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Tropical trees: the potential for domestication and the rebuilding of forest resources

Natural Environment Research Council

G J Lawson.

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Preface

Domestication of 'Cinderella' species as the start of a woody-plant revolution

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We are all aware that the pressures on tropical ecosystems are increasing daily: that human and livestock populations are rising, and that the stock of productive land is finite and dwindling as a result of misuse. Deforestation is reducing species diversity and eroding the genetic base of many tropical tree species, including those used traditionally by local people for products that fulfil many of their domestic needs. Forest degradation is also having negative impacts on soil fertility, and is modifying climate by local/regional influences on the albedo and hydrological cycle, as well as by the emission of trace gases to the atmosphere.

Together, the above consequences of deforestation combine to reduce the area of productive land needed by growing human populations, and to increase poverty and the incidence and severity of famine. At present, the demand for farm land is met by opening up new areas of forest to agriculture. It is therefore important to increase the resource of trees in deforested areas, so as to meet the traditional needs of local people, including the urban populations. Somehow a way has to be found to make the land more productive and to rehabilitate degraded areas in a way which will diversify production, promote genetic conservation, enhance the development of sustainable land use and contribute to domestic, regional and international trade.

Great progress was made with food crops in the 1960–80s, as a result of the 'green revolution', but now there is a need to diversify into new crops, many of which could be tree crops. This diversification is desirable ecologically and economically, to reduce the dependence on commodity crops with falling product prices. In addition, without genetic engineering, further large increases in the yield of the current narrow range of crop species are unlikely.

Throughout the tropics there are numerous perennial woody species that have provided indigenous peoples with many of their needs for millennia. Many of these people have now left the land for the concrete jungles of urban life, but would still like supplies of traditional food, medicines and other natural products. These traditionally important woody plants are virtually undomesticated, ignored by the 'green revolution', yet probably have great genetic diversity. They also play a key role in the biological, chemical, physical and hydrological cycles of the soil and the atmosphere, protecting soils from damage and acting as a buffer against environmental change. These same plants are the ones that are cut down indiscriminately to relinquish a few valuable logs per hectare, to clear land for 'development' projects or to provide a subsistence living for a year or two. These overlooked and often highly desirable trees are the 'Cinderella' species of our forests.

'Cinderella' species are often ignored by agriculturalists of the developed world in favour of a handful of exotic species which have been domesticated and grown artificially on a large scale. The choice is often made without much thought for the environment, and, perhaps, with thought only for relatively short-term economic gains. The same scenario has occurred in forestry. While planting and domesticating a few exotic fast-growing trees for pulp and paper, the majority of the hardwood species forming the basis of the timber trade have not, for a variety of reasons, contributed significantly to reafforestation programmes. Surprisingly, therefore, the absence of even beautiful and commercially important timber trees such as mahogany from man-made forests allows them to be classed as 'Cinderella' species. The resources of these 'Cinderella' tree species can be tapped by the process of 'domestication', which has been applied so successfully to agricultural and horticultural crops.

One of the objectives of this Conference is to raise the profile of the 'Cinderella' species, and, particularly, to draw attention to a growing effort to domesticate a much wider array of tree species and introduce them into agricultural and forestry systems. The domestication of traditionally utilised 'Cinderella' species providing fuelwood, poles, timber, fruits, gums, nuts, resins, fibre, pharmaceutical products, etc, can now be rapidly achieved by applying some of the techniques described in these Proceedings. This approach has the added environmental benefit of diversifying the species grown on farm land and in forest plantations. In addition, domesticating these species will go some way towards reducing economic dependence on a few 'commodity' species. In this way, a start is being made to initiate a 'woody-plant revolution', which could provide some cheer in the otherwise gloomy outlook for tropical forests. Opportunities are currently being lost because of a lack of awareness of the potential to domesticate forest tree species for the production of timber and non-timber products.

What are the issues that have to be resolved to trigger this new revolution? From the viewpoint of a farmer, there are:

- *the political and social issues,* such as how to acquire the right to own and protect a piece of land and the trees on it, and the need for incentives to plant trees;
- *the economic issues,* such as what is the value of these trees in terms of their wood, other products and environmental services;
- *the biological issues,* such as how to grow the trees wanted by farmers; how they can be made more desirable and productive, to the extent of satisfying the farmers' needs and even providing a surplus which could be sold to urban populations.

This Conference is about solving the biological issues concerned with the provision of timber, food and other domestic necessities. However, there are also direct economic and social benefits, such as improving community welfare through the market-place. To plant and grow trees on a scale necessary to have any impact on either the environmental or social consequences of deforestation, it is essential that farmers, communities and companies see financial and other incentives accruing from tree planting. The incentive of greater profitability is proposed as a powerful means of promoting the planting and growth of tree species. Genetic improvements in yield and quality should increase the value of the products of a tree crop, while increased growth rates in timber trees will allow a shortening of the rotation, and hence a more rapid return on invested capital. It should not be at the expense, however, of the environmental benefits of tree planting.

There has been a recent awakening to these biological issues, and significant progress has been made in the past 10–15 years. It has been realised that it is possible to capture the genetic variation inherent in tropical tree populations, and that this can be used to domesticate trees rapidly for timber as well as non-timber products for sale in local, regional and even international market-places. It has also been realised that there is a need to improve management systems if new cultivars are to be as productive as they could be, and if they are to be used to rehabilitate deforested land. Options include systems which rehabilitate the environment on a local scale, by improving soil structure and fertility. Other systems may have more wide-scale effects, such as beneficial impacts on the regional hydrology or global climate, by the creation of complex canopies which mimic natural forests.

There is also a growing realisation that the domestication of these 'Cinderella' trees involves protecting their genetic resources and growing them wisely and efficiently to protect the environment. Perhaps a 'woody-plant revolution' of this sort could contribute significantly to the rehabilitation of our planet and the feeding of its population. Hopefully, the Proceedings of this Conference will inspire fairy godmothers, particularly policy-makers and donors, to mobilise their glass carriages and get Cinderella to the ball.

Dedication

These Proceedings are dedicated to Douglas G B Leakey, who as a forester in Kenya all his career tried to encourage the planting of trees for environmental protection. It was this awareness of the importance of trees that led him to write a paper in 1948 for a conference in the Belgian Congo, which subsequently inspired Professor Anthony Young of the International Centre for Research in Agroforestry to commend him as one of the early advocates of agroforestry.

(See *ICRAF Newsletter* (October 1986), **18**, 5.)

Domestication: a definition

The concept of a domesticated species is familiar to most people in terms of farm animals and household pets, but is not so common in plants. However, it is well known that modern grain cultivars have been bred over generations from wild grasses, and that our gardens and orchards are stocked with woody plants that have similarly been subjected to selection and breeding. Foresters have been slow to see the need to domesticate their crops. Until relatively recently, foresters have collected seeds from the wild and used them without selection. The use of provenance selection, an early stage in the domestication process, gained international importance in the 1960s, although techniques such as clonal selection have been used for centuries in a limited number of species – *Salix, Populus, Cryptomeria japonica,* etc.

The following are definitions which help to explain the processes which are involved in the domestication of a plant species.

- To domesticate is to naturalise; make fond of home; bring under human control, tame; civilise (*Concise Oxford Dictionary*)
- Domestication is closely linked to the idea of selection, of fitness for purpose, of pushing nature into a higher gear and in a particular direction (Palmer, pp16–24)
- Domestication is a two-stage process in plants: the bringing into cultivation of wild plants or exposing them to some form of management, and subjecting these to differential production or selection (Janick *et al.* 1982)
- Domestication is human-induced change in the genetics of a plant to conform to human desires and agroecosystems, culminating in the plant's loss of its ability to survive in natural ecosystems (Harlan 1975)
- The four elements of the domestication process in forest trees (Libby 1973):
  - the original genetic variability
  - selection of the desired trees or genes
  - a packaging of those genes in the plants to be used
  - converting those gene packages into the growing trees which are harvested as a renewable resource.
- There are several stages to the domestication of crops (described by Clement & Villachica, pp230–238):
  - managed species
  - semi-domesticates
  - full domesticates

At the Conference, the full 'domestication' of a tree species was taken to encompass the identification and characterisation of its germplasm resources; the capture, selection and management of genetic resources; and the regeneration and sustainable cultivation of the species in managed ecosystems (Figure 1). In the papers presented, it is clear that the starting point can vary considerably depending on the approach taken, which in turn seems to depend on whether the domesticator is a peasant farmer or a research scientist. Many of the species described can, thus, at best be described as semi-domesticates.

In forestry, the term 'domestication' has mostly been applied to the genetic improvement of trees for industrial plantations, but one message from the Conference is that the domestication process in trees also has a strong social involvement, seen clearly from the examples of non-timber species. The need to develop this social aspect has recently been recognised in the strategic plan for the new Centre for International Forestry Research (CIFOR) prepared by the Australian Centre for International Agricultural Research. CIFOR is the newest institute of the Consultative Group for International Agricultural Research.

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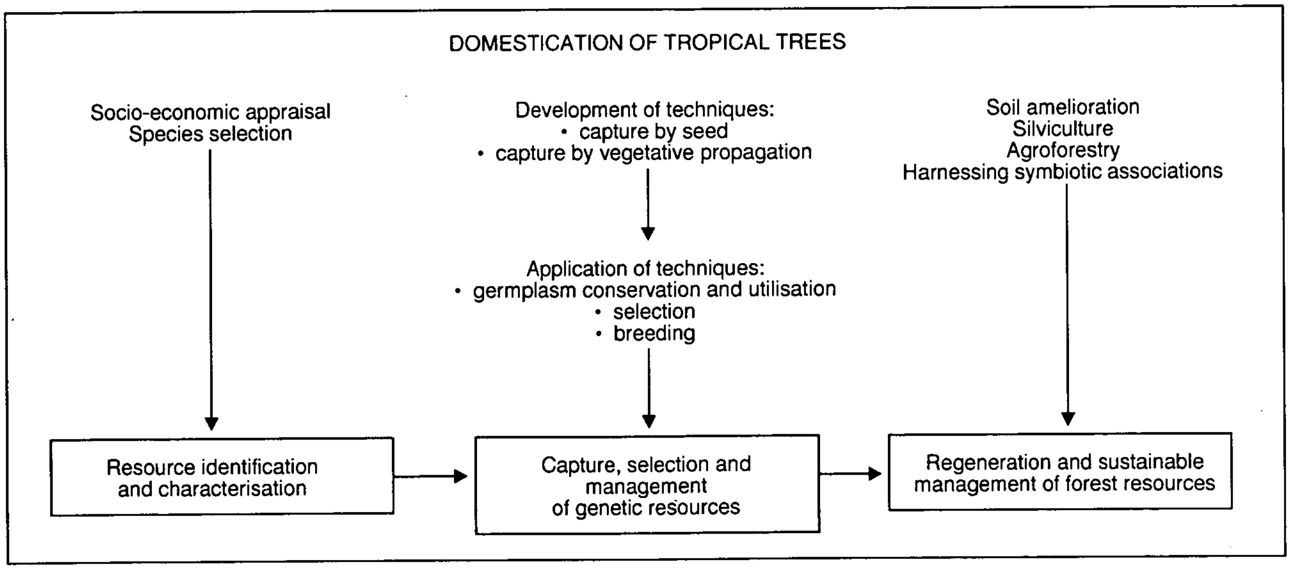

Figure 1. Stages involved in the domestication of tropical trees

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The resource of useful tree species: identification of priorities for domestication

Amazonian tree diversity and the potential for supply of non-timber forest products

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ABSTRACT

The huge diversity of tree species found in the Amazon rainforest presents both an opportunity and a problem for the exploitation of non-timber products. The diversity offers a vast array of potential harvestable crops but this also means that they are sparsely distributed. A few crops, such as the Brazil nut and rubber, have been exploited for many years with little harm to the forest, but other crops have been extracted in a destructive way, such as rosewood and the various species providing balata latex. It is not the most species-diverse forests which have the most potential for non-timber products; in certain areas under adverse environments, such as swamp forests and transition forests where there is a dominance of one or a few species, there is considerable opportunity to use non-timber products. The single most important plant family for such products are the palms, which often dominate the species-poor habitats. However, there are many other plant species from the species-diverse forest with potential for domestication; a number of these are described in this paper.

INTRODUCTION

In this paper it is intended to place the importance of non-timber forest products (NTFPs) firmly on the agenda. Non-timber products, such as medicines and fruits (see Waterman, pp42–48; Okafor & Lamb, pp34–41; Maghembe *et al.*, pp220–229; Clement & Villachica, pp230–238), are relevant to all systems of management, not just to extraction from otherwise untouched forest, where there are severe limits to the possibilities of extractivism. Consequently, the relevance of NTFPs to timber plantations, to agroforestry systems and to the domestication of new forest crops in Amazonia will also be considered.

THE DIVERSITY OF THE AMAZON RAINFOREST

The Amazon rainforest is a potential source of many NTFPs because of its enormous species diversity (Table 1). The highest diversity recorded is from Yanomono in Peru (Gentry 1988), where 300 species of 10 cm diameter or greater were recorded in a single hectare. In addition to tree species, there is a wealth of herbs, shrubs, epiphytes, and parasitic species that add considerably to the total diversity of the forest. In the Rio Palenque Reserve in western Ecuador, Gentry and Dodson (1987) found 365 species of vascular plants in a tenth of a hectare; in the forests of Costa Rica, Whitmore, Peralta and Brown (1985) found 233 species in 100 m^2. These findings equate to a sixth of the British flora in an area smaller than a tennis court! Many of these species have some potential use, as is apparent from studies of a quantitative inventory of forest used by the Amazon Indians (Prance *et al.* 1987).

Boom (1985a, b) made a quantitative inventory of forest use by the Chácobo Indians of the Bolivian Amazon, and found that they have a use for 75 out of the 91 tree species (82%) on a sample hectare. This included 95% of the individual trees (619 out of a possible 649). Similarly, Balée (1986) found that the Ka'apor Indians of Maranhão, Brazil, had a use for every single species of tree on a sample hectare. The uses included food, fibres, fuel, material for construction and crafts, medicines and rubber latex. If the Indians know of so many ways in which to use the forest, it would indicate that there are many more products to be marketed or species to be domesticated than the few

Table 1. Data on tree species diversity from inventories of Amazon rainforest

Locality	No. of trees >10 cm diam ha^{-1}	Source
Yanomono, Peru	300	Gentry (1988)
Mishana, Peru	289	Gentry (1988)
Yasuni, Ecuador	228	Balslev *et al.* (1987)
Cocha Cashu, Peru	189	Gentry (1988)
Manaus, Brazil	179	Prance, Rodriques & da Silva (1976)
Xingu, Brazil	162	Campbell *et al.* (1986)
Breves, Brazil	157	Black, Dobzhansky & Pavan (1950)
Alto Ivon, Bolivia	91	Boom (1986)
Pantanal, Mato Grosso, Brazil	35	Prance & Schaller (1982)

species producing timber, latex and nuts currently harvested from the region.

EXTRACTION OF NON-TIMBER PRODUCTS

Extraction of NTFPs for export from Amazonia is nothing new. It began in the 16th and 17th centuries when such products as cacao (*Theobroma cacao*), vanilla, sarsaparilla and ipecac were some of the main products. Much has been written in recent years about the advantages and disadvantages of creating extractive reserves in Amazonia and elsewhere. Extractive reserves are areas of forest that, through legislation, have been set aside for the local population to extract NTFPs without clearcutting and which they manage collectively. Through the action of the Brazilian Council of Rubber Tappers and through the work of various activists and scientists in favour of the concept (eg Allegretti 1990; Fearnside 1989; Schwartzman 1989), Brazil has set aside over 3 million hectares as extractive reserves, mainly in the states of Acre, Amapá and Rondônia. This in itself is a measure of the initial success of the concept of extractive reserves. Interest and enthusiasm for this type of reserve were increased by various demonstrations that the economics of extraction compared favourably with alternative land uses such as cattle pasture and timber plantations (Alcorn 1989 for Mexico; Peters, Gentry & Mendelsohn 1989, Peters 1990, Prance 1989a for Amazonia; and Balick & Mendelsohn 1992 for medicinal plants in Belize). The economic calculations of Peters, Gentry and Mendelsohn (1989) were based on the hypothetical market value of a hectare of forest rather than the actual sales, and so these authors themselves pointed out the limitations of their study. Since then, a large number of authors have discussed the difficulties facing extractive reserves (Anderson 1992; Browder 1990, 1992; Fearnside 1989; Pinedo-Vásquez *et al.* 1990; Vásquez & Gentry 1989).

SOME LIMITATIONS OF EXTRACTIVISM

Contemporary extractivism in Amazonia has arisen from the needs of the long-neglected population of rubber tappers, who are the remainder of the rubber boom and the debt peonage system of *aviamento* (see Dean 1987; Prance 1989b; Weinstein 1983). Many rubber tappers outside extractive reserves are still in debt (Whitesell in Browder 1992). Within extractive reserves, the economy is based largely on two products, Brazil nuts (*Bertholletia excelsa*) and rubber. Until recently, in Brazil, the price of rubber was sustained above worldwide market value by subsidies. It has now dropped considerably; 60% of Brazilian rubber demand is now provided by plantations outside the Amazon region, where the rubber trees are not attacked by diseases endemic to Amazonia. The price of Brazil nuts has also dropped in the past few years, despite efforts by many people to expand the market for this product. This instability of the market price of the main extractive products is seriously straining the system, and is leading the dwellers of the reserves to fell more forest for agriculture and even to invest their meagre earnings in cattle.

The extraction of many products from forests has led to over-exploitation rather than to the sustainable use of the resource. While the extraction for Brazil nuts and rubber has been reasonably sustainable despite their other problems, there are many examples of both timbers and NTFPs where extraction has resulted in the virtual elimination of the species from the forest. For example, rosewood (*Aniba roseaeodora*) for the essential oil linalol, caucho (*Castilla elastica*) for rubber latex produced by felling, and sorva (*Couma utilis*) for the latex used in chewing gum have all suffered from over-exploitation, which has reduced these species to near-extinction.

Other extraction products have been through this 'boom and bust' cycle because of changes in the international market. For example, barbasco (*Lonchocarpus* spp.) was used for the production of insecticides until replaced by synthetics; tagua (*Phytelephus macrocarpa*) was used for vegetable ivory until plastic replaced it; and oil produced from copaiba (*Copaifera* spp.) lost favour when it was found to pose health hazards.

Conservationists are succeeding, to a limited extent, in reviving markets for the latter two products, but there is no doubt that the vagaries of the international market are not favourable to extraction products that are only harvested in relatively small quantities. A further limitation to extractivism is the low population density that it can sustain in comparison to such alternative land uses as agroforestry (Anderson 1992; Browder 1992).

OLIGARCHIC FORESTS: WHERE EXTRACTION WORKS

The term 'oligarchic forest' was coined by Peters *et al.* (1989) for areas of forest within Amazonia that, because of some environmental factor, are largely dominated by a single species. If the dominant species in an oligarchic forest is of economic use, then, because of its abundance, many of the constraints of extractive reserves in species-diverse rainforest are removed. Most oligarchic forests in Amazonia are dominated by palm species that are of considerable use, and some cover extensive areas (cf Clement & Villachica, pp230–238).

Oligarchic forests of buriti or aguaje palm (*Mauritia flexuosa*) and of açaí palm (*Euterpe* *oleracea*) occur in excessively swampy areas where little else will grow. There are vast areas of *Mauritia*, such as the area of over 10 000 ha in extent around the Rio Jutaí. This palm is exploited for its edible fruit in Amazonian Peru (Padoch 1988) and for both the fruit and a weaving fibre from the leaf epidermis for craftwork in Maranhão, in eastern Amazonia, Brazil (Prance 1988). It could be a continuing and sustainable resource, but, unfortunately, in both places local people often fell the trees to collect the fruit. As the species is dioecious, it produces stands of only male trees. The açaí palm is particularly abundant in the Amazon delta region in areas flooded daily by tidal back-up of the river. It is a truly multipurpose palm with many uses but especially for the fruit, the pulp of which commands a good price in local markets in Belém. Its harvesting has been studied in detail by Anderson and associates (Anderson 1990; Anderson *et al.* 1985; Anderson & Ioris 1991; Anderson & Jardim 1989). Açaí is also an ideal species for the production of heart of palm, which is canned and exported, because it is a multistemmed palm that regenerates from suckers when cut. However, it is already being seriously over-exploited on Marajó island in Brazil, and is another crop that could head for a 'boom and bust' if not carefully controlled.

The babassu palm dominates large areas of the transitional forests in eastern Amazonia between Amazon rainforest and the *cerrado* formation of central Brazil. It forms oligarchic forests because of its resistance to fire, which can spread into the drier forests of the transition region. The area of babassu forest has increased dramatically in recent years because individuals in deforested areas survive and spread rapidly. Babassu is also a multipurpose palm and has supported a large number of local people for many years. The fruit is divided into three parts, each of which is useful. The outer mesocarp is rich in carbohydrate and is used for flour, the extremely hard endocarp is used to make high-quality charcoal, and an oil that is both comestible and combustible is extracted from the kernel. This oil is almost identical chemically with coconut oil. (For further details, see Anderson & Anderson 1983; Anderson, May & Balick 1991; Balick 1987; May 1990a, b; May *et al.* 1985.)

The last example of an oligarchic forest is that dominated by camu-camu (*Myrciaria dubia*) in the riverside and lakeside areas of the upper Amazon. This member of the Myrtaceae family grows in areas that are inundated for much of the year and where little else can survive. The cherry-like fruit, which is produced as the river level rises, can be easily harvested from canoes; it contains 30 times more vitamin C than citrus. It is already extremely popular in Iquitos, Peru, as a drink and as a flavouring for ice-cream, and has much wider potential if a method for transporting the fruit can be developed. Camu-camu is highly productive, easy to harvest and unlikely to be over-harvested. (For further details, see Peters *et al.* 1989; Peters & Hammond 1990; Peters & Vásquez 1987.)

EVALUATION OF EXTRACTION

Extractive reserves are not a panacea that will save the whole Amazon region, but, if their limitations are recognised, they have an important part to play in the conservation of Amazonia. Extractive harvesting works best in areas of oligarchic forest, which by definition are species-poor, and not in the centres of diversity most in need of conservation. However, improved management of oligarchic forests could deflect some of the pressure from other areas. Extractive reserves in species-diverse rainforest have many social problems (Anderson 1992; Browder 1992; Salafsky, Dugelby & Terborgh 1993), but they should not be under-rated. Nepstad *et al.* (1992) studied the Chico Mendes Reserve at Porongaba in Acre State, Brazil, and showed some biotic impoverishment of game, with one species, the tapir, eliminated. It was also noted that the Brazil nut was not regenerating, allegedly because of over-harvesting. This study also showed that many more rainforest species survived in the extractive reserve of Porongaba than in management systems of logging and ranching with which it was compared. The absence of Brazil nut regeneration is normal because it is a light-demanding species that only develops when there are light gaps in the forest (Pires & Prance 1977).

With human activity there is undoubtedly some biotic impoverishment in extractive reserves. However, this impoverishment does not detract from their value because they have been created in areas where the original forest is particularly threatened by destruction. Most reserves were formed to stop the progress of cattle ranching and in this objective they have been successful. Apart from the conservation of biodiversity, extractive reserves are most important because they maintain forest cover, protecting the soils, regulating the hydrological cycle (Salati & Vose, 1984; Salati, Vose & Lovejoy 1986), and sequestering carbon, rather than releasing it into the atmosphere. We should not under-estimate these roles of extractive reserves.

If extractivism is to work well, markets must be developed for products other than Brazil nuts and rubber, both of which have fluctuating prices. This means that the livelihood of an extractivist is tenuous. The challenge before us is to search for and promote other products from the forest, and to develop markets for them – locally, regionally and internationally.

EXTRACTION LEADS TO DOMESTICATION

Most of the Amazonian trees or shrubs that are now cultivated for their fruit, oils, nuts or other products (eg cacao, rubber) were originally extraction products. To support the concept of extractivism is, therefore, to encourage future domestication. Extractivism needs to keep ahead of domestication, by constantly looking for new products. One of the best-known examples of extractivism is the Brazil nut. Until recently, the entire production was from wild trees, as early efforts to grow plantations were a failure. For example, there is a large area of abandoned Brazil nut plantation near to Aleixo, Manaus.

Early attempts to cultivate Brazil nuts in plantations fared badly because the species does not thrive where the soil has lost its nutrients, and because of a lack of understanding about its intricate pollination mechanism. We now know the pollinators (Prance 1985; Mori & Prance 1990; Nelson *et al.* 1986), and that Brazil nuts need to be planted in clusters or strips near to forest so that the pollinator bees work the plantation. The fact that Brazil nuts naturally are often found in clusters of 50–100 trees (Balée 1989; Prance & Mori 1979) is probably because Indians used this method in the past. Today, there are young Brazil nut plantations in several parts of Brazil, some of which look very healthy. Torres and Martine (1991) indicate that several thousand hectares of Brazil nut plantations have recently been planted in Amazonas and Pará states. Brazil nuts are, therefore, in the process of becoming truly domesticated, and much research is being carried out on their management at the Humid Tropics Agricultural Research Station (CPATU) in Belém (see bibliography in Correa, Pinto & dos Santos 1983).

Another crop that began as an extraction crop, was then grown in many private gardens, and is now cultivated in plantations, is cupuaçu (*Theobroma grandiflora*), one of the most popular fruits of the Brazilian Amazon. The plantations are still low-yielding and are much attacked by witch's broom (*Marasmius perniciosus*), also a disease of the related cacao. Domestication of tropical crops into plantations within their native areas is not always easy because of the endemic diseases. Rubber plantations in Amazonia are entirely unsuccessful because of the leaf rust *Microcylus ulei* and several other fungal diseases. There is a strong argument in favour of domestication through mixed-crop agroforestry systems, such as those described in the next section, rather than in plantations, because agroforestry systems are less prone to disease than plantations, maintain a much greater degree of biodiversity, and retain more carbon, especially in the soil.

Domestication of some extraction products may do a lot to avoid the 'boom and bust' economy that has been the fate of so many. Regular, controlled supplies of a product permit a much better marketing strategy. We should not be afraid of domesticating the most promising extraction products, if this programme is accompanied by adequate conservation measures.

