change the composition of a continually productive orchard gradually by planning on a more or less continuous series of new orchard rows at one end of a seed orchard. As clones age and perhaps decline in relative productivity, they can be replaced along a rolling front of productive ramets that may deviate in genotypic composition as replacement genotypes become available. In all these schemes, the inbreeding and effective population-size problems cannot be overlooked, and questions of unequal genotypic representation that diminish the effective population-size must be addressed.

In multiple-population breeding, the genotypes used in sequences of advanced generations may be entirely derived from the original orchard. While one may think the seeds from an orchard will create the forests from which the next generation will be selected, such objectives may shift. The next generation may come substantially from what might have been considered the progeny of some other orchard's alternate population. The structure of the orchards and generations will undoubtedly become more complex, but management of the variation between and within orchard populations must remain under the breeder's control.

The distinctions that are usually made between the mechanics of orchard management (the job of the seed orchardist), genetic management of the forests to be planted (the job of the tree breeder), and the evolving structure of our future forests (the job of the forest geneticist) are illusory. They are artifacts of traditional divisions between sciences and between laborers and thinkers that scientists would do well to overcome.

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Glossary

allele	one of two or more genes located at the same locus in homologous chromosomes and controlling the same character
allozyme	alternative enzyme forms encoded by different alleles at the same locus broad sense heritability portion of the total variance due to all genetic factors
calcicole	a plant tolerant of high calcium soil levels, normally growing on calcareous soils
calcifuge	a plant intolerant of high calcium soil levels, not normally growing on calcareous soils
crossability	the relative ease with which hybrids can be produced within and between species
dioecious	producing male and female flowers on different plants
diploid	having 2n or two sets of homologous chromosomes
family	the offspring of a single tree after open pollination or of a single pair of trees after controlled pollination
gamete	a haploid generation male sperm cell or female egg cell capable of developing into a zygote (embryo) after fusion with a germ cell of the opposite sex
genotype	the entire genetic constitution, expressed or latent, of an organism or group of organisms
half-sibs	trees with one parent in common (usually the female)
heterosis	hybrid vigor
heterotic	*adj.* for heterosis
heritability	the portion of the total variance due to genetic factors
heterozygous	possessing different alleles at a particular locus; derived from the union of gametes ofdissimilar genotype
homoclime	an imaginary line on a map or chart connecting areas of equal rainfall, temperature, elevation, or other factors
homozygous	possessing the same allele at a particular locus; derived from the union of genetically similar gametes
inbreeding	mating between close relatives; mating in a population consisting of a few individuals
infraspecific level	referring to variation below the species level, e.g., within a given species

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isohyet	a line on a map or chart connecting areas of equal rainfall
isotherm	a line on a weather map connecting points having equal temperatures mass selectio.. phenotypic selection; choosing trees on the basis of their phenotypic performance.
monoecious	bearing separate male and female flowers on the same tree
narrow sense heritability	the portion of the total variance due to genes with additive effects and most indicative of the superiority that can be transmitted by seed
ortet	the original ancestor of a vegetatively propagated clone
outbreeding, outcrossing	mating unrelated parents phenotype the visible characters of a plant, the product of a plant's genotype and its environment
polyad	pollen grains that are formed and dispersed in units composed on more than one grain
polyploid	having more than two complete sets of chromosomes
population	genetically, a group of individuals related by common descent and treated as a unit; the size or amount of variability within a population has no definite limit and does not necessarily connote that populations differ by any set amount
progeny	the offspring of a particular tree or a particular combination of one female and one male tree
provenance	the ultimate natural origin of a tree or group of trees, usually considered synonymous with geographic origin
ramet	any of the members of a clone, descended through vegetative propagation from the ortet
roguing	systematic removal of individuals or families of undesirable genotype, especially from a seed orchard
seed source	the locality where a seed lot was collected
selection index	choosing parents on the basis of several desirable traits, judged according to an index of value calculated by considering the heritability and importance of each trait
self-incompatibility	inability to produce seed following self-pollination
sympatric	taxa occupying the same range without loss of identity from interbreeding
taxon	a taxonomic unit of any size
tetraploid	having 4n chromosomes

The Forestry/Fuelwood Research and Development Project (F/FRED) is designed to help scientists address the needs of small-scale farmers in the developing world for fuelwood and other tree products. It provides a network through which scientists exchange research plans, methods, and results on the production and use of trees that meet the household needs of small farmers. These trees, in project terms, are multipurpose tree species (MPTS).

F/FRED is being carried out by the Winrock International Institute for Agricultural Development. Winrock was established in 1985 through the merging of the Agricultural Development Council (A/D/C), the International Agricultural Development Service (IADS), and the Winrock International Livestock Research and Training Center. Winrock's mission is to improve agriculture for the benefit of people--to help increase the productivity, improve the nutrition, and advance the well-being of people throughout the world. Winrock's main areas of emphasis are human resources, renewable resources, food policy, animal agriculture and farming systems, and agricultural research and extension.

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