AMAZONIAN AGROFORESTRY SYSTEMS

One of the most promising options for parts of Amazonia is agroforestry. It has been little encouraged by developers or by government institutions, but has been widely practised for millennia by indigenous populations and more recently by their successors, the caboclos or campesinos, who have adopted many indigenous techniques. Indigenous systems of agriculture are usually mixed-crop agroforestry, involving a mixed planting of herbaceous and tree crops. A regeneration cycle is started which gradually turns the field into an extraction forest. It is a dynamic successional process rather than a static one-crop or one-phase system. Two Amazonian indigenous systems of agroforestry have been particularly well studied: those of the Kayapó Indians (Hecht 1989; Posey 1982, 1983, 1984, 1985), and the Bora Indians of Peru (Denevan *et al.* 1984, 1985; Denevan & Padoch 1988). A similar system to that of the Bora Indians has been adopted by ribereño communities in Peru, such as the villages of Tamshiyacu and of Santa Rosa (Padoch 1990; Padoch *et al.* 1985; Padoch & de Jong 1989). Agroforestry systems used by the Huastec people of Mexico have also been studied in some depth (Alcorn 1984a, b).

With the Bora Indians, Denevan and Padoch (1988) demonstrated, through a series of illustrations of fields of different ages, the gradual progression from the initial planting to a 19-year-old forest which was still visited by the Indians to harvest 22 useful species and which contained a small orchard of their crop tree, macambo (*Theobroma bicolor*). Similarly, Posey (1982) described the Kayapó swiddens as 'anything but abandoned fields'. Both these systems are intensive, can support a relatively dense population, and produce a wide range of products, including food, oils for cooking, fibres and building materials.

In Tamshiyacu, Peru, the area used for agroforestry is now in the second or third phase of a management cycle which the local people use. The succession from the initial planting to forest and small patches of orchard is allowed to develop for 35 years, and is then felled and the cycle repeated. The skilful use of various components of the system was noted. One of the most marketable fruits, the umari (*Poraqueiba sericea*), is grown in small orchards, and a number of different varieties are utilised. At the end of the cycle, the *Poraqueiba* trees are used for charcoal, another marketable product. Brazil nut trees are also an important part of this system. At maturity a few of the trees are cut for timber and others are left standing in the new cycle to continue the production of nuts, which are not produced until a tree is at least 12 years old. In addition to this productive agroforestry system on upland non-flooded ground, the Tamshiyacenos cultivate rice and beans on the floodplains of the river. These crops grow there well in annual cycles between flood seasons. Alluvial matter enriches the soil so that it can be re-used each year without fertilizers. The most striking result of this study was that the 1987 income of a family in Tamshiyacu was just over US$5,000, a remarkable amount anywhere in Peru.

Another characteristic of both the indigenous systems and that of Tamshiyacu is the number of named varieties of each of their domesticated crops: at least six varieties of cassava (*Manihot*) and four of *Poraqueiba* were observed by this author on a single visit. This point is further emphasised by the report that 130 varieties of cassava are used by the Tukano Indians of the upper Rio Negro (Chernela 1986). This use of genetic biodiversity is the best protection they have for their crops against disease. The fact that varieties exist of crops such as *Poraqueiba* indicates that they are already domesticated for use in local agroforestry systems.

The forests of the Amazon delta region which are dominated by the açaí palm have already been mentioned (see earlier). These oligarchic forests are most effectively used when a form of agroforestry rather than extraction is practised, an aspect that has been studied in detail on Combu Island very close to the city of Belem (Anderson 1988, 1990; Anderson *et al.* 1985; Anderson & Jardim 1989; Anderson & Ioris 1991). In the case of Combu Island and other similar places in the Amazon delta, instead of initial clearcutting as in the Peruvian systems described above, the area is managed by an initial selection thinning of the original forest to encourage the growth of selected species of economic importance, such as cacao and açaí palm. The structure of the managed areas is remarkably similar to the original forest (see profile diagram in Anderson *et al.* 1985). The combination of low annual investment into the system and access to a nearby market made the Combu Island agroforestry system the most profitable so far described. The average landholding of a family is 36 ha. Combu is an area particularly suited to this type of farming system, which is only appropriate to the tidal delta region, and illustrates the need to adapt to local conditions, even within Amazonia, rather than design a single formula for agroforestry throughout the region.

Agroforestry is one of the most important areas for further research and development in Amazonia. It will only succeed if it is based on a diversity of crops, including species producing timber and NTFPs. Agroforestry also offers an opportunity for further domestication of many new plants (such as those listed in the Appendix). It is a relatively intensive land use that can concentrate population density in well-managed areas where agroforestry is appropriate, leaving sufficient room for an adequate number of biological reserves.

NON-TIMBER FOREST PRODUCTS FROM TIMBER TREES

There are many Amazonian timber trees producing non-timber products that can be harvested while the timber is maturing. To make timber trees productive in other ways would enable economic returns to be obtained from a longer growing cycle, and so encourage the harvesting of older trees. The agroforestry system described for Tamshiyacu includes Brazil nut trees, some of which are eventually harvested for their excellent timber. The Brazil nut is one of the many possibilities for a mixed-harvest management system. At present it is illegal in Brazil to use the wood of the Brazil nut, and the law which rightly protects the wild trees might need some modification to allow the use of Brazil nut wood from a managed area.

Some examples of other possible crops from developing timber trees are: (i) andiroba oil from the fruit of *Carapa guianensis*; (ii) pequi fruit and oil from *Caryocar villosum*; and (iii) virola oil from various species of *Virola*. *Carapa* is an important wood in the Meliaceae or mahogany family. From quite a young age the trees produce large seeds, that fall off and can be gathered from the ground to extract the oil which already has many uses in Amazonia and which has had an international market from time to time for use in soaps and medicines. It is now being tested for cosmetics. A small plantation of *Carapa* at the Ducke Forest Reserve near to Manaus is producing abundant fruit. Virola oil, which has been much used locally in soaps and candles, is obtained from species of *Virola*, some of the most important timber trees in Amazonia. Its use has declined mainly because of timber harvesting, but it could instead be a by-product of the timber industry. The wood of *Caryocar* is much used locally in boat-building rather than on the international market. The fruits have an edible outer pulp and the kernel an oil that can be used for cooking or lighting. Abundant fruits are produced in young trees and could easily be harvested during the growth of timber (see Prance 1990).

Other crops that need to be further developed for both agroforestry systems and timber plantations are the herbaceous and shrub crops which can be grown on the forest floor under the shade of the canopy, in a similar way to cacao, a long-established shade crop. Posey (1984) showed that the Kayapó Indians plant many such crops along their trails through the forest to supply their needs as they move about. One possibility is the tuberous species of *Calathea* (Marantaceae), already grown by some tribes.

CONCLUSIONS

Non-timber forest products must receive more attention in future rainforest management systems. They are subject to the same dangers as the timber trade of a 'boom and bust' use pattern (Vincent 1992), as has happened with Amazonian timbers such as mahogany and cerejeira (*Torresia acreana*). A balanced mixture of use of timber and NTFPs could lead to a more stable and sustainable land use pattern. The most successful models of land use developed so far in Amazonia are those based on traditional mixed-crop agroforestry. These systems encourage a natural succession from herbaceous crops through to an extraction forest from which timber can later be harvested.

Much further work is needed in Amazonia on the domestication of further crops, including tree crops (see Appendix for species with particular potential). However, even if further crops are developed, it is vital to have an adequate conservation policy that conserves the genetic material of the indigenous species of the region. If the wild relatives of either existing crops or ones that are to be domesticated in the future are lost, the genetic basis will be seriously weakened, and sustainability may be compromised. While some of the area can be used for extractive reserves and timber harvesting, a large proportion of the forest needs to be conserved in biological reserves, both for the purpose of species conservation and for regulating local, regional and global climate.

I hope that this Conference will have encouraged dialogue and collaboration between researchers interested in timber trees and those interested in non-timber forest products. The systems that are working sustainably are based largely on multipurpose species which can yield both timber and non-timber products.

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APPENDIX

Some non-timber forest products from Amazonia which should be considered for future domestication, and which are not already mentioned in text in detail, are described here.

Araçaíboi – *Eugenia stipitata* McVaugh (Myrtaceae)

A shrub that produces a most delicious juicy fruit with a tasty acidic juice that is mostly used for drinks and ice-creams. This species is cultivated in western Amazonia especially around Iquitos, Peru, and has already undergone some domestication. Field trials near Iquitos have shown that it is highly productive (C Padoch, personal communication). (Details about araça-boi in Chavez & Clement 1983 and Pinedo, Ramirez & Blasco 1981.)

Castanha de cutia – *Acioa edulis* Prance (Chrysobalanaceae)

This large tree of central Amazonia produces abundant large ovoid fruits, the kernels of which are used by local people to extract an oil used for both cooking and soap-making. The kernels are also nut-like to eat raw. The mature fruits fall from the tree and consequently can be easily gathered. (Details in Prance 1973.)

Castanha de galinha – *Couepia longipendula* Pilg. (Chrysobalanaceae)

This widespread tree has a flagelliflorous inflorescence and the fruits hang down from the crown on long peduncles. When it is cultivated out of the forest in open light, it forms a small bushy tree from which the fruits can easily be harvested. The kernels contain a useful oil for cooking or lighting. It was formerly cultivated around Manaus, but is no longer used and is an excellent potential oil plant.

Curupira – *Curupira tefeensis* G.A.Black (Olacaceae)

This large tree from the same region as castanha de cutia, around Tefé in Amazonas, Brazil, is another excellent source of oil that has been much used by local people and has great potential for further domestication.

Sacha mangua – *Grias peruviana* Miers (Lecythidaceae)

This tree of the seasonally flooded forests of Amazonian Peru has an avocado-like fruit that is borne on the trunk and branches. The fruits are rich in vitamin A and are much collected for sale in the market of Iquitos. Large monospecific stands occur in some places; the species is already much cultivated in gardens. This is a fruit of great potential. (Details in Peters & Hammond 1990.)

Sapota – *Matisia cordata* Humb. & Bonpl. (Bombacaceae)

A large tree of the western Amazonian rainforest, it is already semi-domesticated and produces a large yellow fruit on the trunk and branches with a thick tasty pulp. This is one of the unsung fruits of the Amazon but deserves much greater attention. Its local name causes confusion with members of the Sapotaceae, the sapodillas, with which it should not be confused because it is quite a different fruit. (Some details in Hodge 1960.)

Sorva – *Couma utilis* Muell. Arg. – *Couma macrocarpa* Barb. Rodr. (Apocynaceae)

These species produce both a delicious fruit and a latex that has been much used by the chewing gum industry. Unfortunately, until recently, the trees have been felled to collect the latex, so much genetic material has been lost and the species has become scarce in the forest. Sorva is a fast-growing tree that reaches 3 m in height, and begins to produce fruit three years after planting. It also grows well on poor soil. The tree has potential to be domesticated both for fruit and for latex. In 1985 Amazonas exported over US$1 million worth of sorva latex. (Details in Arkcoll 1986.)

Tagua – *Phytelephas macrocarpa* Ruiz & Pavon (Arecaceae)

The fruit of this palm produces vegetable ivory which can be carved and used as a substitute for ivory. It was formerly an important crop in western Amazonia but was largely replaced by plastics. Recent efforts to revive the use of tagua by Conservation International are succeeding. If a sufficient supply of the product is to be provided to the button industry, further domestication is needed.

Titara – *Desmoncus* spp. (Arecaceae)

This is the only genus of South American palms to form vines like the rattans of Asia and Africa. These spinous vines can be used for cane as an excellent substitute for rattan. The split cane is being used for chair bottoms in some places. So far, harvesting is entirely from the wild. Being a vine which needs the support of trees, this species lends itself to use in mixed cropping systems. (Details in Pinheiro & Balick 1987.)

Tucuma – *Astrocaryum vulgare* Mart. (Arecaceae)

The various species of *Astrocaryum* are one group of the many palms of greater potential for domestication in Amazonia as a source of fruit and of fibre from the leaf epidermis. The fruit has an edible mesocarp that is rich in vitamin A and a kernel that produces an excellent oil for cooking and soap-making. The plants are abundant, especially in disturbed areas, and so it could easily be domesticated. (Details in Lima, Trassato & Coelho 1986.)

Uvilla – *Pourouma cecropiifolia* Mart. (Cecropiaceae)

The fruits of the fast-growing short-lived tree have often been called 'grape of the Amazon'. They are grape-like, tasty and juicy. This species is already an important crop of the Bora Indians and in various agroforestry systems of Amazonian Peru. This is a plant that is most promising and should be one of the highest priorities for future work on domestication.

Bacuri – *Platonia insignis* Mart. (Clusiaceae)

One of the most popular fruits of Pará, Brazil, that is little known elsewhere. The fleshy pulp makes a delicious sweet or ice-cream. It is a tree of secondary forest that easily colonises cut-over areas and is therefore cultivated extremely easily. The related bacupari (*Rheedia macrophylla* (Mart.) Pl. & Triam) is also a tasty fruit with considerable potential for domestication.

Designing commercially promising tropical timber species

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ABSTRACT

Domestication of tropical timber trees would be accelerated by establishing a more rational framework for research and development. The 'ideotype' concept allows for information to be synthesised from a multilevel approach to research with five major phases:

i. selection of end use characteristics and their ranking in order of priority;
ii. ranking of the morphological characteristics of the tree which would give rise to the greater yield (quantity) or highest priority end uses (quality), ie selection for a high 'harvest index';
iii. identification of the physiological processes which affect the preferred morphological characteristics;
iv. determination of the biochemical reactions which drive the physiological processes; and
v. identification of the gene sequences which control the preferred biochemical reactions.

When considering 'ideotype', thought has to be given to the size of the desirable harvested units. Some technologically promising species of tropical timber trees have adequate growth rates and can provide adequate financial returns because of the high value of pieces of small dimensions, which might be secondary products processed from the residues of the primary harvest.

INTRODUCTION

The idea of domestication is closely linked to the idea of selection, of fitness for purpose, of pushing nature into a higher gear and in a particular direction. Surely, square trees in Swiss communal selection forests would have given an even higher yield of violin backs and double bass fronts? Field foresters in every country are fascinated by the variety of breeds of European livestock, and the possibilities of introducing new stock, of cross-breeding, and the advantages and disadvantages which result.

Although there is much justified concern at the loss of traditional crop varieties and ancient breeds of domestic animals, we should not forget that production of new varieties and breeds is being undertaken in a more deliberate and informed manner and at a greater pace than perhaps ever before.

In this paper, the reasons for domesticating wild breeds will be considered in relation to the design of trees for the specific product, timber. At present, our state of knowledge and development about the domestication of promising tropical timber trees is primitive. Is the domestication of tropical timber trees worth the effort?

WHY DOMESTICATE?

It is not hard to explain the great number of varieties of the staple food crops which have been developed over the past 20 000 growing seasons. Selection of desirable cultivars has occurred progressively, from early cultivation of preferred batches of seed to modern breeding backed by high technology.

The number of palatable edible crop species is, however, limited. This limitation itself provides some pressure for selection and breeding of new varieties, but the situation of tree species is different. For those tree species whose products we eat (leaves, flowers, fruits and nuts), the process of domestication has been quite rapid. There are national collections of the varieties of temperate fruit trees: the International Board for Plant Genetic Resources (IBPGR) has produced directories to some of these collections, as well as standardised descriptors for some fruit and nut species (Gulcan 1985; IBPGR 1986). With most horticultural crops, selection for precocious flowering may result in fertile seed in less than five years. The possibilities for breeding new varieties of such crops are obviously more favourable than for those forest tree species which may take one or two decades to produce fertile seed without selection for sexual precocity.

Forest trees with non-edible or unpalatable products have been subject to much less domestication. Even the relatively weak senses of taste and smell of urban people are more powerful discriminating factors in driving the domestication process than are preferences for particular characteristics of wood or timber.

However, all long-established human communities have preferred particular forest species for particular end uses, mostly on the basis of generations of trial and error. Why has this preference not induced more domestication? The explanation may include the following reasons.

- Preferences are relatively weak compared with factors of availability and price, many timbers being at least partly interchangeable for many purposes.
- The end use characteristics of wood required in large volumes are tolerant of the variation between generally similar species.
- The market volumes are quite small when end use characteristics are narrowly defined, and it may be more economic to search for particular species in the natural forest, and to pay the higher costs of harvesting, than to invest in domestication.

Whether domestication is worthwhile, and how much domestication is desirable, is thus an economic question. The question may be complicated by risk factors, which include the relatively long rotations of timber trees and uncertainty over the legal rights to products. If the government of a nation/state claims substantial rights over all trees, whether wild or domesticated, the incentives are small for any one person or community to engage in either the domestication of trees or the care of forests.

Forces which encourage domestication may be grouped into three classes:

i. diminishing availability of wild stocks, such as:
    - physical loss through changes in land use, excessive harvesting, disease and pests, or fire;
    - stocks increasingly remote or sparse, becoming more expensive to harvest.

   Countering diminished availability involves not only the technical matters of conserving biodiversity and multiplication of stocks; security of land and tree tenure must also be resolved. Loss of stocks may be associated with tenurial systems which have failed to adjust to changes in demand and supply of forest products.

ii. unsuitability of wild types for current or foreseen needs;

iii. appreciation of some elements of the range of natural diversity.

The last two factors lead to a consideration of the design of trees.

DESIGN OF TREES FOR PARTICULAR PURPOSES: IDEOTYPES

Major improvements in yields of staple crops have been achieved in part by raising the total biomass, but also by increasing the harvest index: the proportion of humanly useful material in the plant. We could indeed define 'domestication' in part as 'improvement of the harvest index' (Evans 1980).

The idea of a plant model (Donald 1968) was refined for trees in meetings of the International Union of Forestry Research Organizations at Edinburgh (Cannell 1979; Dickmann 1985). The concept is helpful in the domestication process because it provides a goal to which the process can be directed. An 'ideotype' is a plant model which will yield a greater quantity or quality of useful products than will conventional cultivars or wild types. It is associated with predictable performance in a defined environment, which includes the management regime as well as the biophysical site where the plant grows.

The emphasis in the definition is on the word 'useful'. An ideotype may push selection in a direction quite different from that which natural processes might take. For example, the preferred morphological characteristics of a forest tree species planted into a farmer's fenceline might be quite different from those which nature would select in the forest (Cannell 1979). The selection pressures are for utility of product(s) *versus* 'the gene machine'.

There are perhaps five major phases in the design of tree ideotypes:

i. selection of end use characteristics and their ranking in order of priority;

ii. ranking of the morphological characteristics of the tree which would give rise to the greatest yield (quantity) or highest priority end uses (quality): ie selection for a high yield and high 'harvest index';

iii. identification of the physiological processes which influence the preferred morphological characters;

iv. determination of the biochemical reactions which drive the physiological processes; and

v. identification of the gene sequences which control the preferred biochemical reactions.

In our present state of ignorance, we can be much more confident about the grosser aspects of the ideotype than about the gene sequences and biochemistry. However, this multilayered nature of the ideotype allows progress to be made in different fields at different speeds and at different times, all the while contributing to the domestication of the target species. Moreover, because of the conceptual framework provided by the ideotype, interaction between theories of improved yield and practical tests should be improved.

We know already that some preferred characteristics of trees are under stronger genetic control than others. Stem form and branching characters are often strongly heritable, the presence or absence of spines is usually controlled by a single gene, but growth vigour is only weakly heritable. Furthermore, wood yield is a polygenic character and needs to be improved through research on the components.

END USE CHARACTERISTICS

The end use characteristics of timber vary in relation to the precise end use, so it is not appropriate to suggest a general ranking of the 18 characteristics normally applicable to saw timber. The needs of the end user also have to be considered. Furniture for a rural school in the high Andes is less demanding in timber properties than reproduction Chippendale chairs. Most users of saw timber, as opposed to users of poles or pulpwood, would prefer the following characteristics:

- long lengths, with straight, even grain;
- large width and depth, to improve the conversion percentage;
- uniformity throughout the piece;
- minimal differences between sapwood and heartwood, and between earlywood and latewood in any growing season;
- rapid, easy seasoning, with low shrinkage, distortion and checking;
- naturally durable, or easy to impregnate;
- free of inclusions such as calcite, silica and resin pockets;
- free of damage by insect pests, fungal pathogens and forest fires;
- branch knots absent; or few, well scattered, small, tight, round and at right angles to the grain;
- no bark inclusions;
- easy to work by machine or hand tools;
- easy to glue with modern adhesives, with no adverse reaction from wood chemicals;
- no adverse reaction (such as staining, swelling or corrosion) to metal fastenings or chemicals;
- no irritant dust or chemicals released on sawing or other working, and no bleeding of natural resins or gums over time;
- slow to change colour when exposed to light, and resistant to photo-deterioration;
- slow rate of burning, with internal protection by charring of the exterior of a piece;
- easy to match to other pieces of the same timber species;
- strong for mass.

Most of these characteristics would need to be qualified with respect to any particular end use. A furniture manufacturer might value fine figure and high colour more than uniformity of surface appearance. A flooring manufacturer would prefer hard-wearing properties more than freedom from silica, and resistance to chemicals spilled in warehouses more than a constant colour.

For many uses, upper and lower densities and strengths can be specified, together with acceptable limits of shrinkage. In some countries, these specifications are included in building codes (such as Eurocode 5 for timber structures in Europe and BS 5268 for the UK timber code of practice). Developing countries can expect sales resistance against their exported timbers if the pieces do not conform to these and other consumer protection codes. However, some developing countries or treaty areas can now provide at least qualitative indications for matching domestically common timbers to major end uses.

TREE MORPHOLOGY AND GROSS WOOD STRUCTURE IN RELATION TO TIMBER END USE

It is necessary to interpret the end use characteristics in terms of tree morphology and gross wood structure, as opposed to wood anatomy or fine structure. It is, however, recognised that for specific purposes, particularly those which involve fine finishes or applied surface films, anatomical characters may need to be included in the ideotype.

- Long lengths of straight-grained large pieces obviously require long, straight, cylindrical boles developed on monopodial stems. (Incidentally, trunks with square cross-sections would have much more of the undesirable reaction wood at the corners and thus a *lower* yield or harvest index than round-sectioned trunks.)
- Differences in properties between sapwood and heartwood may be associated with provenance as well as species. Impermeable heartwood is not necessarily naturally durable, so there may be a preference for wide sapwood. A distinct pith is usually undesirable, being associated sometimes with weak fibres and a high content of extractives.
- Differences between earlywood and latewood may be amplified by strongly seasonal climates and other environmental factors. Early flushing and late leaf abscission may contribute to a cambium whose activity is relatively constant rather than strongly pulsed.
- Freedom from extractives may aid timber processing and end use but may not be beneficial to the tree. Extractives may help to protect the tree from attack by insects and fungi.
- Well-scattered, small, tight, round knots translate to small branches inserted at right angles to the stem. If knots are to be few, then branch abscission should be early and

efficient. Presence of few and small knots could mean a small and thin crown, photosynthetically inefficient, and so opposed to the preference for rapid growth. On the other hand, a narrow, deep, persistent live crown with branches inserted at an acute angle to the main stem may be conducive to rapid growth but would reduce the yield of clear wood. If knotty timber is favoured for aesthetic reasons, the narrow and persistent crown may be quite suitable.

- Tree boles which are cylindrical, free from buttresses, wings and flutes, and whose branches are small and held horizontally, are unlikely to give rise to inclusions of bark in the wood.
- Strength and density characteristics of wood may be related to speed of growth and to the degree of stress experienced at the growing site, and may be modified by the management regime. Wood showing close and even growth rings has usually been grown under strong inter-tree competition but also equable conditions which change little from year to year. However, dense wood is not invariably associated with slow growth.

So, many components affect the growth rate of trees, and, consequently, many selection strategies are possible. Uniform growth may be obtained by combinations of some of the following silvicultural operations:

- close spacing of trees;
- frequent light thinning;
- modifying crown size through pruning;
- fertilization;
- irrigation.

The proper management of these operations might obviate the need for genetic selection. Alternatively, if the components could be controlled genetically, the need for rigorous management might be reduced. Tree architecture is described elsewhere (see Oldeman & Sieben-Binnekamp, pp25–33), so here it will simply be noted that bud behaviour, modes of branching, leaf types, leaf sizes and leaf orientations can be affected by these silvicultural operations and, in turn, these may affect bole growth rates through alterations to the rate and amount of photosynthesis (see also Ladipo *et al.*, pp239–248).

Long-term studies on bud behaviour of temperate fruit trees, coffee and oil palm at the CIRAD Modelling Laboratory in Montpellier, France, suggest that more attention should be paid to improving our understanding of the plasticity of growth habits of tropical timber trees. Such studies might explain why some valuable timber species seem to need a 'forest' environment in order to maintain a monopodial habit. For example, numerous trials of some of the Brazilian furniture wood species, especially legumes, in open plantations have produced orchard-like trees instead of the hoped-for long clean boles (J R Palmer, personal observation).

Studies on the relationships between tree architecture and wood structure are being extended to a few tropical tree species, but could usefully include many others. It would be especially interesting to examine the wood structure of contrasted tree forms within a single taxon. This information would help to determine whether efforts to pursue greater volumetric yield were adversely affecting the quality of the wood, other than in terms of strength and density which have been broadly studied already.

In tropical forest timber trees, it is common for the usable bole to be only half the total tree height. Could we delay the age or height of crown break until the main stem forms a greater proportion of total tree height? Could the shoot/root ratio be shifted in favour of the shoot? How would this affect early competitiveness of the tree? How would it affect resistance to wind later in the tree's life? Many of these questions have been considered for temperate trees.

PHYSIOLOGICAL PROCESSES WHICH AFFECT THE PREFERRED MORPHOLOGICAL CHARACTERS

Which physiological processes can be controlled or modified, either through the selection of genotypes or through silviculture to improve the harvest index? To date, the physiological processes themselves are rarely selected or modified directly. Control is through selection of particular morphological characters, or their modification. For example, leaf variation between some provenances of *Eucalyptus camaldulensis* can be explained in terms of the wind climate in the regions of origin (CSIRO, unpublished data). This is an adaptive response of leaf shape and orientation to minimise the effects of water deficits and temperature shock. Armed with this knowledge, we can now choose provenances which are better adapted to different climatic zones.

We still know little about the physiology of tropical trees beyond the seedling stage, while information about temperate trees is increasing rapidly. Much of what is known concerns water relations, and the effectiveness of morphological adaptations which allow trees to control water flows. To construct an ideotype for a timber tree on any particular site, it is necessary to know:

- the probability of there being enough water to sustain the tree at its age or size of maximum consumption;
- the nutrient requirements over the technical rotation of the tree, the corresponding

nutrient availability, and what the tree does with the nutrients;

- the size and variability of the various nutrient sinks in different species of tropical trees;
- how they change seasonally and as the tree ages; and
- how they vary in response to site differences and management regimes.

The role of root symbionts in water and nutrient relations of tropical trees also needs to be explored more thoroughly. In some cases, the association is critical to the survival and commercially adequate growth of a tree. This aspect and the matching of trees to their light environments are covered elsewhere in this volume (see Lapeyrie & Högberg, pp158–164; Mason & Wilson, pp165–175; Sprent, pp176–182; Fasehun & Grace, pp148–157).

BIOCHEMICAL REACTIONS AND GENE SEQUENCES

Descriptive information about genetic variation between and within species is increasing rapidly through the use of biochemical, cytological and molecular marker techniques. How these variations are functionally related to the phenotypic expression of traits is still little known. The combination of laboratory techniques with field and herbarium studies has considerably enlarged our knowledge of infraspecific variation in the few tropical species which have been examined so far. These new studies, plus conventional biosystematics and provenance/ progeny trials of tropical trees, tend to confirm what we know in relation to staple crops and the principal breeds of animals: ie there is a wealth of infraspecific genetic variation which we have barely begun to explore and use.

At present, to locate the ideotypes, we search through the natural population for the most suitable phenotypes. In future, we can expect that trees will be genetically engineered to meet the specifications of ideotypes (or that genetic markers will be used to identify appropriate genotypes: selection based on the genotype directly, not phenotype).

If this range and depth of studies for the development of ideotypes seem to be depressingly formidable, one should remember that the framework can be entered at any level. Once the characteristics of the desired end product have been defined, in a sense the rest follows. Because our current knowledge of tropical timber trees is so patchy, even for the better-known species, I conclude that it would not be sensible to advocate a common approach to further studies on domestication. Priorities will vary according to how much is known already about a particular species, and what are the most promising lines to follow as indicated by work on related species. The improvement of cloning techniques for tropical timber trees will, however, allow the capture and use of characterised ideotypes, in the same way as has occurred in horticulture.

DOMESTICATION OF TROPICAL TIMBER TREES

How does the sequence outlined above compare with the way in which tropical timber trees have been domesticated so far? The answer is, very little. Some of the ideas may have been in the minds of the domesticators, but the procedures which have generally been used appear, with hindsight, to have been rather haphazard. The now quite numerous manuals on tree improvement seem to have skipped over the step of clarifying what the users would want and which kind of tree would satisfy those wants.

CASE STUDIES

Teak (*Tectona grandis*)

With few exceptions, the *Tectona* which is now widely distributed in the tropics and subtropics comes from poorly documented sources, and its performance has been worse than was expected. *Tectona* was collected and distributed because of the good name it acquired from its observed growth in some of the natural stands, and because of the good performance of some of the early introductions as an exotic. Documentation is mostly too fragmentary to determine whether the early collectors and distributors of germplasm consciously sought to match source provenances to the intended destinations.

We now know that *Tectona* is quite responsive to soil water and nutrient status and to climate (Kadambi 1972). Trees of the Verbenaceae are tenacious survivors, even when grown far from their optimum sites, although stem form may be abysmal and growth may be poor. In some ways, it has been a disadvantage that even poorly grown and off-site *Tectona* has usually found a profitable market, thereby discouraging attempts to discover whether other provenances or management methods might have been more appropriate. *Tectona* has been well served by the range-wide provenance collections and international trials organised by the Danish Forest Seed Centre, giving some quantitative information about genotype/environment interaction (GEI) in this species (Keiding, Wellendorf & Lauridsen 1986).

American mahogany (*Swietenia macrophylla*)

Swietenia is still a much-favoured and prestigious furniture wood, being easy to process and possessing many desirable features. Neotropical plantations of *Swietenia* have failed repeatedly, mostly because of the persistent and crippling attacks of the pyralid shoot borer *Hypsipyla grandella* (see Newton *et al.*, pp256–266).

After many years of failures, it was noted that with the *Hypsipyla* in the palaeotropics, *H. robusta*, either it did not attack the *Swietenia* or the attacks were much less damaging. As a consequence of this natural resistance, there are now extensive plantations in Java and lesser areas in Fiji and Sri Lanka.

There have been few attempts, perhaps only one, to make even a partial collection of *Swietenia* provenances. The plots managed by the Institute of Tropical Forestry in Puerto Rico probably represent the only source of some germplasm, as the *Swietenia*-bearing forest at some original sites in Central America has now been destroyed. Because of the lack of genetic testing, only fragments of observations about GEI exist for *Swietenia*. This lack of modern research is curious, in view of the value of the world trade in *Swietenia* over nearly five centuries and after the discovery that the shoot borer could be controlled by systemic insecticides.

WHY HAVE FEW TROPICAL TREES BEEN DOMESTICATED?

The early stages of the domestication of most non-food tropical trees seem to have been stimulated either by a great shortage of wood of any kind in a particular area, or by difficulties in regenerating the commercial species. Most attempts to introduce woody species seem to have started in a rather shotgun manner, using seed and cuttings of any species which could be obtained. Some of the more advanced national forestry services then progressed to homoclinal climatic matching and a phased succession of elimination trials.

Where capital-intensive forest product industries provided a demand, domestication was more focused, with a clear idea of the technical properties required in the bark (for tanning) or wood (mostly for pulp) from the trees. In contrast, most timber-using primary processors of forest products in the tropics lack sufficient knowledge of the end use requirements of the timber users, and of the pricing structures of the retail markets, to provide incentives for the domestication of the species which they use. Outside the large-scale afforestation schemes driven by commercial demand, it is rare to find any suggestion that the foresters had a particular product in mind, perhaps because of the difficulty in obtaining adequate survival and growth of *any* species. Problems have arisen from a lack of knowledge about the degree of species/symbiont plasticity in relation to site conditions. Foresters have also tended to underestimate the depletion of the sites which they were planting, after several to many years of inappropriate land use by others.

Tree species which have orthodox seed, are economical with nutrients and water, and grow naturally on old land surfaces in soils depleted over geological time and in harsh climates have generally been much more successful as species for reforestation and land rehabilitation, being amenable to seed storage and having less stringent site requirements. However, now that we have much improved knowledge about seed handling and nursery techniques (including vegetative propagation) and establishment methods, it can be argued that we can be more selective about what we try to domesticate. Attention to ideotypes would provide a focus and enable us to concentrate the effectiveness of our limited resources for research.

One factor deterring foresters from planting either slower-growing quality hardwoods or those which are not robust in the establishment phase has been the small but vocal group of 'whole tree, any tree' advocates. This group takes the view that, on the one hand, wood fibre is not *per se* a scarce commodity in many countries and, on the other hand, processing technology is now capable of taking almost any fibre and reproducing or even improving upon many natural products. For example, knowledge of structural engineering and wood strengths allows substantial houses to be built from small-dimensioned sawn timber; tropical examples date back at least 30 years. Glulam beams can span larger spaces than natural wood beams, with much less use of fibre and more predictable strength properties. In Australia, the 'scrimber' process, in principle, allows almost any size of tree to be formed into a structural member with known engineering properties; unfortunately, it is not yet economical to process natural fibre in this way (A G Brown, CSIRO, personal communication).

Proponents of the 'whole tree, any tree' philosophy argue that processing technology is developing much faster than trees grow. They can point to the shifts in demand which have taken place in less than one timber tree rotation in peninsular Malaysia, from naturally durable heavy hardwoods to medium hardwoods to light hardwoods, as national lifestyles have changed and industries have developed.

Because we can already simulate the appearance of timber of many species, and improve upon natural finishes, the 'whole tree, any tree' group only advocates domestication of species which are amenable to mass-production processing. An industrially bland species, such as *Gmelina arborea*, is thus more useful as a substrate for overlays, than timbers which are less amenable to industrial processing but more valuable for particular purposes.

There are two main contrary arguments.

i. A market exists in industrialised countries for finely finished natural products, including timbers, for which high prices may be paid.
ii. The 'whole tree, any tree' processing technology is usually far from cheap, and so is unlikely to substitute for less traditional sawmills in developing countries.

WHERE ARE DOMESTICATED TREES MOST NEEDED?

We can predict future needs for reforestation only in very general terms, and thus the dangers of over-specifying the ideotypes must be recognised. We can hazard guesses at the altered growing conditions which climate changes might induce. We can be sure that insect pests and fungal pathogens will challenge whatever we domesticate, but we do not know what pest will attack which species, where or when, or what damage might be caused (Cannell 1979).

Demographic pressure alone will tend to restrict large-scale commercial/industrial bulk plantings more and more to marginal sites. These sites may be steep, rocky, saline, sodic, droughty, windy, poorly drained, or otherwise unsuitable for farming. The sites may have been fertile originally, but are now depleted through poor farming practices. A variety of ideotypes may be needed to suit these sites, each with particular physiological adaptations.

However, as forest masses decline, trees are perhaps more likely to be grown deliberately on farms, as single trees, in clumps and small woodlots. This perhaps is a better scenario for domesticated trees, but timber species which are site-demanding are candidates for domestication only if they cause minimal loss of arable crop area or yield. These considerations lead to three distinct ideotypes.

i. The 'crop' ideotype is the model for commercial plantations and smallholder woodlots. Individual trees would be weak competitors with each other, but would be efficient exploiters of their own growing space and better adapted to the range of degraded sites described above. Live crowns would be deep, dense and narrow. Stem growth would be strongly monopodial. Stands would be uniform in appearance, with a narrow range of diameters. Planting spacement would need to be calculated carefully, so that resources in the growing space did not become limiting before the first commercial harvest. If sites were marginal, probably with soils depleted by improper use, initial spacing might need to be wide in order to give the trees enough exploitable nutrient-bearing soil to sustain growth. However, canopy closure should be sufficiently rapid to keep weeding costs bearable.
ii. The 'fenceline' ideotype is for the arable farm. Individual trees would have deep roots, both to provide wind-firmness and for nutrient and water capture without competing with the arable crop. Crowns would be thin and open, to avoid shading of the crop. Fastigiate branching would probably be undesirable because of the reduction in timber quality. Strong monopodial growth would carry the crown rapidly above the crop. Tree species would not be allelopathic to crops. Water requirements would be low. A heavy leaf litter, which could be used as mulch, might be more beneficial than nitrogen-fixing ability, especially if the requirement for deep rooting is contrary to the conditions for abundant N fixation.
iii. The 'shade-tree' ideotype can be envisaged, also for use on-farm. It would be most suitable for taungya-type agroforestry. Farmers might tolerate a moderate-to-heavy crowned timber species standing over the arable crop, if the timber was of high value and if height growth was sufficient to restrict crop-reducing shading to the first year. *Paulownia tomentosa* over wheat in the People's Republic of China is a well-known example. Less well known is *S. macrophylla* over maize in the farms of the Ketchi Maya in southern Belize. More generally applicable might be agroforestry systems of small numbers of timber trees per hectare, standing over perennial tree crops such as coffee and cacao and spices. Many indigenous polycultures of this kind have been documented.

Just as proponents of clonal plantings recognise the need for security by the use of several clones in any one planting area, so foresters might prefer to hedge their bets by using phenotypically plastic genotypes. Such trees could modify their physiology and morphology according to their spatially and temporally changing environments. Detection of such plasticity would require extensive testing of genotypes on a range of sites and under a range of management regimes. The chosen ideotype could, of course, be aided by appropriate silvicultural methods, but for on-farm trees it would be better to assume that farmer care would be minimal.

WHY HAS LITTLE EFFORT BEEN PUT INTO DOMESTICATING TREES?

I suggest that one reason for the paucity of effort to domesticate tropical timber trees is the relative abundance, until recently, of nearly interchangeable timbers. Some 120 species or species groups are used domestically in the

Amazon basin, perhaps 600 in peninsular Malaysia, almost all of them by harvesting from the wild state because it is perceived to be economical. As I said earlier, domestication is an economic decision, and it has not seemed worthwhile in most countries until very recently.

Since colonial times, governments have laid claim to ultimate ownership of forests, whether or not they were able to exert that authority effectively. For a variety of reasons, governments have generally treated forests as a residual use of the land and have made no serious attempts to value the goods and services of the forest in a holistic manner. Some governments continue to subsidise harvesting of trees from the wild, perhaps because of a lack of understanding of the total costs which they are incurring for the nation.

Increasingly, urbanised populations need more, not less, timber per head than rural populations, so domestic demand in developing countries is rising while natural forest resources are generally declining.

Legislation, national accounting and social attitudes in many countries have failed to keep pace with the rapidly changing situation over supply of and demand for timber (and many other forest products). Thus, the law, economics and society appear to conspire against the domestication of tropical timbers. Where governments have taken firm and soundly based steps to stimulate afforestation and reforestation (as in Brazil formerly and Costa Rica presently), the demand for suitable germplasm has greatly exceeded the national capacity to supply domesticated trees, at least in the short term. The absence of current incentives for the large-scale use of domesticated germplasm should not lull national forestry research services into believing that research is not needed.

IS DOMESTICATION OF TROPICAL TREES WORTH THE EFFORT?

There are perhaps three questions which have to be asked to determine whether domestication is worthwhile.

Are there naturally occurring genotypes which correspond to the timber ideotypes?

Extrapolating from our knowledge of genetic variation in some temperate timber trees and tropical multipurpose trees whose geographic distributions have been well explored, it seems likely that satisfactory timber genotypes could be located if the same effort were to be deployed. We can be fairly sure that simple silvicultural techniques, such as mass selection of superior seedlings and vegetative propagation of good phenotypes, will boost both stem form and growth rate.

Are tree growth rates financially attractive?

Rapid growth is a necessary part of the ideotype, because domestication is a process requiring investment and the cost must be recovered. Although slow growth in the post-establishment phase has sometimes been due to neglect of silviculture (eg the stagnated plantations of *Terminalia ivorensis* in Ghana during the years of national economic crisis), problems have more usually occurred because of unsuitable germplasm, poor nursery techniques and off-site planting. There are enough examples of excellent growth of trees in arboreta and trial plots to indicate that timber tree growth rates can be quite adequate.

The idea of timber trees on farms is intrinsically attractive, as a biological bank deposit against future needs. When silvicultural costs are low, harvesting costs become important. Single trees on farms may be more costly to harvest than a block planting on a remote hillside. On the other hand, transport costs may be lower because the farm is likely to be closer to the timber processing plant.

Is the price adequate for the final product? Or, rather, will the price be right when the trees are ready for harvest, and will the prices justify the cost of domestication?

Prices for standing trees in developing countries are often conditioned in part by government fiscal measures which bear little or no relation to the costs of forest or tree management or to the costs of harvesting, transport and processing. Most countries have shelves of reports from consultancies over many years which recommend more rational systems of valuing forest goods and services. Timber growing, even with domesticated germplasm, is a long-term business and needs both incentives and assurances of security to encourage investors.

Even under the present, generally unfavourable, fiscal conditions, the continued willingness of a clientèle to pay high prices for finely finished products from natural timber should provide its own incentive (Johnson 1988). The high value of mahogany products, including small-dimensioned items (Past Times 1991), illustrates this point: a cabinet priced at £10,220 (Prince George's Woodcraft 1990), a George II mahogany commode, valued at £400,000 (Duthy 1989), and a toilet seat and cover in solid mahogany priced at £45 (Woodentops 1983).

Finally, although this paper has considered single-purpose timber trees, we all recognise that residues from timber trees can be used for charcoal and fuel, at the very least. Demographic and other pressures on renewable natural resources are rising so steeply in most developing countries that single-purpose land uses are almost impossible to defend in social terms. For multipurpose use (eg the production of timber and fodder), it may be necessary to domesticate single-purpose lines. This aspect is considered later in this volume (see Felker, pp183–188; Owino, Oduol & Esegu, pp205–209; Simons, MacQueen & Stewart, pp91–102).

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Timber trees: architecture and ecology

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ABSTRACT

In growing timber trees, life-long architectural adjustment of trees to their direct forest environment is topical. Hierarchical systems analysis of trees examines their architecture in terms of architectural models, multiple sets of such models (metamorphosis and reiteration), and the occurrence of specialised light-gathering shoots (phyllomorphism) and shoots which cease terminal activity and thus branch (unstable monopodia). These different crown-forming processes can come together in a way that develops branch complexes that are hierarchical, with one set dominating others, or polyarchical, where the complexes are repetitive and co-dominate. Examination of these different levels of tree architecture allows one to zoom in on trunk formation, the basis of silvicultural management for timber production. Tree architecture differs between tree groups (ie conifers, legumes, Fagaceae, dipterocarps, Myrtaceae and 'miscellaneous'), determining the nature of forests in whole regions of the world. Hierarchical systems analysis can also define the direct tree environment by zooming in from landscapes, to silvatic mosaics, to the conditions around an individual tree (eco-unit level), determined by ecological interference. Domesticating and growing trees for wood are finally examined in terms of architectural strategies. Silviculture should be overhauled and become more ecologically orientated, its present combination of aims – to produce large timber volumes as straight stems of high-quality wood, in the shortest time – being paradoxical.

INTRODUCTION

Trees perform a major feat of natural, biological engineering: their architecture continually adapts to their changing environment. Every tree responds to a *temporal* sequence of environmental conditions as it grows larger (see Oldeman 1989a for an example of *Acacia* species in the rather unpredictable East African climate). This environmental sequence can be roughly predicted. It is not always true, however, that the seedling environment always differs from the surroundings of a fully grown tree crown, even for pioneer tree species. An alternative view is that the tree crosses a *spatial* sequence of environments from the soil to its adult canopy height. However, this assumes the forest environment to be constant over time, which is a very rare condition (Oldeman 1989b).

This paper concerns timber trees, which are those that form long and straight trunks, suitable for extraction as sawlogs. One important silvicultural question, relevant to the process of domestication and the 'ideotype' concept (see Palmer, pp16–24), is how to grow trees to these specifications. The answer is dependent on our understanding of tree architecture, and the process of trunk formation in particular.

The long, straight stems required by silviculturalists most often occur in natural forests. Only a few tree species maintain this form when grown in the open. Indeed, timber plantations are grown to mimic natural forests in this respect.

Both natural forest and plantation ecosystems are complex and alive, with the canopies of timber trees being forced aloft by the living forest surrounding them. Tree trunks may, therefore, be seen as the trees' tools of ascent towards the light available at canopy level.

The term 'environment' was used loosely above. In reality it covers several scales in the hierarchy of living systems. On the one hand, a 'forest environment' refers to the forest ecosystem, which according to Oldeman (1990) exists on at least three nested scales, ie the *eco-unit* ('forest patch', 'gap'), the *silvatic mosaic* (the mosaic composed of interacting eco-units), and the *site mosaic* (composed of interacting silvatic mosaics occurring in a set of different sites). On the other hand, the 'environment' forcing a tree aloft is a subsystem of any 'forest environment', ie that part which directly surrounds an individual tree. Only this *direct environment* can fully explain the selection pressures on tree growth and the process of adaptation (Oldeman 1990, p513).

In the following sections, this paper will consider:

- an outline of tree architecture, its hierarchical organisation and the question of conformity *versus* flexibility;
- the trunk as an architectural component of the main forest-building trees, trunk size and stability, and ways to favour the formation of straight trunks in timber trees;
- the direct environment of a tree *versus* the average stand environment, and architectural

strategy as a response to site dynamics; and

- some conclusions for timber tree form, growth rate, potential size and age obtained in cultivation, in the context of the domestication process.

TIMBER TREE ARCHITECTURE

Trunks, branches, roots

Every tree builds three interconnected vegetative systems. These are the green, branched above-ground assimilation complex, the rooted below-ground assimilation complex, and the trunk as an intermediary transport and co-ordination complex (Oldeman 1974; Hallé, Oldeman & Tomlinson 1978; Hallé 1991). Hallé and Oldeman (1970, p44) defined the trunk and branches as follows: 'From the unique axis in unbranched trees, the trunk mainly conserves the architectural rôle: it ensures the tree's foothold, its mechanical resistance, its extension growth in height through the successive forest storeys, while producing at its apex new leaf-bearing branches which profit from the best light conditions; because it constitutes a central communication and transport system, the trunk gives a tree its physiological coherence; it determines the final stature of the tree on which depends, at least partially, its competitivity and ecological niche . . . The branches in principle take over those functions which the trunk ceases to assume: photosynthesis and the formation of sexual organs. These functions can be fulfilled in many ways, and numerous setups indeed exist both to capture incident light energy and to present the sexual organs to the vectors of gametes'.

Some evidence suggests that the below-ground complex is organised not too differently from the above-ground architecture (Atger 1992). However, no well-developed, large and persistent trunk-equivalent (tap root) seems to be present in most timber trees. This paper will refer to roots only in passing.

Above-ground tree architecture

Seedlings are usually unbranched (Figure 1, *a*). The first branches form a specialised interface for photosynthesis, the exchange of gases and water, and temperature regulation. The *peripheral* branches show such a set of properties lifelong (Edelin 1984). Sapling axes are of the first order (trunk) and of the last order (crown periphery) (Figure 1, *b*,*e*). The crown is later filled out by intercalation of branch orders (Edelin 1984; Atger 1991), until the full inherited number of potential branch orders is formed (Figure 1, *c*,*d*).

If second- and higher-order axes are more or less equivalent, leaf properties determine the green interface between the tree and its environment. Tree architecture then shows a clear difference between skeletal functions (trunk and main branch axes) and assimilation (leaves), and hence can be described (Figure 1, *e*–*g*) by one architectural tree model (Hallé & Oldeman 1970; Hallé *et al.* 1978), or intermediates. If, conversely, the peripheral branches differ conspicuously from the axes between them and the trunk, botanists perceive the formation of an intercalary axis as an abrupt change-over from a small crown to a larger crown built by smaller crowns. Edelin (1984) coined the term 'metamorphosis' for this event (Figure 1, *b*–*d*). The cauliflower-like crowns of SE Asian dipterocarps and neotropical Vochysiaceae are good examples (cf Oldeman & Fundter 1986).

Each tree species has inherited a limited number of differentiated branch orders, five being common (C Edelin, personal communication). When axes of an order above that limit are needed for crown expansion, re-activated meristems yield a first-order axis again, ie they start crown building over again with an axis equivalent to the hypocotyl (Figure 1, *h*). Oldeman (1974) described this process under the name of reiteration, but did not give this explanation.

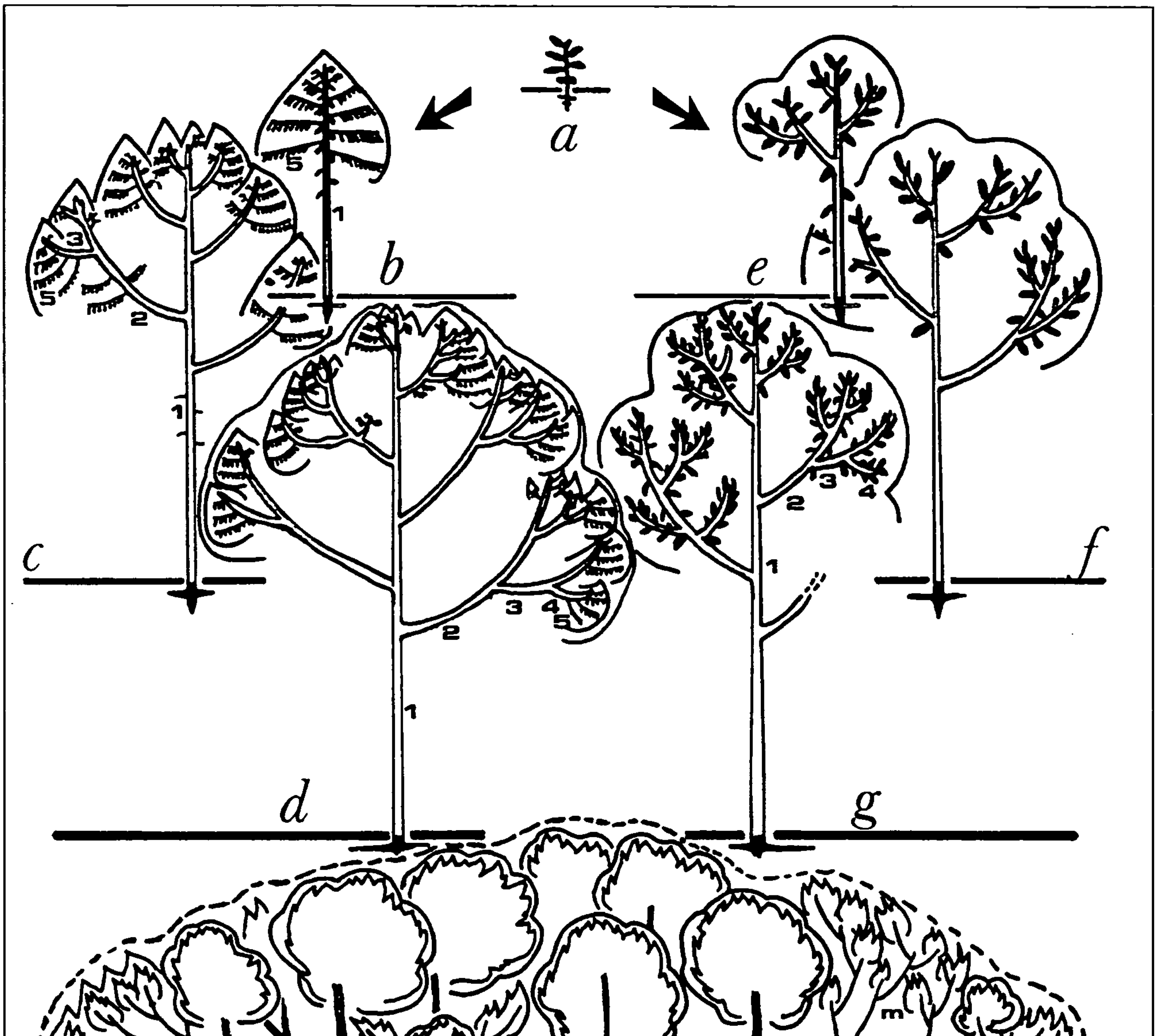
Phyllomorphs and unstable monopodia

Two concepts are important for understanding the ways in which the basic architectural model adjusts to its environment. These are (i) phyllomorphs (Hallé 1967) and (ii) unstable monopodia (Oldeman 1974).

A *phyllomorph* is an axis with many foliar properties, eg small size, limited lifespan, and little wood, while having many chlorophyllic appendages or tissues (leaves, phyllodes, etc). Originally, phyllomorphism was assumed to be closely linked to plagiotropy, but architectural analysis of leguminous trees by Oldeman (1989a) showed that orthotropic short shoots may also be phyllomorphic. It can now be understood that the green interface functions of tree crowns are ensured either by leaves, often on architectural model-like crowns (Figure 1, *e*–*g*), or by phyllomorphs, often on metamorphic crowns (Figure 1, *b*–*d*).

Figure 1. Principles of timber tree architecture

a–*d*	Tree development with metamorphosis (Edelin 1984, 1991); branch order 1 is the trunk, order 5 a peripheral branch (eg twig, phyllomorph), and orders 2–4 are intercalated; sometimes orders 4 or 3 have peripheral characteristics too
a–*e*–*g*	Tree development without metamorphosis (Hallé & Oldeman 1970), the periphery being made up by leaves and the sequence of branching orders so equivalent that intercalation is not proven
h	Reiteration tree with repetitive manifolding of the model (cf 1*g*)
b–*i*	Metamorphic tree with repetitive complication
j	Assemblage tree with both repetitive complication (numbers as for 1*c*) and repetitive manifolding (numbers as for 1*f*) in opportunistic sequences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Selection pressure can make phyllomorphism 'migrate' from the periphery to the trunk. This may happen in a very stereotyped way and cause modular growth, as in Petit's model (eg the rubiaceous sequence from the *Rothmannia* to *Tetrorchidium* species originally studied by Hallé in 1967, cf Hallé & Oldeman 1970), or from Roux's to Aubréville's model (see the sequence from *Trema* to *Terminalia* described by Oldeman and Hallé 1980). In the centre of the tree, the trunk is eventually the only axis left with a considerable size, mass and lifespan (eg 'pagoda trees' such as *Terminalia* spp. – Corner 1952). Foresters speak of 'monopodial branching' in such trees, in which the branches occur on a big, monopodial trunk.

On the other hand, migration of phyllomorphism to lower-branch orders can be opportunistic and disorderly. Leguminous trees in adverse environments (eg the dry tropics or heavy shade under forest) illustrate this behaviour; examples are the *Acacia* species of East African tree savannahs (Oldeman 1989a), the Sahelian mimosoid *Faidherbia albida* (Sterck, van der Zandt & Oldeman 1992) or *Eperua falcata* (Edelin 1991), a caesalpinioid neotropical rainforest tree.

Unstable monopodia, described by Oldeman (1974, eg in Guyanese, very hard-wooded melastomataceous *Mouriri* species), are axes with an easily but unpredictably deactivated end meristem. In this instance, extension growth is often taken over by another unstable monopodium, known in temperate trees as shoot tip abortion (cf Remphrey & Davidson 1991). This phenomenon is in the same strategy as phyllomorphism, for both the smaller size and shorter lifespan of phyllomorphs and early meristem abortion lead to small building blocks in tree architecture. Both phyllomorphism and monopodial instability hence lead to the increasing predominance of sympodial growth over monopodial growth in a tree.

Command hierarchy or polyarchy

From a study on sympodial trees, Edelin (1991) postulated two ways to build trees by branching. His first principle is hierarchical, the second is polyarchical; both are determined by a command hierarchy ('plan d'organisation' sensu Edelin 1991). In hierarchically built trees, an axis commands or dominates the behaviour of its branches, or a branched complex commands or dominates the behaviour of other branched units it bears, such as reiterates (Figure 1). Polyarchical trees are colonies of equivalent units organised by loose, ephemeral mutual interactions.

Systems hierarchy and tree architecture

With the above concepts, the architectural study of timber trees can be reduced to a few clear principles. The following systems hierarchy is defined especially to deal with timber tree architecture.

Stems and architectural unit models

There is frequent confusion between the terms 'axis', 'sympodium' and 'monopodium', so trees will be considered here to be built by 'stems'. A stem is defined as a growing cylindrical organ bearing leaves, meristems or other appendages; it is perceived macroscopically; only its geometric origin, not its meristematic origin, is specified; it can be macroscopically differentiated according to simple criteria of apparent phyllotaxis and orientation (orthotropic, plagiotropic, mixed), size and longevity (trunk, branch, twig, phyllomorph), flowering (none, terminal, lateral), and timing (immediate, delayed or adventitious appearance). More refined criteria are presented by Hallé *et al.* (1978) and Edelin (1984).

All primary architectural unit tree models (eg Figure 1, *a–g*) are defined as theoretical trees originating from seed, the architecture and dynamics of which are described in terms of simple branching patterns determined by woody skeletal stems, ie trunk, branches and their differentiation. This definition is close to, but differs from, those in Hallé and Oldeman (1970).

Repetitive architectural patterns

A metamorph (Figure 1, *a–d*) is an *intercalary*, regularly branched pattern caused by a spatial and temporal combination of stems being formed later within the primary architectural unit tree model (Figure 1, *c,d*). The metamorph is not an initial part of this model (shown in Figure 1, *b*). A reiterate (Figure 1, *h*) is an *apposed* branched complex, corresponding to the total or partial primary architectural unit tree model. The reiterate is not built within but apposed to this model. Reiteration is important for timber trees, because reiteration causes trees to have more than one trunk. The tree has one trunk from the seed and one in each reiterate (word coined by C Edelin, personal communication). In other words, a 'subtree' formed by reiteration also possesses a trunk. Metamorphs make more branches within a tree; reiterates add additional peripheral trunks and/or branches to a tree.

According to the above definitions, all timber trees, throughout their development from germination to senescence, belong to one of four strategic unit tree models: *elementary* trees (Figure 1, *g*), *reiteration* trees (Figure 1, *h*), *metamorphic* trees (Figure 1, *i*) or *assemblage* trees (Figure 1, *j*).

Architectural systems hierarchy for timber trees

Timber trees can now be examined in their ecological context according to a simplified systems hierarchy. As usual in such hierarchies, a system is explained by the interactions between its subsystems, conceived to be situated one level lower than the system itself. A stem is the sum of its parts plus their interactions; a primary or secondary architectural unit is the sum of its stems plus their interactions, as apparent from the branching geometry and dynamics around one central stem; a strategic unit is the sum of its architectural units plus their interactions as apparent from the geometry and dynamics of trunks and major branches; a forest stand is the sum of its organisms plus their interactions as apparent from the distribution and dynamics of its trees.

Conformity and flexibility

Trees can either adjust or adapt (Hallé *et al.* 1978): *adjustment* occurs as a change in growth and architecture of individual trees in response to environmental stimuli; *adaptation* occurs as the result of inherited changes of behaviour and architectural strategy in a tree population in response to the selection of surviving and reproducing members. For the study of the architectural flexibility of timber trees, the behaviour of big woody stems, trunks and branches in primary and secondary architectural units is paramount. In general, the context here is one of architectural conformity, as in the original architectural tree models of Hallé and Oldeman (1970). Gigantism of the primary architectural unit (Hallé 1986) stands for maximal conformity, regardless of what complex subsystems its stems may conceal. It is by repetition that big trees can adjust in a flexible way. The crux of the matter of predicting architecture and growth dynamics of timber trees is, therefore, the nature and number of the architectural units on the one hand, and their sizes and timing of appearance on the other.

TIMBER TREE TRUNKS

In timber trees, a forester or tree farmer prefers the development of one woody stem, the tree trunk, to be straightforward from the seedling stage to maturity for harvest. This development, moreover, should be as fast, as voluminous and as stable as possible. Five tree groups are the superpowers in the forests of the world:

i. Coniferae, forming a major component in many boreal, northern and montane forests;
ii. Leguminosae, abundant in a majority of tropical African and American rainforests, and many dry tropical forests worldwide;
iii. Fagaceae, dominating the main cool and warm temperate broadleaved forests and many montane forests;
iv. Dipterocarpaceae, moulding the basic features of the lowland rainforests of tropical Asia;
v. Myrtaceae, playing a decisive part particularly in Australian forests and in tropical forest plantations.

The trees in these groups represent a success story, because of only a few architectural and other responses to selection pressures (eg Oldeman & Fundter 1986). Another, more diffuse, group contains unrelated trees from various families (eg Meliaceae, Burseraceae, Lauraceae, Celastraceae or Vochysiaceae). Their success stories are unmistakable but rather more individual than collective, often parallelling one or another feature of one of the above major groups. However, in this diffuse group, there also seems to occur one original, rather elementary strategy enabling their success as tropical rainforest trees. This group might be termed 'miscellaneous giants', with the species building or rebuilding tropical rainforests *sensu lato* following major forest clearings or under late pioneer conditions.

Each of the above groups shows a particular formation, size and persistence of the trunk. Conifers are architecturally simple trees during much of their life, their trunks being simply grown-up seedling stems. Coniferous metamorphs seem to be rare, and reiterates occur late, if ever (also see Edelin 1977). Both Leguminosae (Oldeman 1989a) and Fagaceae (Peters 1992; Roloff 1989, 1991) are widely spread over many environments. They show an assemblage strategy with a pronounced tendency to form numerous, quite small metamorphs and reiterates, resulting in compound, unstable trunks and branches with a tendency towards crooked growth and forking. Dipterocarpaceae and Myrtaceae are most often metamorphic trees with some, late, reiteration (Edelin 1984). They conserve and enlarge a stable trunk from the seedling stage onwards for a prolonged period, the complex crown being built mainly by metamorphs. Finally, miscellaneous giants are reiterative trees with a large, stable and orthotropic primary architectural unit and rather few, late and massive reiterates, so that their woody mass is distributed over rather few, massive and stable trunks and branches.

This general survey of the main groups of successful forest trees, many of which are important as a source of timber, illustrates their very different responses to their forest environments. Therefore, both their domestication and their silviculture have to be understood in the light of such specific strategies.

The architectural strategies of conifers and miscellaneous giants give a strong propensity for the formation and persistence of one sturdy trunk. Domestication of such trees for timber includes selection of genotypes in which this trunk-building tendency is maintained or enhanced. Silvicultural protection of these trunks against breaking also has to be selected for, because trunk regeneration by early, massive reiteration lowers timber quality. Dipterocarps and Myrtaceae (including *Eucalyptus* spp.) should be selected in the same way, but their susceptibility to repetitive architectural complication needs to be studied. Nutrients and energy have to be invested in the trunks, not excessively in the crown mass, and this feature also requires appropriate silvicultural selection. Finally, Fagaceae and Leguminosae are not programmed to form straight trunks, because they pile up metamorphs and reiterates opportunistically, their environment dictating the compound trunk shape. The latter, therefore, depends on the silvicultural system used, as exemplified by two centuries of *Quercus* (oak) and *Fagus* (beech) silviculture in Europe.

TIMBER TREE SITES

The folded forest model

Big trees exert a large influence on their environment below, but big trees start life as small trees. This statement defines the essential points of 'inner' forest environment dynamics, to which all forest organisms other than mature trees are partly or totally subjected (Oldeman 1983; Uribe 1991). Forest environment dynamics are analysed at different scales below.

The green mass of vegetation covers the land in irregular folds of forest, tree row, agricultural field or meadow (Figure 2, *a*; also cf Oldeman 1992b). Within a forest, the canopy surface is itself folded by regeneration dynamics and the resulting patterns (cf Gómez-Pompa, Whitmore & Hadley 1991), such as large and small, open, aggrading and biostatic or mature patches (Figure 2, *b*) (see Oldeman 1990). This patchwork or silvatic mosaic acts as an irregular sieve on incoming climatic factors, such as light, wind and precipitation (Figure 2, *c,d*).

Ecological factors are usually dynamic, hence no clear ecological limits exist between eco-units. Geometrical limits (such as those proposed by Brokaw 1982, p102, later contested by Bongers & Popma 1988) are indeed irrelevant for timber tree ecology, although valuable in forest diagnosis (Koop 1989; Oldeman 1990).

Light, just like turbulent or rain-laden wind, penetrates into a forest through large gaps, through small openings between neighbouring crowns, and through interstices between leaf masses borne by reiterates, metamorphs or large branches (Figure 2, *c*). The distribution and repetitive redistribution of light or other factors create a very mobile and heterogeneous microclimate, manifest among others in the mobile and elusive sunfleck pattern in the undergrowth. These patterns permit the calculation of the light available to plants in a certain spot in the forest. However, temporal resolution has to be kept low, eg by using monthly figures of spotwise accumulated available irradiation. A spot is defined in a spatial grid with quite a high spatial resolution, eg by fish-eye photograph scanning and simulation. Horizontal and vertical light-and-shade patterns depicted with high spatial and low temporal resolution are highly non-linear. They invalidate the concepts of straight horizontal strata or vertical gap patterns, even as approximate working hypotheses. In man-made forests, such simple patterns might be created temporarily. However, a recent and realistic simulation of simple, pure *Pinus sylvestris* (Scots pine) forest plantations in The Netherlands shows that their heterogeneity as sieves for climatic factors increases with time (Leersnijder 1992).

Small volumes of light or shade accumulating over time in a non-linear model, as in the SILVI-STAR light climate simulation (Figure 2, *c,d*; Koop 1989), produce seemingly random points, accumulating over time like pixels producing fractal images on a computer screen.

Self-similarity of the climatic effects of stepwise decreasing canopy openings also intimates fractal mathematics (Oldeman 1992a). Such forest microclimate patterns are generally repetitive enough on a local scale that plant and animal species can live and reproduce in such forests from generation to generation. This kind of dynamic *status quo* brings to mind the climatological 'Lorenz attractors' (Gleick 1989; also, F Lutz, personal communication). There are no data as yet to check these hypotheses. This checking would be worthwhile, however, because of the promise of new methods for the calculus of predictive models, based on ecosystem geometry.

Direct environments of timber trees

Using the cruder, hand-made approximation (Figure 2, *c*), however, forest environments nested within the whole-forest mosaic, down to the direct environment around one tree, can be discussed. First, folding of the forest surface is the consequence of different gap forms and sizes and eco-unit development (Oldeman 1990, 1992b). Second, all forest folds have a canopy, high or low, thin or thick. This canopy rises slowly, reaches its highest level, and then collapses, on an eco-unit scale.

In large eco-units (Figure 2, *a*, L), the gap phase is all but devoid of a functional canopy. It gradually develops and diversifies into a climatic sieve, usually built by fast-growing, rather short-lived pioneer trees. Generally, these trees neither reach their highest level, nor die, at the

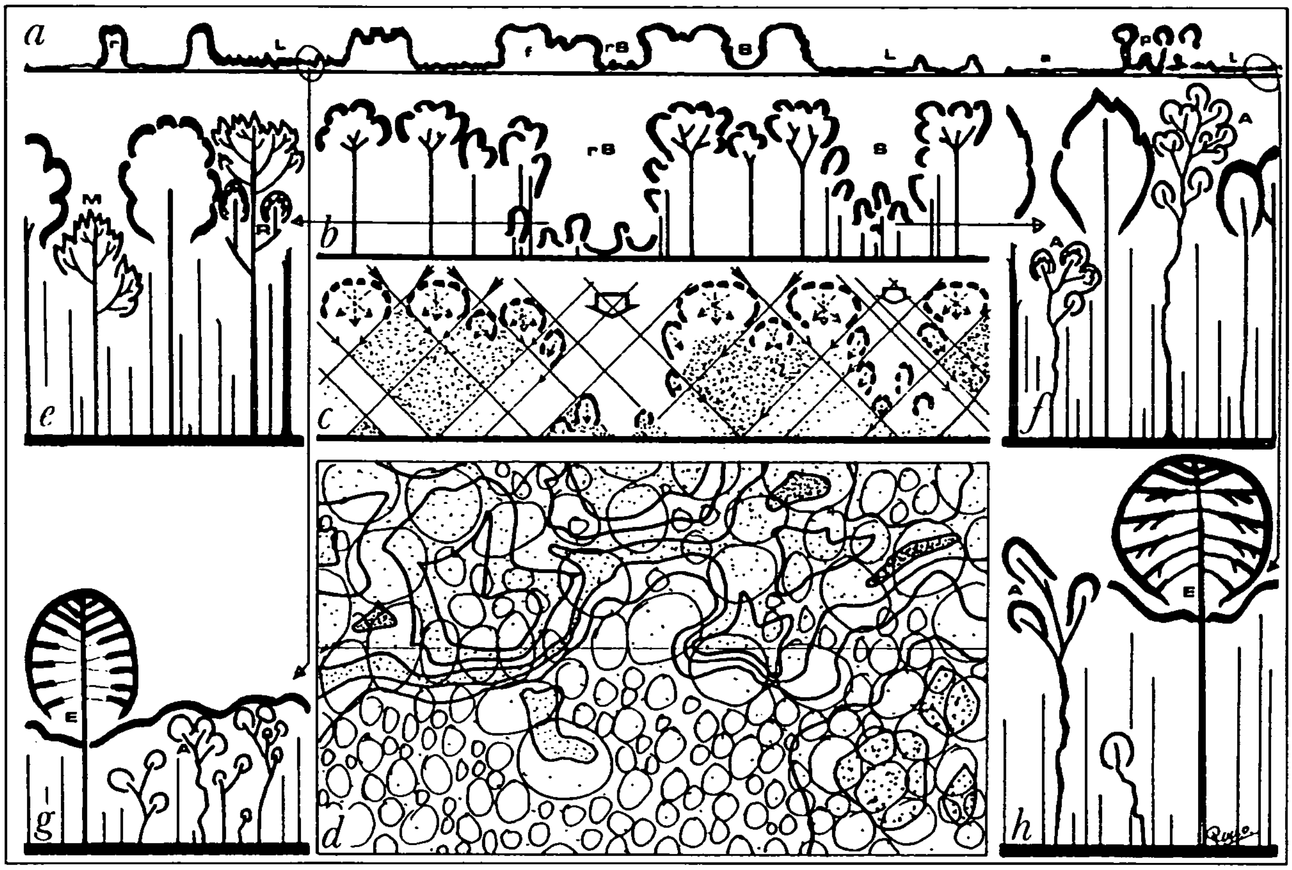

Figure 2. Principles of nested tree environment dynamics

a	Land covered by a folded green carpet (after Oldeman 1992b). r, row of trees; L, large surface pioneer forest; f, forest; rS, rather small forest gap (young eco-unit); S, small gap (young eco-unit);a, agricultural canopy; p, park canopy
b	Folds are folded again by crowns, these are folded again by subcrowns (for formation see Figure 1); abbreviations as for Figure 2, a
c	Folded canopy acting as an ecological sieve (cf Oldeman 199b), eg for light; open arrows, light through gaps; black arrows, light through chinks between crowns; stippled arrows, light between subcrowns, the latter two usually being included in 'indirect light' measurements; note pattern not at all as in gaps defined as discrete 'holes', light not vertical and canopy neither homogeneous nor opaque; shading denser where darker
d	SILVI-STAR-like, hypothetical pattern (cf Koop 1989) of lighter and darker patches on the forest floor caused by the transmission patterns as given in Figure 2, c; shading denser when darker; thick lines approximate isoluxes, thin lines crown projections; upper half of Figure forest as Figure 2, b, lower half large-surface pioneer forest
e	Metamorphic timber trees (M) with later some reiterates (R), such as Asian dipterocarps, grow in rather small openings
f	Assemblage trees (A) develop in small, highly dynamic openings, such as legume trees in tropical Africa and America
g & h	Development of elementary pioneer trees (E), such as Moraceae, above the pioneer forest canopy and assemblage trees (A), such as legumes, in that canopy; note repetitive phenomena coupled with decreased size of architectural units

same time. After the pioneers, the large eco-unit splits up into a finer-meshed mosaic, with smaller gaps as the origin of smaller eco-units. The latter range in size from one to a few trees (Figure 2, *a*, rS and S). This development may take one or more decades. Meanwhile, in and under the canopy, a first degree of non-linear complexity is born, with shaded and illuminated spots and regions. This pattern does not conform to a simple mosaic of illuminated gaps *versus* shaded undergrowth. The interference of large and small light, wind and humidity gradients creates a diverse array of microclimatic conditions in which the seedlings become established (for interference, see Oldeman 1989b, 1992b).

From the seedling populations come the saplings that shape the eco-units arising in small gaps. These trees modify the climatic sieve formed by the canopy once they start to participate in its formation. The more a forest develops beyond the pioneer stage, the more differentiated its internal environment can become. There are two limits to this complexity. The first limit is wholesale forest elimination, such as by fire, clearcutting, or other major event. Pioneer development may then start all over again. The second limit is over-diversification, when environmental heterogeneity reaches the point where a particular species population can no longer survive because appropriate niches become too few and far between.

Architectural strategies in the context of the domestication of timber trees

The domestication process requires that genetically improved timber trees are able to express their potential productivity; to this end, there is a need for silviculture to create the appropriate environment for growth (see Fasehun & Grace, pp148–157). Timber tree domestication is, therefore, inseparable from the choice or design of forest-like ecosystems in which such trees are to be cultivated. It is futile, for instance, to select *Eperua* genotypes (Leguminosae) for simple plantations and clearcutting, because they would never yield straight timber, but only crooked firewood. This is the intuitive base of the classical choice of species related to their 'light requirements'. However, forest ecoclimates are less straightforward than is suggested by contrasting 'light-demanding' against 'shade-tolerant' species. Forest trees include architectural strategies opposing programmed conformity to near-total flexibility, but also admit combinations in order to survive in dynamic environments (Oldeman 1990; Oldeman & Van Dijk in Gómez-Pompa *et al.* 1991).

Silvicultural systems have been designed to favour the ecosystem's carrying capacity for chosen tree species at the expense of others. Selective silviculture usually eliminates pioneer trees to a large extent. Mixed-plantation timber silviculture is usually considered difficult, being intermediate between natural regeneration and artificial regeneration. With the above concepts, it can be implemented. Among the best examples are tropical agroforestry systems utilising multipurpose, non-timber species (see Simons, MacQueen & Stewart, pp91–102) and the mixed dipterocarp silviculture in East Kalimantan (see Oldeman & Van Dijk in Gómez-Pompa *et al.* 1991).

The crux of the matter is timing. Foresters and timber farmers want a high timber volume of the best marketable tree species in as short a time as possible, unless they work in a multiple-use forestry context. There are inbuilt paradoxes in this set of aims. They can only be achieved either if the desired species have pioneer characteristics, such as short lifespan, high growth rates and straight trunk formation, or if the combination of rotation and volume is adapted to maximise tree size, rather than the volume per year per hectare. Domestication of 'new' timber tree species makes sense only if the concept of timber production itself is thoroughly overhauled (Oldeman 1991), adopting principles of ecological forestry.

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Fruit trees: diversity and conservation strategies

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ABSTRACT

Fruit-producing trees contribute significantly to the species diversity of tropical forests. Their contributions to the nutrition and local diet in developing countries are great, and their diversity is considerable. The availability and consumption of native fruits are declining in most regions, partly because of the greater attention given to research, development and marketing of exotic fruits. Population growth and severe forest degradation, arising from over-exploitation and infrastructural development, also adversely affect the availability of native fruits.

Strategies which can address the situation include conservation, domestication and enhanced utilisation of wild fruit trees, through the establishment of cottage industries and land use applications involving local participation. In this paper, priority species are recommended for domestication in countries of Malaysia and West Africa, and include durians, rambutans, mata kucing, bush mango, African pear and African breadfruit. The domestication effort should be complemented by *in situ* conservation practices, such as establishment of forest reserves for the protection of genetic diversity. Increased taxonomic, phenological and propagation studies are necessary to enhance identification, conservation and sustained use of fruit trees.

INTRODUCTION

The term 'fruit' is broadly applied here in both its horticultural and botanical senses to include the succulent and non-succulent portions of ripened ovary or ovaries which are eaten fresh or used in various cooked food preparations. Apart from trees, other tropical woody plants such as erect shrubs and climbers also provide edible fruits. In addition, trees, shrubs and climbers are also sources of edible leafy vegetables, edible flowers, mushrooms, and other foods and beverages.

Wild fruit trees form an important part of the species diversity of tropical forests. The diversity of tropical fruit trees is related to the range of families, genera and species involved, as well as the extent of intraspecific variation. For example, in Borneo, considered to be the centre of diversity for many plant genera, the genus *Garcinia* (Guttiferae) consists of 50 species or more, while *Baccaurea* (Euphorbiaceae) comprises at least 25 species (Wong & Lamb 1990).

The wide range of edible products obtained from wild fruit trees includes nuts and seeds used as staple foods or main dishes; those used as minor food supplements; condiments; thickening agents and flavours; leafy vegetables; fresh fruits; fresh seeds; edible oil; spices; fruit drinks and non-alcoholic beverages; and alcoholic drinks. These edible forest products constitute important and cheap sources of vitamins, minerals, protein, carbohydrates and fats and their contribution to the diet of local people is often great. Their dietary contribution is increased because they are available during most seasons, including strategic periods in the year when the conventional staples and vegetables are scarce (Okafor 1991). The potential of these wild plants for overcoming food availability problems in tropical countries is enormous (Getahun 1974; Jong, Stone & Soepadme 1973; Okafor 1975a, 1980a, b, 1981a; Okigbo 1977; Roche 1975a; Wong & Lamb 1990).

Notwithstanding their diversity, nutritional and dietary importance, the availability and consumption of wild fruit trees appear to be declining in many regions, partly because of the greater attention given to research, development and marketing of exotic fruits rather than to indigenous ones. Another important contributing factor is the declining availability of edible forest products, owing to human population growth and severe forest degradation. To redress the situation it is necessary to intensify programmes on the identification and genetic improvement of species with high potential, and on the development of strategies for conservation, development and production of both traditional and innovative products (Okafor 1991). These objectives form the focus of this paper, based largely on work and field experiences in Malaysia and countries in West Africa.

TAXONOMY OF EDIBLE WILD PLANTS

There are few taxonomic studies on edible wild plants of the tropics. Available information comes mostly from general notes and casual remarks in *Floras* and more general texts, and from oral reports as commonly documented in ethnobotanical and socio-economic surveys (Okafor 1989, 1990a; Shepherd & Okafor 1991; Thomas *et al.* 1989). Okafor (1981a) presented an account of 171 indigenous woody plants (53 families and 119 genera) of nutritional importance within the forest zone of Nigeria.

Species diversity of wild fruit trees in the forests of Sabah is illustrated by the genera *Artocarpus* (Moreaceae), *Durio* (Bombacaceae) and *Mangifera* (Anacardiaceae) (Wong & Lamb 1990). There are at least 13 species of *Artocarpus* indigenous to Sabah, out of some 25 species which are found in Borneo (Jarrett 1959a, b, 1960). The durians (*Durio* spp.) are represented by about 28 species in SE Asia, while in Sabah 14 species are recorded out of the 19 species found in Borneo (Korsterman & Soegeng-Riksodihardjo 1958). Of these 14 species, there are seven which have edible fruits. Similarly, in the genus *Mangifera*, there are some 19 species (with one introduced) in Sabah, out of a total of 24 found in the whole of Borneo (Bompard 1988). Other fruit species representing 33 families and 65 genera, cited by Wong and Lamb (1990), further illustrate the overall diversity of the wild and semi-wild fruits found in the forests of Sabah. Many of these families and genera are also represented in West Africa (Table 1). For example, the family Sapindaceae includes many important edible fruits both in Sabah and elsewhere. The akee apple (*Blighia sapida*), which occurs in West Africa, is a commercially important fruit tree, while the best-known fruits of this family in Sabah are the rambutan, meritam or pulasan (genus *Nephelium*) and mata kucing (genus *Dimocarpus*). The most commonly eaten rambutan is *N. lappaceum*.

THE EXTENT OF INTRASPECIFIC VARIATION

Examples of intraspecific variation abound in tropical fruit tree species. For instance, *Dimocarpus longan* (mata kucing) is very variable morphologically, especially in Borneo, where 30–40 local races can be distinguished (Van Welzen, Lamb & Wong 1988). All these Bornean races belong to the subspecies *malesianus*, which is divided into two varieties: var. *malesianus* and var. *echinatus*. The two species of *Nephelium*, *N. lappaceum* and *N. cuspidatum*, are also very variable in appearance. *N. lappaceum* is divided into three varieties, namely var. *lappaceum*, var. *pallens* and var. *xanthioides*, all three occurring in Sabah. *N. cuspidatum* has six varieties of which var. *robustum* (with large glabrous leaves) and var. *eriopetalum* (small and hairy leaves) are also found in Sabah.

The existence of natural variation within fruit trees is a crucial factor in efforts aimed at the domestication of edible forest species (Whitmore 1976; Okafor 1980a). Examples of varietal delimitation in West African fruit trees, such as *Irvingia gabonensis* (Okafor 1975b), *Treculia africana* subsp. *africana* (Okafor 1981b) and *Dacryodes edulis* (Okafor 1983), have indicated high prospects for extending the period of fruit availability, increasing the yield, and choosing the desired pattern as well as season of yield (Okafor 1978, 1981a; Okigbo 1977). If the two varieties of *I. gabonensis*, which fruit in the rainy (var. *gabonensis*) and dry (var. *excelsa*) seasons respectively, were each to be developed, the

Table 1. A list of some genera producing edible fruits in Nigeria, West Africa, that are also reported to occur in Sabah, Malaysia, by Wong and Lamb (1990). NB Several genera (and species) which occur in West Africa but were not cited in Wong and Lamb (1990) have been excluded. For a more detailed list, see Okafor (1979)

Family	Species	Local name	Product	Potential for development
Annonaceae	*Uvaria chamae*	—	Fruit	Low
Burseraceae	*Canarium schweinfurthii*	Ube-okpoko	Fruit	Medium
	Dacryodes edulis	African pear	Fruit	High
	D. klaineana	—	Fruit	Low
Ebenaceae	*Diospyros iturensis*	—	Fruit	Low
	D. elliotii	—	Fruit	Low
Euphorbiaceae	*Antidesma venosum*	—	Fruit	Low
Guttiferae	*Garcinia kola*	Bitter kola	Pulp and seeds	High
	G. smeathmannii	—	Pulp and seeds	Medium
Leguminosae	*Dialium guineense*	Velvet tamarind	Seed aril	High; very rich in vitamin C
	Parkia biglobosa	Locust bean	Fruit pulp, seed	High; rich in vitamin C
Moraceae	*Ficus capensis*	—	Fruit, leaves	Low
	F. exasperata	—	Fruit	Low
	F. vallis-choudae	—	Fruit	Low
Palmae	*Nypa fruticans*	Nipah	Fruit	Low
Sterculiaceae	*Sterculia oblonga*	—	Seed	Low

combined period of availability of the products would be significantly extended (Okafor 1991).

PROPAGATION TECHNIQUES

Large-scale production of fruit trees requires the development of nursery procedures involving the use of seeds or vegetative propagation, either for the production of stockplants to be used for budding (budgrafting), or for seedling trees to be outplanted in seed orchards or plantations. For example, in Nigeria, standard nursery practices have been developed for several species including *Dacryodes edulis, Irvingia gabonensis* and *Treculia africana* (Okafor 1981a, 1990b).

Seed propagation

Traditionally, tropical trees are propagated and conserved by seed, either by establishing plantations or by encouraging natural regeneration. There are three main advantages of seeds.

- Large numbers can usually be obtained easily.
- Spare seeds can be stored for later use.
- Variation is retained in succeeding generations, although this may not strictly be regarded as an advantage if a uniform product is desired.

Vegetative propagation

Vegetative multiplication is an alternative to the use of seeds as a method of raising planting stock of young trees. The advantages of this method are as follows.

- Genetically uniform planting stock may be produced.
- When mature adult budwood is used, early fruiting and fruit set at low height can be achieved.
- Superior genotypes can be selected and multiplied, leading to improvements in quality and yield.
- Selection and conservation of clones that are resistant to pests and diseases may be possible, and clones may be developed that are suitable for a particular region, site and end use.
- Conservation of genetic variation (such as hybrids produced by breeding) can be achieved through vegetative multiplication, in the form of clone banks of both 'adult' and 'juvenile' material.

The main objection to the development of clonal tree crops is the increased risk of biotic or physical catastrophe which is associated with the narrowing of the genetic base (Barnes & Burley 1987). However, frequent introduction of new clones and the maintenance of genetic diversity should reduce risk (see Foster & Bertolucci, pp103–111). The advantages of vegetative propagation techniques are greatest when there are problems with seed availability or storage, when only the male or female plant of dioecious species is required, or when there is a particularly high value attached to certain individual trees (see Barnes & Burley 1987).

Van Welzen, Lamb and Wong (1988) successfully produced cultivars of rambutan with constant quality by using budding techniques (Forkert method). In a study in West Africa, some 26 species of trees producing edible products were found to be buddable in experiments using scions from mature trees (Okafor 1978, 1980a, 1981a) (Table 2). Budded trees of some of these species (*Chrysophyllum albidum, Dacryodes edulis, Dialium guineense, Irvingia gabonensis, Pentaclethra macrophylla, Spondias mombin* and *Treculia africana*) produced viable fruits close to ground level after only two to four years (instead of five or more years in trees raised from seed).

Table 2. Trees with edible parts, successfully propagated by budgrafting in West Africa (source: Okafor 1981a)

Species name	Family
Afzelia africana	Caesalpiniaceae
A. bella var. *bella*	Caesalpiniaceae
*Bosqueia angolensis**	Moraceae
Canarium schweinfurthii	Burseraceae
Ceiba pentandra	Bombacaceae
Chrysophyllum albidum	Sapotaceae
Cola acuminata	Sterculiaceae
C. gigantea	Sterculiaceae
C. hispida	Sterculiaceae
Dacryodes edulis	Burseraceae
Detarium microcarpum	Caesalpiniaceae
Dialium guineense	Caesalpiniaceae
Hildegardia barteri	Sterculiaceae
Irvingia gabonensis	Irvingiaceae
Monodora myristica	Annonaceae
Myrianthus arboreus	Moraceae
Parkia biglobosa	Mimosaceae
Pentaclethra macrophylla	Mimosaceae
Pterocarpus mildbraedii	Papilionaceae
P. santalinoides	Papilionaceae
P. soyauxii	Papilionaceae
Spondias mombin	Anacardiaceae
Tetrapleura tetraptera	Mimosaceae
Treculia africana	Moraceae
Vitex doniana	Verbanaceae
Xylopia sp.	Annonaceae

* Now *Trilepisium madagascariense*

Propagation by stem cuttings (without application of auxin) using adult shoots was also successful for 21 West African tree species (Table 3). Fruiting was subsequently recorded in trees of *T. africana* subsp. *africana* var. *inversa* and *D. guineense* derived from stem cuttings. With juvenile cuttings, R R B Leakey (personal communication) recorded 69% rooting of *T. africana* under intermittent mist, using a 0.2% solution of IBA in 95% ethyl alcohol.

Table 3. Woody plants with edible parts, successfully propagated by stem cuttings (source: Okafor 1981a)

Species	Family
Ceiba pentandra	Bombacaceae
Cola gigantea	Sterculiaceae
Detarium microcarpum	Caesalpiniaceae
Dialium guineense	Caesalpiniaceae
*Dioscoreophyllum cumminsii**	Menispermaceae
Ficus capensis	Moraceae
Gnetum spp.*	Gnetaceae
*Gongronema latifolium**	Asclepiadaceae
Heinsia crinata	Rubiaceae
Hildegardia barteri	Sterculiaceae
Monodora myristica	Annonaceae
Lasianthera africana	Icacinaceae
Myrianthus arboreus	Moraceae
*Piper guineense**	Piperaceae
Pterocarpus mildbraedii	Papilionaceae
P. santalinoides	Papilionaceae
P. soyauxii	Papilionaceae
Triplochiton scleroxylon	Sterculiaceae
Tetracarpidium conophorum	Euphorbiaceae
Treculia africana	Moraceae
Vernonia amygdalina+	Compositae

* Woody climber; + Shrub

Research studies on vegetative propagation have also been carried out on a number of tropical timber species (see Leakey, Newton & Dick, pp72–83). For timber production, juvenile shoots are usually preferred for ease of rooting and for vigorous shoot growth, while, for fruit production, adult scions are used in order to obtain early fruiting at low heights. Furthermore, a plagiogeotropic growth habit, which may be a topophytic or 'adult' character, is regarded as undesirable for timber species, except for seed production in clonal seed orchards. Such traits may, however, be desirable for fruit tree production. It is, therefore, necessary to develop propagation methodologies and selection criteria specifically for fruit trees (see Okafor 1990b), even when the same species is important for both fruit and wood products.

CONSERVATION OF THE GENETIC RESOURCES OF FRUIT TREES

Conservation of genetic resources can be implemented by adopting both *in situ* and *ex situ* methods (Roche 1975b). Forest reserves, strict natural reserves (SNRS) and protected fetish groves contain fruit trees and serve as potential reservoirs of the various species. However, owing to high rates of forest clearance, natural reserves are no longer dependable sources of the genetic material of fruit trees. As a result of bush burning, farming, grazing and infrastructural development, over 26 000 ha of high forest are lost annually in the forest zone of Nigeria (Ola-Adams & Iyamabo 1977), and more than 90% of natural forest vegetation has already been cleared (World Wide Fund for Nature 1989). These losses adversely affect the availability of fruit trees in Nigeria and elsewhere in the tropics.

The density of fruit trees in rainforests is usually low, sometimes around three trees per hectare (Jong *et al.* 1973; Okafor 1981a), indicating that large areas are needed for sustainable *in situ* conservation (Roche 1979; Okafor 1981a). This fact also emphasises the need for *ex situ* conservation, which may involve seed storage, establishment of clone banks, tissue and meristem culture techniques, and the establishment of living collections (see Tompsett, pp61–71; Engelmann, pp49–52; *Khuspe et al.*, pp53–60; Ladipo *et al.*, pp239–248). Varietal selection must form a key part of such conservation programmes for fruit trees.

The adoption of agroforestry practices holds good prospects for *ex situ* conservation, especially in the support zone of national parks, such as Cross River National Park in Nigeria and the Korup Project in Cameroon (Okafor 1989, 1990a). Agroforestry can contribute to the conservation of biodiversity if people are encouraged to cultivate local forest species, especially edible varieties, in their farming systems (Okafor 1991). Species which can be used in agroforestry systems such as alley farming and intercropping include *Treculia africana, Ricinodendron heudelotii, Dacryodes edulis, Irvingia gabonensis, Cola acuminata*, etc (Okafor & Fernandes 1987).

OPPORTUNITIES FOR COMMERCIAL DEVELOPMENT OF INDIGENOUS TROPICAL FRUIT TREES

The large number of species of fruit trees in various parts of the tropics and the wide range of their food products have been well documented (eg Van Welzen *et al.* 1988; Abbiw 1990; Falconer 1990; Getahun 1974). In addition to the direct nutritional contribution of these local fruit trees, there is significant potential for developing cottage industries based upon them. These industries, in turn, could enhance the improved use of their edible products, as well as promote the development and conservation of the species for the large-scale supply of raw materials (see Prance, pp7–15; Clement & Villachica, pp230–238; Maghembe *et al.*, pp220–229). A number of food products that could be produced commercially from lesser-known tropical fruits are described below.

Jams and jellies

Suitable species include *Irvingia gabonensis* var.

gabonensis, Chrysophyllum albidum, Dialium guineense, Ficus sycomorus, Sclerocarya birrea and *Nephelium lappaceum* (rambutan) (Okafor 1973; Okafor & Okolo 1974; Van Welzen *et al.* 1988).

Fruit juice

The following species are suitable: *Irvingia gabonensis, Parinari curatellifolia, Tamarindus indica, Parkia biglobosa* (Okafor 1980a).

Confectionery

Breadfruit flour, processed from *Treculia africana*, can be used to produce a variety of baked foods (Anazonwu-Bello 1981).

Beverages

Recently, Ejiofor, Obiajulu and Okafor (1988) have prepared a non-alcoholic beverage from powdered *T. africana* seeds. Various fruits are also suitable for brewed alcoholic drinks, including *Spondias mombin, Uapaca kirkiana* and *Diospyros mespiliformis.*

Composite seasoning

Several indigenous seeds can be blended into seasoning. Suitable species include *Afrostyrax lepidophyllus* (country onion), *Monodora brevipes, Piper guineense* (bush pepper), *Tetrapleura tetraptera* and *Xylopia aethiopica* (Ajayi 1986).

Fats and oils

The high fat and oil content of the fruits of *Dacryodes edulis, Elaeis guineensis, Butyrospermum* spp., *Baillonella toxisperma, Irvingia gabonensis, Ricinodendron heudelotii* and *Nephelium lappaceum* (rambutan) indicates their suitability for commercial production of cooking oil and margarine, manufacture of soaps and pharmaceutical preparations, etc (Okafor & Okolo 1974; Udeala, Onyechi & Agu 1980; Van Welzen *et al.* 1988).

Livestock feeds

Kernels of *Dacryodes edulis*, which contain 3.2% protein (Okafor & Okolo 1974), and fruit head pulp and bran of *Treculia africana*, which contain 9.4% and 5.7% protein respectively (Ejiofor *et al.* 1988), can be used in livestock feed formulations.

Medicinal uses

Many fruit trees are used in traditional medicines. For example, seeds of *Garcinia kola* (bitter kola) are useful in the treatment of coughs and hepatitis (Iwu *et al.* 1987). The roots of *Nephelium lappaceum* (rambutan) are used in decoctions for treating fever, the fruit for digestive problems, and the leaves in poultices for headaches (Van Welzen *et al.* 1988).

PRIORITIES FOR DOMESTICATION

Many tropical wild fruit, nut and spice trees have been selected by generations of local people in various tropical countries, and have become part of their everyday life in food supply and farming systems. For example, in Borneo, the commonly cultivated fruit trees include the tampois (*Baccaurea macrocarpa*), the rambais (*B. motleyana*), the rambutan group (*Nephelium* spp.), mangosteen (*Garcinia mangostana*) and durians (*Durio* spp.). In West African countries such as Nigeria and Cameroon, commonly cultivated fruit trees include bush mango (*Irvingia gabonensis*), African pear (*Dacryodes edulis*), monkey kolas (*Cola lepidota, C. pachycarpa*), kola (*Cola acuminata, C. nitida*), and African breadfruit (*Treculia africana*), among others.

The collection of fruits and other products from the species listed above represents a start to the domestication process, but much greater progress could be made with some well-targeted research. Domestication of such species should help overcome the problems enountered when the only source of the fruit is from natural forest, such as the lack of information on periods of fruit maturity, irregular fruit supply, variable product quality, and the sparse density of fruit trees. Economically important species which provide a range of useful products and which are easily propagated should be accorded highest priority for domestication. Similarly, species which have restricted distribution, sparse density or are threatened with extinction should also be the focus of research attention (see Table 4).

CONCLUSIONS

Despite the importance of indigenous fruit trees as sources of food products and cash income to local people in tropical countries, the future of such trees appears bleak, because of the ever-increasing pressures on the tropical forest resources base, caused by increasing population, intensification of various land use practices, infrastructural development, and associated environmental problems. Many of the tropical wild fruit trees are fast disappearing, and many may soon face extinction if not conserved or protected. In addition, many tropical wild fruit species are markedly under-exploited. To illustrate this point, according to Zakri, Saw and Rajanaidu (1989), there are approximately 12 000 species of seed plants recorded in Malaysia, out of which only about 300 species (or 2.5%) are currently being used. The rest are still relatively unknown (Wong & Lamb 1990).

Efforts are currently being made by the Department of Agriculture in Sabah, Malaysia (Wong & Lamb 1990), and the Forestry Commission, Enugu, Nigeria (Okafor 1981a), towards the conservation and domestication of the wild fruit trees in these countries, by developing suitable propagation techniques and by collecting wild species and planting them in

Table 4. Fruit tree species with apparent high potential for selection and genetic improvement

Species	Local name	Family
Malaysia (eg Borneo, Sabah)		
Artocarpus spp.	Breadfruits	Moraceae
Baccaurea spp.	Tampois	Euphorbiaceae
Canarium spp.	Dabai, kembayau, kedondong	Burseraceae
Dacryodes spp.	Kembayau	Burseraceae
Dimocarpus spp.	Mata kucing	Sapindaceae
Durio spp.	Durians	Bombacaeae
Garcinia spp.	Bebata, kandis, mangosteen	Guttiferae
Mangifera spp.	Mangoes	Anacardiaceae
Nephelium spp.	Rambutans	Sapindaceae
West Africa (eg Nigeria, Cameroon)		
Afrostyrax lepidophyllus	Country onion	Styracaceae
Baillonella toxisperma	Shellnut	Sapotaceae
Chrysophyllum albidum	African star apple	Sapotaceae
Cola acuminata, C. nitida	Kola	Sterculiaceae
C. lepidota, C. pachycarpa	Monkey kola	Sterculiaceae
*Dacryodes edulis**	African pear	Burseraceae
Dialium guineense	Velvet tamarind	Caesalpiniaceae
Garcinia kola	Bitter kola	Guttiferae
*Irvingia gabonensis**	Bush mango	Irvingiaceae
Monodora spp.	Nutmeg	Annonaceae
Parkia biglobosa	Locust bean, dorewa	Mimosaceae
Pentaclethra macrophylla	Oil bean	Mimosaceae
*Piper guineense**	Guinea pepper, uziza	Piperaceae
Ricinodendron heudelotii	Groundnut tree	Euphorbiaceae
Spondias mombin	African hog plum	Anacardiaceae
*Tetracarpidium conophorum**	Conophor, ukpa, kasu	Euphorbiaceae
*Treculia africana**	African breadfruit	Moraceae

*Species among the priority list of 20 under-utilised species considered as needing immediate attention by a symposium on conserving biodiversity held at the International Institute of Tropical Agriculture, Ibadan, Nigeria, in 1990

orchards. To complement these efforts, the *in situ* conservation of wild fruit trees in strict natural reserves (Wong & Lamb 1990) needs to be properly maintained and expanded to cover more areas, for the protection of genetic resources of the species. This work should be supplemented by further *ex situ* conservation.

Vegetative propagation techniques and nursery procedures developed for several fruit tree species have great potential as tools for domestication and *ex situ* conservation, including incorporation of fruit tree species in agroforestry systems. The involvement of local communities is necessary for the identification, design and implementation of such agroforestry programmes. Development and utilisation of food and industrial raw materials based on indigenous tropical fruit trees should be undertaken as a purposeful conservation strategy for the species. Such tree species should also be used in land use, management and development options, to enhance the sustainable supply of edible products and their role in environmental protection.

Ethnobotanical surveys, including taxonomic and phenological studies involving local fruit trees, are required in tropical countries, in order to identify species and variants with high potential, and their traditional uses. Improved knowledge about tropical fruit trees will facilitate their conservation and efficient use.

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Trees for drugs and other extractives: future prospects

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ABSTRACT

Historically, plants and their extracts have been exploited as medicines and for a range of other uses, such as dyestuffs, perfumes and industrial adjuncts. In the majority of cases, supplies have been obtained by collection from wild plants. Relatively few species have been cultivated to any great extent. *Hevea* and *Cinchona* are two exceptions. In the past, the absence of reliable (*Strophanthus* spp.) or sustainable (*Rauvolfia serpentina*) sources significantly harmed the success of potentially valuable medicinal plants.

Currently, in the search for new lead molecules for drug development, there is a major increase in the screening of plant extracts. The major developments taking place in screening technology (high throughput and very specific screening targets) will ensure that re-assessment of the bioactivity of an extractive can take place over and over again in the coming years. Evidence from our own participation in such screening exercises suggests that there will be a significant 'hit rate', demanding further, more detailed, investigation of the active extracts.

For the Western pharmaceutical industry, the follow-up to these hits will be directed toward identification of the active component(s) and subsequent development of a 'manageable' product. 'Management' will, by preference, be by synthesis, but, if a non-synthesisable natural product is required, it will be produced by biotechnology. Only where both synthesis and biotechnology fail would domestication be contemplated. There may be greater opportunities for domestication in relation to herbal medicines and non-medical products, such as perfumes.

INTRODUCTION

Historically, plants and extracts or pure compounds isolated from them have been an important source of medicinal substances, as well as dyestuffs, perfumes, tannin substances and various industrial adjuncts and foodstuffs. In this paper, the current situation is reviewed and consideration is given to what might happen in the future, restricting the discussion more or less to tropical tree species and to their potential value in the pharmaceutical and allied sectors. First, however, a few generalisations are made about attitudes and philosophies that currently exist with regard to plant-derived pharmaceuticals.

CURRENT ATTITUDES

As pointed out previously (Waterman 1989), there has not, in the pharmaceutical context, been any decrease in the use of drugs derived from natural sources during the period from 1930 to 1988 because of the advent of antibiotics and developments in the use of animal products and semi-synthetic derivatives of natural products (notably antibiotics and steroidal drugs). There has, however, been a very considerable change in emphasis away from the use of powdered plant materials and extracts toward the use of isolated pure compounds, because of the greater control this allows in maintaining product quality and dosage.

Today, in many pharmaceutical companies, there is a re-awakening of interest in the living world as a source of lead compounds for drug development programmes. This interest must not be interpreted as a change in emphasis away from synthetic chemistry. When a drug discovery team identifies a novel compound with therapeutic potential, the most likely response will be, simultaneously, to find out how it works and to find a way of synthesising it. If the results are of sufficient interest, this stage will then be followed by a major synthetic programme aimed at producing analogues which maximise the required activity while minimising side-effects and toxicity. The final marketed product will generally be wholly synthetic. Only on those occasions where an isolated metabolite is the compound of choice, or where the marketable product is a semi-synthetic derivative that defies total synthesis, would the original natural source be likely to retain lasting importance.

One recent example is the new anti-cancer drug taxol (Figure 1), which was originally obtained by extraction from the bark of *Taxus brevifolia* (Taxaceae). The structural complexity of taxol

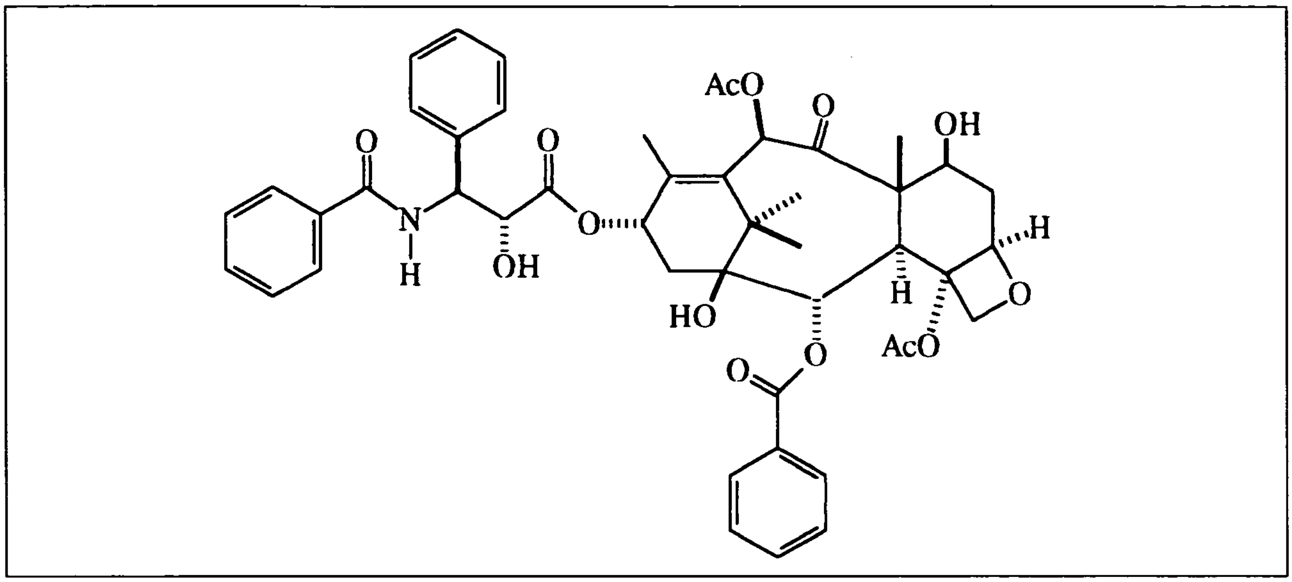

Figure 1. Chemical structure of taxol

means that synthesis of the compound is not currently a viable option, but there is scope for producing a wide range of semi-synthetic derivatives (Kingston, Samaranayake & Ivey 1990). Unfortunately, as it is estimated (Kelsey & Vance 1992) that 2000–3000 trees are needed to produce 1 kg of taxol, there is currently a severe supply problem which is limiting availability of the drug. As a result, other species of *Taxus* have been studied and taxol and/or allied compounds have now been obtained from the leaf as well as the woody parts, giving hope that a supply can be maintained from a resource that is renewed annually (Kelsey & Vance 1992). However, at present, the only source for taxol recognised by the US Food and Drug Administration is the bark of *T. brevifolia*. Harringtonine (Figure 2) from *Cephalotaxus harringtonia* (Cephalotaxaceae) is another promising anti-tumour compound that seems to present similar problems.

Undoubtedly, a major effort will be made to produce taxol under controlled laboratory conditions. If this cannot be achieved by synthesis, then tissue culture and other biotechnological methods will certainly be attempted. To date there has been much effort in this area but limited success. Shikonin (Figure 3), a dye and antiseptic from *Lithospermum erythrorhizon* (Boraginaceae), berberine from *Coptis japonica* (Ranunculaceae), and the alkaloids of ergot (*Claviceps purpurea*) are currently produced commercially by tissue culture (Samuelsson 1992), but it is fair to say that, despite all the efforts that have gone into this technique, there have been relatively few successes. Given all the problems confronting production, there has been some suggestion of cultivating *T. brevifolia*, but as yet there is no serious programme to bring this about.

These arguments reflect the attitudes of Western pharmaceutical companies producing products that are aimed primarily at a developed world market. The option of a developing country being able to supply its own pharmaceutical requirements by growing medicinal plants is a very different matter, as evidenced by the importance placed on growing medicinal plants in the People's Republic of China (Hikino 1989) and in India (Aslam 1989). The Chinese, in particular, are also great importers of medicinal

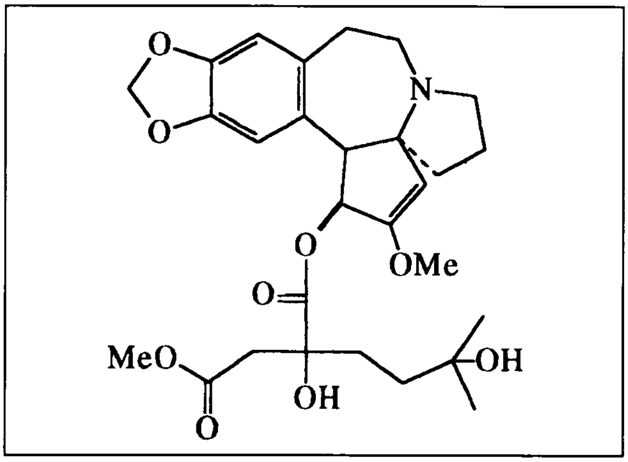

Figure 2. Chemical structure of harringtonine

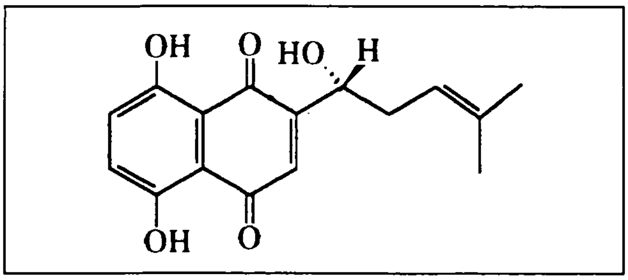

Figure 3. Chemical structure of shikonin

plants from other parts of the world, and there is obviously considerable scope for improving the quality of materials to meet this demand.

If the preferred strategy of the Western pharmaceutical industry seems largely unsympathetic to tropical forestry and agroforestry, the opposite is true for other products which can be labelled as 'green' or herbal medicines and health foods. Whatever the scientific basis for the advocacy of these materials, the fact they they are 'natural' is a major attraction to a subset of the population of the developed world. The problems with many such products is that their popularity is often transient, which is not conducive to long-term development. A 'fad' is all too often accompanied by the rapid exploitation of limited natural resources by haphazard collecting from the wild population. One example, seen in Kenya in the 1980s, resulted in the harvesting of *Aloe* species, such as *A. marsabitensis*, to a state of near-extinction. However, where interest is sustained, as in the case of ginseng (*Panax* spp.), then there is very considerable scope for the development of cultivated material (Evans 1989).

There is currently a more balanced situation in allied areas, such as perfumery, and in spice and gum production, where stable, long-term markets exist. Among the most important spice trees are cinnamon (*Cinnamomum verum*) which is now extensively grown in Indonesia, Sri Lanka and the Seychelles, nutmeg (*Myristica fragrans*) from Indonesia, Malaysia, Sri Lanka and Grenada, and clove (*Syzygium aromaticum*) for which Malagasy, Brazil and Malaysia (but not Zanzibar) are now the most important sources. Other well-established crops are those producing gums, particularly for confectionery, and tanning materials.

THE PRESENT SITUATION

Pharmaceuticals, resins and major spices

In the past, there have been some notable successes in the domestication of trees containing pharmaceuticals, the most widespread being a number of species of *Cinchona* (Rubiaceae), the source of quinine (the first anti-malarial), and quinidine (useful against some forms of heart disease) (see Figure 4). It is arguable whether the protection that *Cinchona* bark extracts provided against the ravages of malarial fever contributed very significantly to the colonisation of the tropics by European peoples. Originating in South America, *Cinchona* was initially collected from wild plants and soon became locally extinct. Seeds obtained by the Dutch were taken to Java where through an extensive breeding programme hybrids were produced with a much-elevated alkaloid content (pharmaceutical-grade bark must have a minimum of 6% alkaloids, and some strains are recorded as reaching the astonishing level of 15%). Because of the other use of quinine, as the bitter principle in tonic water, its cultivation and production continue to be a major industry. In addition to Indonesia, there is now appreciable production in Bolivia, Guatemala and the Congo, and plantations exist in many other countries.

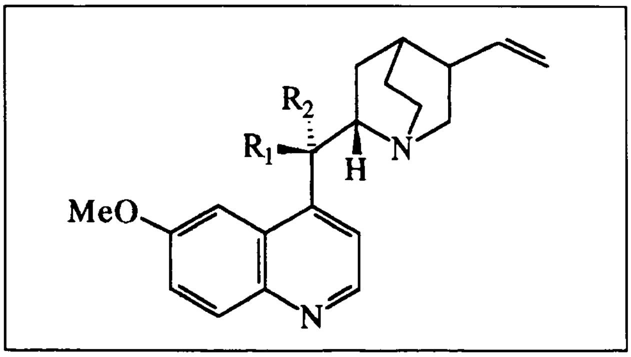

Figure 4. Chemical structure of quinine (R_1=OH, R_2=H) and quinidine (R_1=H, R_2=OH)

The continued buoyancy of the *Cinchona* industry is not, unfortunately, matched by many of the other drug plants that have been important components of the *materia medica*. A list of some of the tree species of the tropics which have been or are still cultivated for medicinal products is given in Table 1. Their use is generally in decline in the developed world as their products become less important in medicine (senna and the spices are exceptions), or occasionally, as in the cases of tragacanth and acacia gum, demand outstrips supply.

Some materials, such as the burseraceous resins from *Commiophora* and *Boswellia* species (frankincense, myrrh, bissabol, opopanax), may have only small Western markets but are in heavy demand in the Far East, both as incense and as ingredients in Chinese medicine. According to Thulin and others (Thulin & Warfa 1987; Thulin & Claeson 1991), they are among the major exports of Somalia and are also collected extensively in north-east Kenya and southern Ethiopia. Throughout their range the collection of these resins appears to be based more or less entirely on wild plants, and there is either a total lack of, or inadequate, quality control of what is collected and sold, except in Ethiopia. As a consequence, material for export from Somalia and Kenya is almost always of variable quality, a fact that buyers are able to exploit to keep the price low. This seems to be a classic example of an industry that would benefit from rationalisation, selection and development of appropriate varieties and cultivation, and from the production of standards

Table 1. Pharmaceutical products (with uses, where appropriate) obtained from cultivated tree species in tropical or subtropical countries (source: Evans 1989)

Species (family)	Product	Source
Styrax benzoin (Styracaceae)	Balsamic gum	Indonesia
Styrax paralleloneurus	Balsamic gum	Thailand
Myroxylon balsamum (Leguminosae)	Balsamic gum	Cuba, Colombia*, Venezuela*
Myroxylon pereirae	Balsamic gum	Guatemala, Honduras, San Salvador
Liquidambar orientalis (Hamamelidaceae)	Balsam	Turkey
Astragalus sp. (Leguminosae)	Tragacanth gum	Turkey*, Iran*, Iraq*
Acacia senegal (Leguminosae)	Acacia gum	Sudan
Sterculia urens (Sterculiaceae)	Sterculia gum	India, Pakistan
Cassia senna (Leguminosae)	Purgative	Sudan, India
Rhamnus purshianus (Rhamnaceae)	Purgative	N America*
Myristica fragrans (Myristicaceae)	Carminative, flavour	Indonesia, Malaysia, Sri Lanka, Grenada
Cinnamomum verum (Lauraceae)	Carminative, flavour	Sri Lanka (widespread)
Cinnamomum cassia	Carminative, flavour	S China
Cinnamomum camphora	Rubefacient	S China, Japan, India, Georgia
Syzygium aromaticum (Myrtaceae)	Antiseptic, stimulant	Madagascar, Indonesia, Brazil, Tanzania
Eucalyptus spp. (Myrtaceae)	Decongestant	Widespread
Commiphora myrrha (Burseraceae)	Antiseptic	Somalia*, Ethiopia*
Boswellia carteri (Burseraceae)	Incense, fumigant	Ethiopia*, Yemen*
Garcinia hanburii (Guttiferae)	Veterinary purgative	SE Asia*
Pistacia lentiscus (Anacardiaceae)	Medical paints	Greece
Quillaja saponaria (Rosaceae)	Emulsifier	Chile*, Peru*, Bolivia*, USA, India
Picrasma excelsa (Simaroubaceae)	Bitter tonic	W Indies*
Prunus africana (Rosaceae)	For prostate treatment	Africa*
Erythroxylum coca (Erythroxylaceae)	For ENT surgery	Peru, Bolivia, Colombia, Indonesia
Cephaelis ipecacuanha (Rubiaceae)	Expectorant, emetic for amoebic dysentery	Brazil*, India
Physostigma venenosum (Leguminosae)	Anti-mydriatic	W Africa*
Strychnos nux-vomica (Loganiaceae)	Respiratory stimulant	India
Rauvolfia serpentina (Apocynaceae)	Anti-hypertensive	India, Pakistan
Rauvolfia vomitoria	Anti-hypertensive	Africa*
Voacanga spp. (Apocynaceae)	Anti-hypertensive	Madagascar*, Indonesia*
Pausinystalia johimbe (Rubiaceae)	For sexual inadequacy	W Africa*
Cinchona sp. (Rubiaceae)	Anti-malarial, bitter tonic, for cardiac disease	Indonesia, Tanzania, Kenya, Guatemala, Bolivia
Pilocarpus sp. (Rutaceae)	For glaucoma	S America

*Probably collected entirely from wild populations

for identifying and quantifying the monoterpene, sesquiterpene and diterpene components of the resins.

As already observed, there is currently an upsurge of interest in medicinal plants and their products; one of the most tangible results is the present interest in taxol. Unfortunately, the taxol situation points out the problems for plant breeders when faced with the sudden rise to prominence of a previously obscure species. The pharmaceutical industry needs taxol *now*, not in 10–15 years' time. The situation with taxol is appreciably different from that which followed the discovery of the last major anti-cancer drugs to be derived from a plant source, vinblastine and vincristine (Figure 5), which were isolated from the Madagascan periwinkle (*Catharanthus roseus*, Apocynaceae). These have proven, as taxol currently appears to be, intractable to synthesis. However, the Madagascan periwinkle is a weed that will grow prolifically in more or less any moist tropical or subtropical climate. Yet, despite

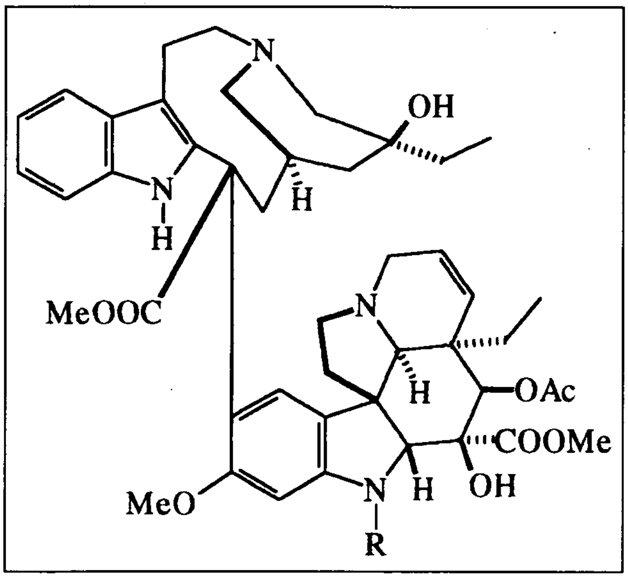

Figure 5. Chemical structure of vinblastine (R=Me) and vincristine (R=CHO)

the ease of cultivation, there have still been enormous efforts to produce these alkaloids under controlled conditions: in this case, through tissue culture. It has proved to be a difficult and frustrating process, and is still not a viable proposition after some 20 years of research.

The demand for an immediate supply of a plant species and the pressures this demand places on natural populations are currently being seen with the harvesting of seeds and bark of *Voacanga* species (Apocynaceae) and the bark of *Prunus* (*Pygeum*) *africana* (Rosaceae) in tropical Africa. Both provide extracts that are being used in medicines popular in continental Europe; both are collected entirely from wild plants. According to Cunningham (1990), during the 1980s an average of about 800 tonnes of *Prunus africana* bark were exported annually from Cameroon to France, a level of output that can no longer be sustained from easily accessible material. These two taxa, and *Prunus* in particular, while not immediately endangered, will be lost over part of their ranges if the problem of indiscriminate collection is not overcome. This is the challenge that tropical forestry faces: what can it do to answer the demand for species like *Prunus*?

Gums

There are major problems with the traditional sources of natural gums. Tragacanth, from *Astragalus* species (Leguminosae), has never been widely cultivated; over-collection and political problems (native to Iran and Iraq) have led to a major reduction in its availability. Production of acacia gum, from *Acacia senegal* (Leguminosae), is centred in Sudan, but current supply is unable to keep pace with demand, a problem which is magnified by political and worsening climatic conditions. In response to the problems that have affected tragacanth and acacia production, there has been a considerable upsurge in the use of the gum of *Sterculia urens* (Sterculiaceae), a species presently cultivated primarily in India. Where supplies of gums fail, semi-synthetic materials (methoxycellulose) or by-products of crop plants (legume seed gums) have been taking an increasing market share, but the traditional products are still sold at a premium price. The traditional gums are all produced as exudates from injured bark. Two further species of Leguminosae also produce gums of commercial value: *Ceratonia siliqua* (carob) and *Cyamopsis tetragonolobus* (guar). Both guar and carob gums are obtained from the seed.

At first sight, the market seems ripe for the introduction of further natural gums. However, there is another set of problems which must be confronted by someone wishing to produce a new product to replace and compete with the traditional gums, which are at present approved by regulatory authorities. Acacia gum, for example, if it were to appear on the market as a new product today, would have to run the gauntlet of examination by bodies such as the Food and Drug Administration in the USA. There must be severe doubts that it would prove acceptable in the raw state on the grounds of variable quality and microbial contamination. It escapes censure primarily on the basis of prolonged use without strong evidence of deleterious effects. To overcome these presentation difficulties, spray-dried acacia, produced from imported crude material, is becoming common in Western countries; one suspects that any new large-scale introductions would need to be presented in some comparable, modified, form.

Because of the pitfalls that surround the introduction of a natural replacement for the edible gums, the answer seems to lie with the development of better management and control of those currently in use. Of these the most important is acacia. There certainly seems to be plenty of scope for such developments. Astonishingly, according to Evans (1989), 'apart from some "acacia gardens", wild, self-sown plants are the main source of the gum', with Sudan and, to a much lesser degree, Senegal and Nigeria providing the best product. Given the shortfall in supply and the apparently safe long-term need for such gums (for the food industry as well as pharmaceuticals), acacia, and perhaps some of the others as well, seem to be strong candidates for development as crops for arid and semi-arid areas in the Sahel.

Tannins

Historically, the use of plant-derived tannin extracts to make leather has been a major item of commerce throughout the world. Numerous species have been used to produce tannin, from various plant parts (barks, woods, leaves, fruits and galls). Most of the major sources have been listed by Haslam (1989). Among the most important are *Acacia* species (wattle, babul, cutch), *Eucalyptus* species (wandoo), *Cassia* species (avaram), *Caesalpinia* species (divi-divi, algarobilla, tara), *Terminalia* species (myrobalans), *Quercus* (valonea, aleppo, garouille), various Anacardiaceae (*Schinopsis* – quebracho; *Rhus, Anogeissus*–sumach), *Castanea* species (chestnut), *Uncaria* species (gambier), and various monocotyledonous tree species (*Picea, Tsuga, Pinus, Larix*).

In the UK, vegetable tanning has now been supplanted to a large degree by mineral tanning. Tannin from vegetable sources (most commonly from oak, *Quercus* spp.) is used largely for speciality fashion wear and for orthopaedic equipment (Haslam 1989). More vegetable tannin is now probably imported into the UK for commercial uses other than for use in the tanning industry. However, elsewhere in the world, vegetable tannins remain important. In the USA, about 15% of all leather tanning still uses vegetable materials (Seigler *et al.* 1986). In 1976, approximately 18.5 million lb (8400 t) of wattle (*Acacia mearnsii*) derivatives, 30 million lb (13 600 t) of quebracho and a small amount of European chestnut were imported into the USA to meet the need for vegetable tannins. India is estimated to import some US$124M worth of vegetable tannin, which is made up primarily of wattle, quebracho, oak galls, gambir and myrobalans (Devi & Prasad 1991).

One of the major sources of wattle for the American market has been Kenya, which in 1978 had 14.3 kha under plantation with *Acacia mearnsii*. However, despite the fact that the price of wattle increased five-fold between 1977 and 1986, the area under wattle plantations decreased in the same period to 9.8 kha (Mugedo & Waterman 1992) because of the need to convert to food-producing farmland. If current trends continue, then Kenya will soon need to import vegetable tannin to support its own tanning industry, rather than export it.

As a result of the realisation that there will soon be a serious shortfall in vegetable tannage, attempts have been made to identify new sources. The focus has been *Acacia*, with surveys being carried out of species indigenous to the USA (Seigler *et al.* 1986), India (Devi & Prasad 1991) and Kenya (Mugedo & Waterman 1992). In each case, species have been located with promising yields of tannins and which will grow in situations unsuitable for the growth of food crops (usually semi-arid environments). There is clearly considerable scope, as well as need, for the development of new sources of tannins. However, this development must be done carefully and with close co-operation between tannin chemist and forester. It is not just the quantity but also the quality of tannin produced that is important in selecting species, and assessing quality in a tannin is a very difficult procedure.

THE FUTURE

At the present time, the potential for drug discovery based on natural products is higher than it has been at any point in the past 30 years. The development of high-throughput screens and the identification of target receptors and enzymes on which to base highly selective screens, are the subject of major efforts by drug companies. Many of these screens are capable of assaying crude extracts, as well as isolated natural products or synthetic chemicals. Each time a new screen target is developed, then each extract needs to be tested again, irrespective of past record of activity or inactivity. To help feed these screens, many drug companies are accessing natural biodiversity. A current topical example is the agreement between the American company Merck and the Institut Biodiversidad of Costa Rica (INBio), whereby Merck have agreed to pay INBio US$1M for exclusive access (for a limited period) to an agreed number of species (plant and animal). The payment will be used to help conserve and protect Costa Rican biodiversity. The desired outcome is the identification of useful bioactivity and the isolation, synthesis and patenting of an active compound. The key is access to maximum biodiversity, and only when there is a coincidence of:

- optimal bioactivity in an extract or natural product, and
- intractability to synthesis

will there be any chance of cultivation for a new product. Even when this coincidence occurs, it seems increasingly likely that the solution will be found in the realms of biotechnology, and not in traditional methods of production.

In looking to the future and trying to identify new opportunities for forestry, it seems best to disregard the Western pharmaceutical industry. However, there are plenty of opportunities in other areas. These include:

- improving the production of already established crops for food and pharmaceutical industries, notably among gums and resins for both Western and Far Eastern markets;
- identifying regional needs in the developing world and ensuring continuity of supply of drugs for local markets; and
- identifying and establishing new sources of tannins.

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Techniques to domesticate trees

In vitro systems for the conservation and utilisation of germplasm

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ABSTRACT

The use of *in vitro* techniques is essential for the safe conservation of numerous plant species which have recalcitrant seeds or are vegetatively propagated. For medium-term conservation, growth reduction is achieved by modifying various environmental variables (temperature, culture medium, gaseous environment). These techniques are now routinely employed in many laboratories. For long-term conservation, cryopreservation (in liquid nitrogen at -196°C) is the only method available. Cryopreservation protocols have been set up for more than 70 plant species under various forms (cell suspensions, calluses, meristems, somatic and zygotic embryos). However, the large-scale application of these techniques is exceptional at present. Conventional cryopreservation protocols are generally complex and comprise numerous successive steps which have to be determined for each new material. In the past two years, simpler techniques (encapsulation/dehydration, desiccation, vitrification) have been developed which may facilitate the long-term conservation of the germplasm of numerous plant species.

INTRODUCTION

For seed storage purposes, plant species have been divided into two categories (Roberts 1973): those with orthodox seeds and those with recalcitrant seeds. Orthodox seeds can withstand extensive dehydration to low water contents and can be stored in the dry state at low temperatures for extended periods of time. Recalcitrant seeds, which have a high moisture content, are sensitive to dehydration and remain viable only for a short time (weeks or months), even if stored optimally (high humidity and temperature). Species with recalcitrant seeds are predominantly of tropical and subtropical origin and include different groups of plants (fruit trees, beverage crops, oleaginous crops, spices, horticultural and medicinal species) which are often of great economic value. Long-term seed storage is also difficult for many forest trees because they have a very long juvenile phase and do not produce seeds for several years. The conservation of species which reproduce asexually also poses considerable problems.

PRESERVATION OPTIONS

In situ conservation is often problematic because of the widespread destruction of natural vegetation and the disappearance of large wild areas. *Ex situ* conservation is limited by various parameters, notably the size of the samples necessary to retain genetic diversity (from 20 plants for a single population to 5000–20 000 plants to maintain the heterozygosity of a species). Consequently, the land requirements and the cost of maintaining the *ex situ* field sites can become very extensive, particularly in the case of large plants such as forest trees. Furthermore, plants preserved in natural conditions remain exposed to pests, pathogens, natural and man-made disasters such as hurricanes, fire, etc, which can be especially serious for *ex situ* conservation areas. An alternative, therefore, is to develop laboratory-based storage systems, such as seed stores (see Tompsett, pp61–71) or *in vitro* culture.

IN VITRO CULTURE FOR GERMPLASM PRESERVATION

The use of *in vitro* techniques, which have now been applied to more than 1000 plant species, is of great interest for the collection, storage, exchange and multiplication of plant germplasm. Such techniques are particularly useful for recalcitrant seeds or for species which reproduce asexually. Tissue culture techniques have the additional advantage that they provide the opportunity for very high multiplication rates in an aseptic environment. Moreover, the space requirements and labour costs are very considerably less than those of *in vivo* systems. Finally, tissue culture techniques greatly facilitate the international exchange of plant germplasm, reducing the volume to be shipped and satisfying phytosanitary regulations by providing sterile conditions.

Depending on the duration of storage required, the conservation methods employed vary. For short- or medium-term storage, the aim is to reduce the growth rate of the plant material, usually by lowering the culture temperature. For long-term conservation, cryopreservation in liquid nitrogen (−196°C) arrests all metabolic events and cell divisions. The plant material can thus be stored without any alteration for unlimited periods of time. In this instance, the cultures are also stored in a small volume and protected from contamination.

There is an extensive literature on *in vitro* conservation techniques for plant germplasm, covering general aspects, the use of different culture systems (Kartha 1985; Dereuddre & Engelmann 1987) and their application to different groups of plants, such as woody and horticultural species (Aitken-Christie & Singh 1987; Engelmann 1991a) and tropical crops (Zakri *et al.* 1991; Engelmann 1991b). This paper briefly presents the classical short- and long-term storage techniques, and then discusses more extensively the new *in vitro* conservation technologies and their potential for germplasm conservation, focusing on tropical woody species.

USE OF *IN VITRO* TECHNIQUES FOR COLLECTING GERMPLASM

The use of *in vitro* methods when collecting germplasm has many advantages and applications (Withers 1987). For example, these technologies are ideal when only vegetative explants are available, when clonal genotypes are required, or when collecting missions fail to coincide with the time of seed production. Similarly, the collection of mature embryos of recalcitrant seeds can help to prolong their viability and, at the same time, reduce their bulk. *In vitro* techniques can be carried out under field conditions using minimal equipment. To date, *in vitro* techniques have been used to collect germplasm of *Gossypium* sp., *Manihot* sp. and *Cocos nucifera*. They are also being tested for other species such as *Citrus*, *Theobroma cacao*, *Musa* spp., forage grasses and temperate fruits; techniques are under development for *Persea americana* and *Vitis* spp., and are planned for *Coffea* spp. (Withers 1991).

SHORT- AND MEDIUM-TERM STORAGE USING SLOW GROWTH

Technical approaches

Various conditions can be modified to reduce the growth of plant cell cultures and to extend the intervals between successive transfers. The most successful storage conditions for slow growth are those which result in as few modifications as possible, in comparison with standard culture conditions. In most cases, the culture temperature is reduced. For example, with temperate woody species, the temperature is decreased to between 2°C and 20°C, allowing a conservation duration ranging between ten years and four months, depending on the species (Mascarenhas & Agarwal 1991). For tropical species which are generally cold-sensitive, other modifications have to be sought. Slow-growing species such as *Coffea* can be stored in standard conditions and transferred only every six months to one year (Bertrand-Desbrunais & Charrier 1990). Alternatively, the composition of the culture medium can be modified by reducing the content of mineral elements and/or sugar, or adding compounds such as osmoticums or growth retardants (Engelmann 1991b). Another option is to reduce the quantity of oxygen available to the cultures. This reduction can be achieved by covering the material with mineral oil, as with calluses (Augereau, Courtois & Pétiard 1986) or shoot cultures of *Coffea* (Jouve, Engelmann & Charrier 1991) and *Costus* (Dekkers, Rao & Goh 1991). The use of controlled gaseous atmospheres has been successfully tested by Bridgen and Staby (1981) with *Nicotiana tabacum* plantlets and by Engelmann (1990) with somatic embryos of *Elaeis guineensis*.

Desiccation represents another promising approach. It was first investigated by Nitzsche (1980) with carrot calluses. Recently, McKersie *et al.* (1990) and Lecouteux *et al.* (1992) successfully stored desiccated somatic embryos of *Medicago sativa* and *Daucus carota*, respectively, for eight months.

Present development of slow-growth storage techniques

Slow-growth techniques are presently used routinely in many commercial laboratories, as well as in conservation centres for the storage of germplasm as shoot cultures. The assumption is that they are considered the best methods. However, there are no well-documented data available concerning the stability of shoot cultures or conformity to type during storage. Similarly, nothing is known of the possible selection and adaptation processes which may take place during the prolonged conservation of shoot cultures (Withers 1991). Other types of material, such as callus, can be interesting for conservation purposes, but are known to be very unstable, even under slow-growth conditions (Seitz 1987). There is, therefore, a need to develop alternative conservation techniques.

LONG-TERM STORAGE USING CRYOPRESERVATION

Technical approaches

Up until now, most plant material has been cryopreserved using classical techniques, involving a cryoprotective treatment and controlled freezing (Dereuddre & Engelmann 1987). In the past three years, new techniques such as vitrification, encapsulation/dehydration and desiccation have been developed. These facilitate the cryopreservation of numerous plant tissues (Dereuddre 1992), such as cell suspensions, calluses, meristems and embryos, which are considered separately below. The difficulty of defining an efficient cryopreservation process increases with the structural complexity and cellular heterogeneity of the material.

Cell suspensions and calluses

Cryopreservation of cell suspensions is still routinely performed in many laboratories, using or adapting the classical protocol (including pre-growth and slow cooling) proposed by Withers and King (1980), although simpler freezing techniques can be developed in particular cases (Tessereau *et al.* 1990). Similar techniques, derived from those used with cell suspensions, can be applied to calluses.

Meristems

Meristems are very complex structures: consequently, the application of standard techniques generally leads to poor and non-reproducible results. Dramatic improvements have now been made using vitrification and encapsulation/dehydration (Dereuddre 1992). During the vitrification procedure, the experimental conditions induce the formation of an amorphous glassy structure which replaces the intracellular water, thus avoiding the detrimental formation of ice crystals which can disrupt cellular structure. Vitrification has been notably applied recently to different cultivars of *Malus* and *Pyrus* meristems (Niino *et al.* 1992). However, the high toxicity of the cryoprotective substances employed may reduce the routine application of this technique.

Encapsulation/dehydration uses synthetic seed technology, encapsulating the structure to be frozen in an alginate bead which protects it during the successive steps of the cryopreservation procedure. This approach seems the most promising in the case of meristems, and has enabled high survival rates with shoot tips to be obtained repeatedly, notably with *Pyrus* (Dereuddre *et al.* 1990), *Vitis* (Plessis, Leddet & Dereuddre 1991) and *Eucalyptus* (Monod *et al.* 1992). Finally, partly desiccating stem segments of *Asparagus* allowed them to withstand freezing in liquid nitrogen (Uragami, Sakai & Nagai 1990)

Embryos

Zygotic and somatic embryos also represent complex structures for cryopreservation. For these tissues, especially somatic embryos, the freezing procedure consists of the classical technique. A simpler process, involving desiccation followed by rapid freezing, is mainly used for zygotic embryos. A combination of both methods is used in particular cases. The cryopreservation of woody plant embryos has been applied to a wide range of species (see review by Engelmann 1992) and most recently to zygotic embryos of *Coffea* (Normah & Vengadasalam 1992; Abdelnour-Esquivel, Villalobos & Engelmann 1992) and *Citrus* (Normah & Hamidah 1992).

In summary, cryopreservation techniques have now been developed for a wide range of species, including many tropical crops (Engelmann 1991b). However, these techniques have only rarely been applied to these crops. One successful example concerns the cryopreservation of somatic embryos of around 150 oil palm clones (Engelmann 1991c).

CONCLUSIONS

In vitro conservation techniques for the safe storage of plant germplasm have become technically more feasible, particularly as a result of recent progress in cryopreservation. However, for many tropical tree species, there are several prerequisites which have to be fulfilled before the application of cryopreservation techniques is possible. A minimal knowledge of the biology and physiology of the species to be conserved is needed in order to define the necessary *in vitro* culture conditions. Moreover, the germplasm must be evaluated, in order to store a representative sample of the genetic variability of the species. Finally, practical problems such as the provision of minimal tissue culture facilities, trained personnel, etc, have to be overcome in order to apply these techniques in many tropical countries. In the near future, efficient techniques for the reliable storage of tropical tree germplasm should be developed with the continuing efforts of various international institutes.

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Capture of genetic resources by *in vitro* culture: field evaluation and precocious flowering

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ABSTRACT

Clonal propagation using either plant tissue culture or rooted cuttings can now be achieved with several species. This paper deals with results obtained under two tissue culture programmes initiated in our laboratory on propagation and field evaluation of different tree species. The objectives under these programmes were to capture the maximum gains in biomass production and timber quality, utilising explanted material from proven mature trees of *Eucalyptus* spp. *In vitro* precocious flowering in bamboos was an additional method employed to reduce conventional regeneration cycles, and increase the rate of genetic improvement. Field trials have been conducted at several locations and growth rates evaluated over periods ranging from two to ten years. In general, plantlets derived from tissue culture showed a high degree of uniformity, with an increased biomass capacity compared to seedlings. The advantages of *in vitro* culture methods are discussed in the light of these results.

INTRODUCTION

The world consumption of wood today is around 3 billion tonnes, nearly half of which is used as fuel. The total wood consumption is more than that of steel and plastics combined, and in another decade the world's population will be using over 4 billion tonnes of wood annually. The total forest loss on the earth is over 12 Mha every year, which is roughly the area of England. To meet the increasing demands for forest raw materials in India, emphasis has been laid on increasing the productivity of our forests from the present low average yield of 0.5 m^3 ha^{-1} yr^{-1}. This increase is being planned through rational land policies, technological innovation and improved management. Tree improvement programmes for the genetic improvement of planting stock are also being introduced by several forestry-based companies to increase productivity. These programmes involve:

- raising seedlings only from selected mother trees;
- producing clonal planting stock of selected plus-trees, through the conventional rooting of cuttings or by micropropagation;
- creating seed orchards for the production of plants which combine the selected traits from the best parents and show high vigour at the nursery stage; and
- applying and integrating biotechnological methods (Cheliak & Rogers 1990).

Considerable progress has been made over the past two decades in developing tissue culture methodologies from explants of juvenile and mature trees for industrially important species, and applying them to forestry (Mascarenhas *et al.* 1988; Dunstan 1988; Mascarenhas & Muralidharan 1989). An integrated approach to reforestation involving the application of clonal techniques offers a realistic hope for enhancing forest production. However, the success of such an approach is limited by the efficiency with which selected trees can be reproduced vegetatively and by the high production costs of such plants, relative to likely gains. Woody species in the juvenile phase are generally easy to clone from embryos and young seedlings via conventional vegetative methods and micropropagation (Whitehead & Giles 1977). However, the ease of propagation tends to decline as trees mature to a stage where a more reliable evaluation of their crop potential can be made. This problem is especially serious in plants whose cuttings are difficult to root by conventional means. In such cases, tissue culture can be extremely useful for the production of clonal material for testing and/or the establishment of clonal germplasm banks.

A large number of tropical tree species have now been propagated *in vitro* using juvenile tissues (eg *Khaya ivorensis* and *Nauclea diderrichii*; see Newton *et al.*, pp256–266). More recently, a few species have been cultured following rejuvenation of the trees by special treatments such as *in vitro* subculturing (Von Arnold, Clapham & Ekberg 1990), and spraying with benzyl amino purine (BAP), eg *Eucalyptus ficifolia* (Magalewski & Hackett 1979). Similar effects can also be obtained by serial rooting or grafting on juvenile rootstocks (Franclet *et al.* 1987) and by repeated hedging (Campinhos &

Ikemori 1983). These latter methods are time-consuming and may be more expensive than rejuvenation induced by *in vitro* subculture.

In addition to developing the procedures for micropropagation, there is now an increasing awareness of the importance of the field evaluation of plants raised *in vitro*. However, the number of reports on such studies is limited and, with a few exceptions (Table 1), examples are confined to a few temperate coniferous (Frampton & Amerson 1989; Horgan & Holland 1990; Ritchie & Long 1986) and broadleaved tree species (McCown & Amos 1979).

Table 1. Observations from field evaluation of micropropagated tropical trees. The list is not comprehensive

Tree species Source of explant	Observations	Reference
Dendrocalamus strictus (bamboo) Seedlings	Early culm formation Number of culms higher	Mascarenhas *et al.* (1988, 1989) Ramanuja-Rao & Rao (1990) Mishra *et al.* (1990)
Eucalyptus spp. Mature trees	Increased early growth rates in some clones Uniformity	Khuspe *et al.* (1987) Mascarenhas *et al.* (1988, 1989) V Patil & T N Bhandari (personal communication)
Hevea brasiliensis Seedlings and mature trees	Higher growth rates	M P Asokan & M Sethuraj (personal communication, 1992) M P Carron (personal communication 1992)
Tamarindus indica (tamarind) Seedlings	Early flowering Uniformity	Mascarenhas *et al.* (1988, 1989)
Tectona grandis (teak) Mature trees	Increased early growth rates	Mascarenhas *et al.* (1988, 1989)
Populus deltoides Seedlings	Higher growth rates	H C Chaturvedi (personal communication, 1992)

This paper is restricted to the results of field evaluation studies conducted on tissue culture propagules obtained from: (i) mature trees of three *Eucalyptus* species which are important for rapid production of woody biomass and also, in some species, for their oil, and (ii) seedlings of bamboo (*Dendrocalamus strictus*). Studies carried out on the *in vitro* precocious flowering and seeding of bamboos as an alternative method of propagation are also described.

CULTURE PROCEDURES

The experimental culture procedures followed to induce, grow and multiply roots and shoots from trees of *Eucalyptus tereticornis*, *E. torelliana* and *E. camaldulensis* and from *Dendrocalamus strictus* (bamboo) seedlings have been described in earlier publications (Gupta, Mascarenhas & Jagannathan 1981; Gupta, Mehta & Mascarenhas 1983; Gupta & Mascarenhas 1983, 1987; Nadgir *et al.* 1984). The ages of the *Eucalyptus* trees from which vegetative buds were collected for initiation of cultures were between ten and 20 years. Both apical and axillary buds were collected from the crown regions of the trees. The rooted plantlets or microcuttings of both *Eucalyptus* and *Dendrocalamus* were transferred to polyethylene bags (2.5 cm diameter x 10 cm height), containing autoclaved sand, and placed in a greenhouse maintained at 30°C with a relative humidity of 80–90%. On attaining a height of 10 cm, they were transferred to larger bags (10 cm x 20 cm) containing river sediment, and further incubated in the greenhouse until their transfer to different locations for the establishment of field trials.

FIELD EVALUATION OF *EUCALYPTUS*

Seedlings *versus* clones: field trials of *E. tereticornis* and *E. torelliana*

Individual trees were selected on the basis of their phenotypic traits (an apparent rate of biomass production ten times higher than the average) in forest plantations. Clones were subsequently produced by tissue culture methods, and then grown on a pilot scale (30 trees) in Pune, Maharashtra, India, in 1983. The clones were compared with plants raised from seed according to a non-replicated experimental design described previously (Khuspe *et al.* 1987). Plants of both species grown from tissue culture showed height, diameter and biomass values higher than control plants over the first few years. With *E. tereticornis*, the biomass yields of tissue-cultured plants at 12, 34 and 52 months were 220%, 60% and 16%, respectively, higher than controls (Table 2). After the same time intervals, the biomass yields of *E. torelliana* were 900%, 115% and 105% higher than controls, respectively (Table 3). After 84 months' growth of *E. torelliana*, biomass yield was reduced below that of the seedling controls, while in *E. tereticornis* yields remained higher than controls even after 108 months. Density of the wood at 52 months was similar to that of six-year-old seedlings (Mascarenhas *et al.* 1988).

These clones did not achieve growth rates to match their estimated (ten-fold) superiority, except perhaps during the first few months, when, in addition to culture conditions, many other factors, such as acclimation (Boulay 1987), planting stock, size at planting, etc, would have a major effect. It could be argued that these plus-tree tissue-cultured plants were genetically superior to the control seedlings, but that this advantage was lost owing to the onset of earlier maturation. In this study, the tissue-cultured plants started flowering after 24 months, when 3 m tall, whereas the seedlings did not flower until they were 42 months old. However, the general morphology of the plantlets resembled that of seedlings with respect to colour and shape of leaves, stem growth, branching habit and canopy. This study demonstrates the difficulties associated with phenotypic plus-tree selection for fast-growing clones, and emphasises the need for proper genetic testing in clonal trials before selecting superior material for multiplication by tissue culture.

Table 2. Growth and biomass evaluation of *Eucalyptus tereticornis* plants produced by tissue culture (TC) (average based on 30 plants)

Location	NCL, Pune
Planting date	July 1982
Flowering date	TC – July 1985 Control – January 1987
Observation date	July 1992

Age	Height (m)		Diameter at breast height (cm)		Biomass plant^{-1} (kg)	
(months)	TC	Control	TC	Control	TC	Control
12	6.0	3.9	4.5	4.6	1.6	0.5
34	8.2	6.8	6.9	5.0	4.8	3.0
52	10.3	8.5	9.4	8.3	18.5	16.0
84	11.5	10.8	9.6	8.7	53.4	37.1
108	12.9	11.6	11.0	9.9	83.4	65.0

Table 3. Growth and biomass evaluation of *Eucalyptus torelliana* plants produced by tissue culture (TC) (average based on 30 plants)

Location	NCL, Pune
Planting date	July 1982
Flowering date	TC – July 1985 Control – January 1987
Observation date	July 1992

Age	Height (m)		Diameter at breast height (cm)		Biomass plant^{-1} (kg)	
(months)	TC	Control	TC	Control	TC	Control
12	5.8	1.1	4.8	2.5	2.0	0.2
34	8.9	6.0	7.4	6.0	6.7	3.1
52	11.3	8.6	8.6	6.9	42.5	20.7
84	13.0	11.9	9.1	9.1	55.7	49.0
108	13.2	12.8	10.1	10.1	68.8	80.3

Clone/site interaction in field trials of *E. camaldulensis*

Clones from four candidate trees of *E. camaldulensis* (R–6, ERK–4, APFDC(R–5) and NSPR, collected from Andhra Pradesh) were grown in a replicated trial to compare the growth performance of different clones. The candidate trees ranged from ten to 20 years old, and were 13–22 m tall with girths of 30–65 cm. The trial was conducted at Nasik, India, in April 1991 and replicated at six other sites (Table 4). Seed-raised plants were used as controls. Rooted plantlets were potted and repotted in December 1990 and February 1991, respectively, then planted out in April 1991. Maximum increases in height and girth measurements were observed in clone ERK–4 followed by R–6 and APFDC (R–5) (Table 4). The uniformity in height and girth measurement was also striking. Clone NSPR displayed very poor growth. These results clearly demonstrate the importance of testing a range of different clones. At other locations (Pune and Tirupati), ERK–4 was also the clone which displayed the highest growth rate. Assessment of the growth performance of these plants over a longer period will be necessary to arrive at more definite conclusions about their relative performance.

Table 4. Comparative field trial of four clones of *Eucalyptus camaldulensis* produced by tissue culture

Location:	Kundewadi, Nasik, MS
Nos of replications	4
Nos of plants/replication	16
Planting date	April 1991
Observation date	May 1992

Treatments	Height (m)	Girth (cm)
R-6	2.6	8.8
ERK-4	3.7	11.7
NSPR	1.2	–
APFDC(R–5)	2.5	7.8
Control	2.1	7.3
SE	±0.2	±0.1
CD (5% level)	0.6	0.4

Effects of subculturing tissue-cultured clones from mature *Eucalyptus* trees

In this study, plant propagules were produced from one elite tree of both *E. tereticornis* (Clone T–8) and *E. camaldulensis* (Clone R–3) after different numbers of subcultures. Ten plantlets were field-grown at each subculture to test whether any significant differences occurred in growth performance. In *E. camaldulensis* and *E. tereticornis*, plants were tested from the fourth to seventh and ninth to eleventh subcultures, respectively. A striking uniformity was seen between subcultures (Table 5) in both species

Table 5. Effect of number of subcultures on growth of micropropagated *Eucalyptus camaldulensis* and *E. tereticornis* plants (average based on ten plants)

Location	NCL, Pune		
Age of plants:	36 months		
Subculture number	Height (m)	Girth (cm)	Biomass plant^{-1} (kg)
E. camaldulensis			
4	8.2	15.5	10.5
5	8.1	15.8	10.4
6	8.2	15.5	10.4
7	8.2	15.3	10.2
E. tereticornis			
9	6.5	12.5	5.2
10	6.6	13.4	5.9
11	6.5	12.5	5.2

after 36 months' field growth. This experiment highlights the possibility of utilising plantlets from repeated subculture. In *Eucalyptus* this is an important factor because initiation of fresh cultures from mature trees is beset by two major problems: (i) the very low percentage of buds sprouting even in the best seasons, and (ii) the long initiation period with primary explants. These results indicate that multiplication in the laboratory can be carried out throughout the year without any seasonal influences on culture initiation or field performance. No evidence was found in this study for rejuvenation by serial subculturing.

Mature clones of *E. citriodora* for essential oil production

Eucalyptus citriodora is important for its foliar oil, which is used in the cosmetic and pharmaceutical industries. The important ingredients of the oil are citronellal (90–95%) and citronellol (5–10%). The oil content varies from 0.5% to 4% in the green leaves in different trees, suggesting the immediate application of vegetative methods of propagation and clonal selection (Gupta & Mascarenhas 1987) to capture this variation. Tissue-cultured plants were raised from a 20-year-old parent tree containing high concentrations of oil and citronellal, and growing at an altitude of over 2000 m in Ootacamangalam, Tamil Nadu, in the south of India. The regenerated plants were grown at Pune, Maharashtra, India, and the oil and its ingredients were analysed when the plants were one and three years old, as described by Gupta and Mascarenhas (1983). The concentrations of oil (3.5%), citronellal (90.0%) and citronellol (5.0%) in one- and three-year-old micropropagated plants were more or less similar to those of the parent tree. These results indicate the advantages of tissue-culturing mature trees to obtain early returns in one-year-old plants. Seedling plants take three to four years before the oil contents stabilise. The micropropagation of elite trees, therefore, has great potential for high value chemical production (Mascarenhas *et al.* 1988).

Early flowering in micropropagated *E. tereticornis*

Plantlets were produced from an elite tree, K(1)–37 of *E. tereticornis*, collected from Shimoga (Karnataka), India, and planted at two locations, Neyveli and Pune, India. The heights of tissue-cultured plants after 13 months at Pune were significantly greater than those of control seedlings (121 *versus* 80 cm; P). Similar growth rates were observed at Neyveli. Interestingly, these plants flowered within six months after planting, at both Pune and Neyveli. Although early flowering has been recorded in tissue-cultured plants, the reason why this phenomenon occurred only in clone K(1)–37, 18 months after transfer to polythene bags, is unclear, and is currently being investigated. In order to determine whether soil factors influenced flowering, soil samples from Neyveli were compared with samples collected at Pune using the analytical methods of Perur *et al.* (1973). The main difference observed was the higher potassium content of the Pune soils.

The time required for forest trees to reach sexual maturity has implications for the breeding, selection and propagation stages. In the former, the major influence is the time of first flowering and, consequently, the time required to provide the next generation in the breeding programme. In the latter, if propagation is to be *via* the sexual process, then not only is the initiation of flowering important but so are the consistency and scale of flowering (Cheliak & Rogers 1990).

The treatments to promote flowering in forest trees include drought, root pruning, girdling, high temperature, and the application of nitrogen fertilizers and appropriate external growth regulators, such as gibberellins. There is some evidence that flowering can be initiated earlier through *in vitro* culture. For example, Hackett (1983) reported that somatic embryos derived from callus from roots of mature *Panax ginseng*, and from the callus of zygotic embryos of date palm flower in the embryoid stage, whereas sexual embryos do not flower for several years. McKeand (1985) reported that two-year-old tissue-cultured plantlets of *Pinus taeda* grown in the field exhibited high growth rates and morphological characters typical of mature trees. This result was not expected as the plantlets originated from juvenile embryonic tissues. As mentioned earlier, the causes of the early flowering response in *Eucalyptus* in the present studies could be attributed to the origin of the explants from mature trees, but it is also possible that flowering was promoted by the ingredients present in the culture medium.

FIELD EVALUATION OF MICROPROPAGATED *DENDROCALAMUS STRICTUS* (BAMBOO)

A number of bamboo species flower gregariously and unpredictably. Most bamboo species are monocarpic, ie they flower once before culm death (McClure 1966). The production of seed in bamboo is irregular because, in the majority of species, flowering cycles range from four to 120 years (Janzen 1976). Most bamboo species have considerable economic and social importance. Some of the best qualities of paper are produced from bamboo. Throughout Asia and other tropical regions, bamboo is a vital source of lightweight rot-resistant wood used in the construction of houses, furniture, tools, baskets and other household items. Bamboo hay, which has four times the protein of other fodder grasses, is a staple for livestock.

Bamboos are propagated by seed or vegetatively. Conventionally, offsets, rhizomes, cuttings or layering have been used for this purpose (Seethalakshmi, Venkatesh & Surendran 1983; Banik 1985) and have given successful results. Micropropagation methods through organogenesis, from embryonic tissue and seedlings, have also been developed recently (Ramanuja-Rao & Rao 1990; Mascarenhas *et al.* 1990; Nadgir *et al.* 1984; Yeh & Chang 1986a, b, 1987).

In our laboratory, bamboo plantlets were raised by tissue culture using the procedures of Nadgir *et al.* (1984) and Mascarenhas *et al.* (1990). The cultures were isolated from germinated seedlings. The plantlets were grown in a greenhouse, as described for *Eucalyptus* above, and planted out at Pune, India, in August 1990, using a paired plot design with 16 replications. Significantly increased heights and culm numbers were observed after 16 months. Mishra, Nair and Vidya-Sagar (1990) reported the results of a similar trial conducted at Kumarapatnam, Karnataka, India, with plants collected from our laboratory. The increase in height of cultures and rate of culm production was 20% and 75% respectively, compared with plants raised from seed as controls.

The results of these two experiments indicate the importance of micropropagation in bamboo for obtaining earlier and higher growth rates both in culm formation and in the number of culms. The gestation period of about two years for plants of seed origin can be reduced to six or seven months using tissue-cultured plants (Mishra *et al.* 1990). Moreover, multiplication of plants can be carried out all year round within the confines of a laboratory and need not be determined by the long and unpredictable flowering cycles in this species. Micropropagation can be used to produce sufficient planting material between the flowering cycles when seed is scarce.

Natural stands and plantations of bamboos derived from seedlings show considerable variation, unlike clonally propagated plantations. The totally solid culms of some *D. strictus* clumps fetch much higher prices than hollow ones. It is not known whether this unusual trait is under genetic or environmental control, or both. Even if it proves to have low heritability, by selection and clonal propagation it should be possible to increase the frequency of solid culms in a clump.

There are several examples of spontaneous mutants produced in different bamboo species. Thornless mutants of normally thorny species are known to occur in *Bambusa arundinacea* of India and *Guadua angustifolia* of tropical America. In *B. vulgaris*, culm colour variations are also known. Clonal multiplication by tissue culture, if possible with these species, has great potential for multiplying such selections (Venkatesh 1992).

IN VITRO FLOWERING AND SEEDING IN BAMBOOS

In vitro flowering experiments

In India, the mast flowering cycle for *Ochlandra travancorica* (Venkatesh 1984) is seven years, for *Bambusa arundinacea* 30–40 years, and for *Dendrocalamus strictus* 20–65 years. This infrequent flowering at long intervals has been a major obstacle for the genetic improvement of bamboo by conventional breeding. The Forest Research Institute of Guangdong province in the People's Republic of China has recently produced several artificial interspecific and intergeneric bamboo sexual hybrids by making opportunistic crossings with sporadically flowering clumps of the different species of bamboo (Zhang & Chen 1985). This chance crossing, however, is not as useful as a controlled breeding programme would be.

In our laboratory, using tissue culture techniques, we have recently succeeded in inducing precocious flowering and normal seed setting of three Indian bamboos: *Bambusa arundinacea* and *Dendrocalamus brandisii* (Nadgauda, Parasharami & Mascarenhas 1990), and, more recently, D. strictus. In brief, the steps followed for obtaining flowering and seeding in these species are as follows.

i. Seedlings of the species are raised on White's medium.

ii. Excised seedling segments are transferred to Murashige and Skoog's liquid medium with

BAP and coconut milk (MS–1) for initiation of shoot cultures and for the first three subcultures.

iii. After three passages on the above medium, vegetative shoots develop an inflorescence containing panicles of normal spikelets in 70% of *B. arundinacea* and 40% of *D. brandisii* shoots.

iv. On separation of inflorescence segments and subculture to MS–1 medium, they multiply, giving rise to an inflorescence culture for repeated seed production.

v. In 30–50% of the cultures, seed set was observed with viability of 3–5%.

Recently, the *in vitro* flowering of *D. hamiltonii* has also been reported (Chambers, Heuch & Pirrie 1991). These preliminary results suggest an alternative approach for obtaining a continuous year-round supply of seed, provided the extent of seed production and seed setting can be increased.

The causes of low seed set in bamboo raised *in vitro*

In order to determine the cause for the low seed setting in the flowers of bamboo species raised *in vitro*, experiments were carried out with *Bambusa arundinacea*. This species had flowered extensively at Pune and so allowed a comparison of morphology and pollen fertility of flowers raised *in vivo* and *in vitro*. Pollen fertility was determined by following Alexander's staining procedure (Alexander 1969). Floral parts of flowers raised both *in vivo* and *in vitro* were complete. However, the opening of tissue-cultured flowers was only partial; in 60–70% of the flowers, the lemma and palea were closed. Anthesis and pollen fertility in flowers raised *in vivo* were almost 100%, compared to the very low values for flowers raised *in vitro*. These preliminary data suggest an explanation for the low fertility of flowers produced *in vitro*. Moreover, it is also reported that *in vivo* the stigmas are receptive before pollen production in some bamboo species. This characteristic could explain the outcrossing that is assumed to occur.

The main goal of flower induction technology is to provide flowering on demand, with consistency and predictability. In the bamboos, this is extremely important because of their long vegetative phase before flowering and seeding, and the difficulties associated with their vegetative propagation. The discovery of a means to stimulate precocious flowering and seeding in four bamboo species opens up the prospect of:

- controlled breeding by a systematic intercrossing between different species to produce intraspecific or interspecific hybrids with desirable characteristics;
- continuous supplies of bamboo seeds for planting during the long inter-mast periods where seed is scarce (this method can be combined with micropropagation procedures);
- the continuous availability of anthers (pollen) for production of haploids;
- studies of the mechanisms for the unpredictable flowering of bamboos, and of their reproductive development.

By inducing synchronous flowering and seeding, it will be possible to apply conventional breeding and hybridisation procedures to the genetic improvement of bamboos.

CONCLUSIONS

Modern agricultural techniques require crop uniformity. Plants of the same height make for the easier placement of agricultural chemicals and for weeding by machines. Crops which mature at the same time with uniform fruit or cob size facilitate machine harvesting or plucking. In the limited number of field tests reported to date, the morphological appearance and the performance of micropropagated plants of forest tree species have varied considerably from species to species. Results with *Eucalyptus* species and *Dendrocalamus strictus* are similar to some of the results obtained with other species, and are marked by a higher degree of uniformity with a rapid early growth rate. As has been observed in our studies, it seems feasible to increase the productivity of forest lands before the trees reach their biological limits. Although micropropagation may not be justified immediately for producing millions of plants by organogenesis, at a low unit cost it still has the following genetic and economic advantages:

- the exploitation of the early flowering behaviour of superior mature trees to capture their general combining ability for mating at random in a seed orchard (in this way superior individuals could be bred within a shorter period);
- the production of plants in very high numbers and within shorter timespans than is possible by conventional vegetative propagation methods;
- increased gains in biomass per tree (however small, these can result in highly significant absolute gains when the annual planting numbers are considered).

In India, the forestry plantation programme involves several million *Eucalyptus* plants annually. With a regeneration programme of this magnitude, even small gains per tree represent significant absolute gains. To capitalise fully on clonal forestry there must also be a means of conserving germplasm, ensuring that it is maintained in a state capable of subsequent propagation for a length of time commensurate with its field testing regime (see Engelmann, pp49–52).

Bridging the widening gap between supply and demand of firewood, timber and raw materials for pulp and fibre is possible only through well-conceived, highly efficient production technologies, involving high-yielding certified planting stock, under the aegis of agroforestry and industrial forestry programmes. Although our results already indicate the possibility of obtaining higher gains in biomass in *Eucalyptus* and bamboo, there are several other factors which have to be studied in far greater detail. The factors which influence field performance of micropropagated plants can be summarised as:

- culture conditions involving origin of explants, period in culture, etc;
- greenhouse and ultimately agroclimatic conditions in which the propagules are planted; and
- the agricultural practices adopted.

These factors, individually or in combination, can raise the biological limits of productivity in genetically superior planting stock, and ensure sustainability.

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Capture of genetic resources by collection and storage of seed: a physiological approach

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ABSTRACT

Seed provides the most natural vehicle for the collection, transport and storage of genetic variation, often avoiding the technical difficulties and expense inherent in other methods. Consideration is given to the advantages and limitations of using seed, with examples drawn from the Meliaceae, Dipterocarpaceae and Araucariaceae families. The importance of placing seed into desiccation-intolerant ('recalcitrant') or desiccation-tolerant ('orthodox') storage physiological categories is emphasised, and progress in this regard is reported. Handling procedures to ensure maximum viability for the two types are discussed in relation to moisture content, temperature and gaseous factors. It is concluded that long-term conservation of some tree species as seed is a feasible strategy, but that other species may require further research to ensure maximum viability at harvest and greatest possible longevity in storage. Achievement of high initial viability will compensate for the shorter natural longevity of tree seed compared with seed of herbaceous crop species.

INTRODUCTION

Relevant general articles on seed storage include those by Bonner (1990), Stubsgaard (1992), Willan (1985) and De Muckadell and Pilim (1983). The present paper is based mainly on personal experiences of the author. The term 'seed' is used herein to encompass fruit. Availability, collection and storage topics are covered, with the emphasis on physiological rather than genetic aspects; sampling strategies have been considered by Turnbull (1978) and by Willan, Hughes and Lauridsen (1990).

'Orthodox' and 'recalcitrant' seed types

A consideration of supreme importance in deciding practical handling methods is the storage physiological category of the seed; 'orthodox' seed can be stored dry and cold, whereas 'recalcitrant' seed cannot be dried to low moisture contents without loss of viability and so must be stored moist (Roberts 1973). Orthodox seeds tend to be small and are produced on both woody and herbaceous species; recalcitrant seeds are generally large and are found mainly, if not exclusively, on woody species. Assessment of storage type is accomplished by determining the relationship between germination and moisture content, preferably using several desiccation methods; misclassification can occur if detailed studies are not carried out. Recalcitrant seed cannot be stored for long periods so cannot be considered as a means for genetic conservation. Seed of orthodox species can be stored for much longer, and its use in conservation is discussed below.

Percentages of species possessing recalcitrant seeds are 35%, 94% and 33% in the Meliaceae (Table 1), Dipterocarpaceae (Tompsett 1992) and Araucariaceae (Table 2), respectively, for those members examined so far; the percentage with recalcitrant seed for all three families combined, calculated by pooling all data in the above sources, is 72%. The extent to which this small sample represents woody species as a whole is hard to assess. However, the probability that there is a large percentage of recalcitrant-seeded species in rainforests, combined with the known high species density in these forests, indicates that this figure may not be entirely unrepresentative.

Recently, a third 'intermediate' type of seed storage physiology has been proposed, which has desiccation characteristics intermediate between those of the orthodox and recalcitrant types (Ellis, Hong & Roberts 1990, 1991). In addition to the partial desiccation tolerance exhibited by this category, three further differences relating to dry seed were reported to differentiate it from the orthodox type: cool temperatures near 0°C were more damaging than warm temperatures; freezing temperatures were likewise more damaging than warm temperatures; and, within a range extending approximately from 5% to 10% moisture content, the usual improvement in longevity observed on drying orthodox seed was reversed. The question of whether this new category is physiologically distinct from the orthodox type is considered later in relation to earlier research on *Araucaria columnaris* (Tompsett 1984b).

Table 1. Lowest-safe moisture contents (LSMC), mass values and optimum recorded storage conditions for Meliaceae seed; storage temperatures, and moisture contents are given with the best final germinations (germ.) achieved. Seeds were supposed mature. Mass is that at or near LSMC. Authorities are those of Pennington and Styles (1975) for subfamilies, tribes and genera (data are those of P B Tompsett (unpublished) unless otherwise stated)

	Orthodox or recalcitrant	Lowest-safe moisture content (%)	Mass (g)	Optimum storage recorded				Comment
				Period	Temperature (°C)	Germination (%)	Moisture content (%)	
MELIOIDEAE								
i. Melieae tribe								
Azadirachta indica[1]	O	NA*	0.3	12 yr	–20	80	4	–
ii. Trichileae tribe								
Trichilia[2]								
T. monadelpha	R	38	0.3	120 d	18	50	38	Storage at 99% rh in PB*
T. megalantha	R	32	1.0	221 d	18	87	42	Storage at 99% rh in PB
T. prieureana	R	38	0.3	106 d	18	50	47	Storage at 99% rh
T. dregeana[3]	R	30	?	35 d	15	97	–	Storage at 40% rh
Pseudobersama								
P. mozambicensis	O	NA	0.1	–	–	–	–	Seed can be dried to <7% MC*
Ekebergia								
E. senegalensis	O?	NA	0.2	–	–	–	–	Seed can be dried to <19% MC
iii. Guareeae tribe								
Guarea thompsonii	R	43	2.2	44 d	18	85	50	Storage at 99% rh in PB
SWIETENIOIDEAE								
i. Cedreleae tribe								
Cedrela odorata	O	NA	0.01	369 d	2	86	4	–
ii. Swietenieae tribe								
Khaya								
K. senegalensis	O	NA	0.2	3 yr	2	81	6	–
K. ivorensis	O	NA	0.2	2 yr	2	44	6	–
Entandrophragma								
E. angolense	O	NA	0.4	150 d	2	76	5	–
E. candollei	O	NA	0.4	2 yr	2	96	4	–
E. utile	O	NA	0.3	240 d	2	92	4	–
Swietenia								
S. humilis	O	NA	0.6	2 yr	–20	93	4	–
S. macrophylla	O	NA	0.5	2 yr	–20	100	5	–
iii. Xylocarpeae tribe								
Carapa procera	R	<34	10.4					
		>16		–	–	–	–	No viability at 16% MC

*NA, not applicable; PB, ventilated polythene bags; MC, moisture content

[1] P B Tompsett, K Manger & R D Smith (unpublished)

[2] Arils removed before testing or storage

[3] Choinski (1990)

The need for tree seed conservation

The seed stores currently existing in forestry and allied institutions provide material for breeding and plantation programmes in the short to medium term. Long-term tree seed storage facilities, as employed for the conservation of herbaceous crop species, are almost non-existent. Physiological studies have revealed that, on average, tree seed appears to possess an inherently shorter storage life than crop seed; long-term storage is nonetheless feasible for at least some species. This approach is urgently needed where a species is under threat of extinction in the whole or in a part of its range, as is the case for *Entandrophragma* and *Khaya* spp. Although *in situ* conservation is the method of first choice, and *ex situ* conservation stands have been established for many species, it is recognised that other *ex situ* conservation methods should be more closely examined National Research Council 1991). The present paper considers the role seed can play in the *ex situ* conservation and utilisation of tropical trees.

Table 2. Lowest-safe moisture contents, mass and optimum recorded storage conditions for Araucariaceae. All details except those concerning taxonomy are as in Table 1. Genera and species sections are given for *Araucaria*. Germinations are not adjusted for percentage empty seed, which averages over 50% in orthodox species (data are of P B Tompsett (unpublished) except where otherwise stated)

	Orthogonal or recalcitrant	Lowest-safe moisture content (%)	Mass (g)	Optimum storage recorded			
				Period	Temperature (°C)	Germination (%)	Moisture content (%)
ARAUCARIA							
i. *Eutacta*							
A. montana	O	c12	0.30	80 d	2	17	15
A. cunninghamii[2]	O	<2	0.15	8 yr	−15	43	Air dried
A. rulei	O	c12	0.32	80 d	2	9	<9%
A. nemorosa	O	c12	0.54	80 d	2	16	15
A. scopulorum	O	c12	0.27	80 d	2	23	12
A. heterophylla	O?	c12	1.42	–	–	–	–
A. columnaris	O	c12	0.41	8 yr	−20/−70	12	7
ii. *Intermedia*							
A. husteinii	R	32	0.54	80 d	6	80	45
iii. *Columbea*							
A. angustifolia	R	37	4.74	496 d	2	67	43
A. araucana	R	38	3.25	961 d	2	88	44
iv. *Bunya*							
A. bidwillii[3]	R	35	10.10	–	–	–	–
AGATHIS							
A. australis[4]	O	<5	–	>6 yr	6	c80	5
A. australis[5]	O	<6	–	1 yr	−10	62	10
A. macrophylla[4]	O	<13	–	>6 yr	−13	c20	7

[1] In the case of orthodox seed, some damage may occur on drying if seed is either immature or over-mature

[2] Storage data from Shea and Armstrong (1978)

[3] D Doley (personal communication)

[4] R D Smith and J B Dickie (unpublished)

[5] Preest (1980)

Objectives of seed storage studies

The objectives of seed storage studies may be viewed as two-fold:

- to improve short-term storage for maintenance of viability during transport and temporary holding for use in species trials and plantation programmes; and
- to enable long-term genetic conservation in seed form.

COMPARATIVE MERITS OF SEED AS A CONSERVATION MEDIUM

Advantages

First, seed is the natural vehicle for gene dispersal and has advantages in *ex situ* gene conservation, being immediately available for seedling production. Alternative methods, such as those involving tissue culture and pollen, require intermediate processes before seedlings can be produced. Second, for cross-pollinated species, each propagule may have a wider range of genes than vegetative material from the same tree. Third, maintaining material as seed is less expensive than other methods such as tissue culture slow growth; in addition, seed storage is genetically more stable. Fourth, conservation by pollen storage entails the uncertainties of pollination and seed production (or equivalent tissue culture procedures) before seedlings can be finally produced.

Disadvantages

The problems associated with moist storage (for example, premature germination) imply that any long-term *ex situ* conservation of recalcitrant-seeded species must probably be in forms other than whole seed. Second, for some species seed is produced only at intervals of between two and five years in any particular location, as for example in the case of rainforest dipterocarps, creating difficulties in acquiring material. Third, some orthodox-seeded species have propagules requiring particular harvesting and handling procedures to ensure successful desiccation for safe storage; such seed may include the so-called intermediate category (discussed below). With adequate research, however, the latter problems can be alleviated. Fourth, the male parent may be unknown for seed of cross-pollinating species, adding an element of uncertainty not present when vegetative materials are collected. Fifth, large-seeded species may be relatively expensive to store, because of the volume they occupy, although storage of the de-coated dry embryo may provide a cheaper alternative. Sixth, seedlots of tree species sometimes contain a high percentage of empty (embryoless) seeds; in some cases, separation from sound seed is impracticable (eg *Araucaria cunninghamii*). Finally, many tree species have special processing requirements, such as the de-pulping of drupaceous fruits (see Maghembe *et al.*, pp220–229); further research is needed to assess optimum procedures.

SEED AVAILABILITY

Periodicity of seeding

As referred to above, availability can be limited by infrequent seeding, particularly in relatively moist environments; examples are provided by *Dipterocarpus grandiflorus* and *D. retusus*. In seasonal areas, however, some seed may be produced every year, as for example with *D. intricatus* and *D. tuberculatus* in dry dipterocarp forest.

Amount of material available

When fruiting occurs it may be prolific, as with *Azadirachta indica* or *Swietenia* species, or it may be more restricted, particularly for species with larger propagules such as those of *Shorea macrophylla* (the illipe nut) or *Dipterocarpus grandiflorus*. Obtaining the required spread of genetic material can be more difficult when only a restricted quantity is available.

Crown accessibility

The large crowns of many species provide difficulties in attaining the necessary fresh, viable seeds. *Araucaria hunsteinii*, which can exceed 80 m in height, is an example of a species needing skilled collectors, leading to high cost of the seed. Seed shaken from tall trees possessing wind-dispersed seed, such as *Hopea foxworthyi*, can also provide problems, in that abscised seed may be hard to locate.

Parasite infestation

Pest problems can restrict availability. Species such as *Shorea amplexicaulis* and *Dipterocarpus tuberculatus* can have seed which approaches 100% infestation with insect larvae.

Premature abscission

Failure of the flowers or young fruit to develop may be caused by dry conditions. In addition, localised high winds associated with rainfall near the end of the hot season in Thailand have stripped *Shorea roxburghii* trees of seed; similarly, young *Hopea foxworthyi* seed has been lost during a typhoon in the Philippines in 1992.

Geographical and topographical isolation

Separation of seed sources from population centres by great distances or by physical features such as mountains or rivers can reduce availability. Collection of dipterocarps in Papua New Guinea is difficult because rugged terrain hinders the location of suitable seed-bearing trees.

SEED COLLECTION

It is not proposed to cover collection techniques in detail; information on this topic may be found elsewhere. Broadly, seed can be collected from the ground after abscission, from the crown using ground access, and from the crown by climbing. Many dipterocarps have large fruits which fall directly below the mother tree and can be easily collected from the ground. Such material, even if selected for apparent freshness, can, however, be of poor quality; crown collections by climbing are preferable. Collecting from the tree by hand picking is feasible for low branches of small individuals of *Azadirachta indica* and *Melia azedarach*. Rifles may be used to shoot down branches (Green & Williams 1969), a technique applicable for harvesting seed of trees in open habitats. Flexible saws are suitable for severing fruit-bearing branches on medium-sized trees (Robbins 1984). A recent relevant review is that of L Thomson and colleagues at the Food and Agriculture Organisation (Guarino, Rao & Reid 1993).

SEED STORAGE

Viability constants for orthodox seeds

The most important storage characteristics of orthodox seeds relate to the mathematical relationships between longevity, temperature and moisture content; these relations were originally worked out for barley (Ellis & Roberts 1980a, b). A detailed exposition of the reasoning is given in Ellis (1984). Within a range of moisture contents (lower limit 2–6% and upper limit 15–28% according to species), longevity increases in a predictable way as moisture content is reduced. In addition, for temperature within the range from about −13°C to 90°C, longevity increases as temperature is reduced, again in a predictable manner. The relationship found to fit the observed data best takes the form:

$$\log_{10}\sigma = K_E - C_W\log_{10}m - C_Ht - C_Qt^2$$

where K_E, C_W, C_H and C_Q are species constants, t is temperature in °C and m is percentage moisture content. Longevity is represented by σ, which is the reciprocal of the slope of the relationship between the probit of germination percentage and time (d) during storage. Following the work of Ellis and Roberts, this equation was shown to apply to tree seed using *Ulmus carpinifolia* and *Terminalia brassii* (Tompsett 1986a).

The most important concept on which this equation rests is the statistically normal distribution of seed deaths over time for a seedlot held under constant storage conditions. The seedlot must be homogeneous, having been collected at the same time and place and at about the same stage of maturity. A consequence of normal distribution is the existence of a sigmoid shape to the relationship between percentage germination and time; accordingly, when this relation is plotted on a scale of normal equivalent deviates (probits), a straight line is produced. The slopes of many of these probit lines must be assessed for a large number of combinations of temperature and moisture content, the results being subjected to multiple regression analysis in order to produce accurate species viability constants.

A quicker method for determining the viability constants has, however, been published (Dickie *et al.* 1990). The method uses the results from a set of probit lines determined at several moisture contents using a single high temperature for storage. The slope of $\log_{10}\sigma$ against $\log_{10}$ moisture content for this temperature is then taken as C_W, from which K_E can be derived. The values of the temperature constants, C_H and C_Q, have been found not to differ significantly among a wide range of species (Dickie *et al.* 1990), and may thus justifiably be used in conjunction with the values for K_E and C_W obtained. Most of the values for the constants in Table 3 were obtained in this way.

A fifth viability constant, K_i, represents the probit of percentage germination at the start of storage, and is a characteristic of a particular seedlot. It is important in determining the future storage life of the seedlot.

A further notable consideration is the relationship between longevity and moisture content of ultra-dry seed. It has been found that, below a moisture content of around 5%, there is a lower moisture content limit below which no further increase in longevity occurs, but no decrease is found either (Ellis *et al.* 1990).

Experimental approaches

There is not enough space to describe all materials and methods used by the author; most details can be found in the publications cited. On receipt, a new species is assessed for its seed storage physiology; desiccation for this purpose is generally achieved in a drying room

Table 3. Viability constants for seeds of ten tree species. Values in parentheses are those obtained when K_E and C_W are calculated from an experiment including very few temperatures and combined with the best available temperature constants (Dickie *et al.* 1990 describe the method)

Family/species	K_E	C_W	C_H	C_Q	Source
COMBRETACEAE					
Terminalia brassii	5.00	2.15	0.035	0.000413	Tompsett (1986)
MELIACEAE					
Swietenia humilis	5.19	2.45	0.033	0.000499	Tompsett (unpublished)
*Entandrophragma angolense**	(4.60)	(2.21)	(0.033)	(0.000478)	Tompsett (unpublished)
*Khaya senegalensis**	(4.76)	(2.15)	(0.033)	(0.000478)	Tompsett (unpublished)
ARAUCARIACEAE					
Araucaria cunninghamii	(7.49)	(3.73)	(0.033)	(0.000478)	Tompsett (unpublished)
Araucaria columnaris	(5.66)	(2.68)	(0.033)	(0.000478)	Tompsett (1984b)
DIPTEROCARPACEAE					
Dipterocarpus alatus	(5.92)	(2.69)	(0.033)	(0.000478)	Tompsett (unpublished)
Dipterocarpus intricatus	(6.18)	(2.77)	(0.033)	(0.000478)	Tompsett (unpublished)
ACERACEAE					
Acer platanoides	(7.22)	(4.23)	(0.033)	(0.000478)	Dickie *et al.* (1991)
ULMACEAE					
Ulmus carpinifolia	5.71	2.97	0.034	0.000408	Tompsett (1986a)

*Preliminary results

at 15°C and 15% relative humidity, sampling at many moisture contents. If the seed is orthodox, viability constants are then determined. The viability constants for prediction of longevity in Table 3 are based on at least four accurately determined survival curves (ie the relationships between viability and period of storage for combinations of moisture content and temperature). The value of CW is assessed using only the linear part of the relationship between $\log_{10}\sigma$ and $\log_{10}$ moisture content. The author's results for the longest storage periods achieved (Tables 1 & 2) are based on survival curves determined in hermetic dry storage for orthodox seed.

For recalcitrant seed, a range of moist storage conditions is tested. Results for seed which was subjected to weekly ventilation are presented in Tables 1 and 2; in the experiments in Table 1, a temperature of 18°C was employed, the seeds being retained in small rib-channel type plastic bags with a high volume ratio of air to seed, the bags in turn being kept in a Conviron G30 germinator at approximately 99% relative humidity. Lowest safe moisture content provides a guide for use in practice, and is defined as the moisture content below which a reduction in germinability first appears (Tompsett 1986b). The effect of gaseous environment was assessed by continuously passing the relevant moisturised gas through the seedlot to maintain a constant gas composition in the environment and constant moisture in the seed.

Assessments of relationships between relative humidity and seed moisture content at equilibrium were made with a Michell S4020 dewpoint hygrometer.

Theoretical considerations

In the following sections, consideration is given to the possibility of adapting the present short-term seed storage practice to achieve long-term storage for conservation purposes. Suitable seed moisture contents will need to be determined for this to be undertaken. The present section gives some background to theoretical considerations.

The original research contributing to the predictive viability equation above was conducted using conventional moisture content assessment to represent the water status of seed. However, a more accurate measure of seed water status in relation to physiological activity is seed water potential, which is in turn related to the relative humidity producing, at equilibrium, the moisture content under consideration. These relationships have been considered in connection with storage life by Roberts and Ellis (1989). The reason why relative humidity is of importance may be illustrated by considering the influence on longevity of the reserves in an oily seed. For a species with an oil content of 50%, ageing-associated physiological responses would be predicted at a moisture content which is about half the moisture content for the same responses in a non-oily seed, provided all other factors are identical; this is because of the hydrophobic nature of the oily reserve. The relative humidity value at equilibrium, however, would be expected to be similar for the seed of both species for the same predicted physiological responses. Other chemical factors besides oil content may affect the relation between moisture content and relative humidity at equilibrium. Appreciation of the involvement of oil, however, may help understanding of why different moisture contents were selected for inclusion in the calculations contributing to Table 4; *Swietenia humilis* and *Araucaria cunninghamii* have oily embryos, whereas those of *Dipterocarpus alatus* are starchy (P B Tompsett, unpublished), so it is not surprising that optimum longevity tends to be at relatively low moisture contents for the former, compared with the latter. The moisture content values used in Table 4 for *S. humilis*, *A. cunninghamii* and *Ulmus carpinifolia* are based on the author's unpublished work and represent the lowest moisture contents at which the linear relation between $\log_{10}\sigma$ and $\log_{10}$ moisture content applies; equilibrium relative humidity of *U. carpinifolia* at this moisture content is about 6%. The 7% moisture content value for *Dipterocarpus alatus* was chosen because it has proved difficult to dry the seed further at normal temperatures.

Both orthodox and recalcitrant seeds of Meliaceae and Dipterocarpaceae are susceptible to chilling damage below about 16°C when they are moist (P B Tompsett, unpublished), so care must be taken to avoid subjecting seed of either type to low temperatures at high moisture contents.

The genetic stability of material stored as seed has not been found to be a severe problem for lettuce (Rao *et al.* 1987), but research to assess genetic changes in stored tree seed would be advantageous. Storage at subzero temperatures of dry orthodox seed should enable seed to survive over long periods. The question whether temperatures much below −13°C convey significant benefit requires further attention; Tompsett (1986a) found similar longevity for *Ulmus* seed stored at −13°C and −75°C.

ARAUCARIACEAE

The Araucariaceae family contains the two genera *Araucaria* and *Agathis*.

Desiccation tolerance and mass

Desiccation experiments summarised in Table 2 have indicated that there are at least six orthodox- and four recalcitrant-seeded *Araucaria* species (Tompsett 1982, 1984a). The small seed of *A. cunninghamii* (mean 0.15 g dry mass) could be dried to 2% moisture content without loss of germinability. The medium-sized seed of five New Caledonian species (mean 0.35 g dry mass) could be dried to about 12% moisture content, and those of four recalcitrant species (mean 4.7 g dry mass) to a mean 35% moisture content. One species, *A. heterophylla*, remains of uncertain type.

At first, the intermediate desiccation tolerance of the New Caledonian species casts doubt on the storage physiology category of this seed. However, subsequent studies on *A. columnaris* clearly showed the usual relations among longevity, moisture content and temperature; for this reason, a decision was taken not to create a new storage category (Tompsett 1984b). A sudden drop in viability on placing dry material in freezing temperatures was indeed observed, but this drop may have been due to the presence of small proportions of seed in the seedlots which were at an above-average moisture content and which were unable to survive freezing. This explanation is supported, first, by the absence of any further loss over a 20-month period of subsequent storage and, second, by the fact that the driest seed sustained no loss of viability on freezing. Seed of *Agathis australis* has similarly been found to suffer a loss of some viability on drying to 5% moisture content (R D Smith & J B Dickie, unpublished).

Seed longevity

Orthodox *Araucaria* seeds are relatively long-lived (Table 2) (Tompsett 1984a). Seed of *A. cunninghamii* has been stored for 12 years with little viability loss (P B Tompsett, unpublished). The seed is predicted to remain at above 85% viability (on a full-seed basis) for over 3000 years, provided initial viability is 99.4% (Table 4) and ideal conditions are maintained. Relatively great longevity is suggested by the K_E and C_W constants in Table 3; these figures are relatively high for *A. cunninghamii* with the consequence that, if all other factors in the above equation are constant, a relatively greater longevity is achieved for this species than for all others in the list, except *Acer platanoides*. In general, either K_E or C_W can indicate relative longevity among species for two reasons: first, K_E appears to be linearly related to C_W for the eight best-determined species (P B Tompsett, unpublished); and, second, C_H and C_Q probably have the same values for all species (Dickie *et al.* 1990). However, this method of longevity comparison does not take into account such factors as seed oil composition, as explained above.

The low viability of many *Eutacta* species in Table 2 after six months' storage is a consequence of low initial germination rather than of loss during storage. The related species, *Agathis australis*, can be stored for over 11 years (Table 2).

Recalcitrant seeds of *Araucaria* have been stored at Wakehurst Place, Surrey, UK, for longer than those of recalcitrant dipterocarps, the period amounting to over two years for *A. araucana*. Such seeds are not subject to chilling damage at 2°C, unlike the moist seeds of Meliaceae and Dipterocarpaceae. Cool storage is a means of reducing the germination rate of recalcitrant seeds, which maintain metabolism for a long period provided chilling damage does not occur.

Effect of the gas environment

Detailed studies concerning the effect of the gas environment on the recalcitrant seed of *A. hunsteinii* have revealed a decrease in longevity as oxygen concentration is reduced from 21% to zero, and a reduction in longevity in an atmosphere with 0.01% ethylene (Tompsett 1983). Ventilation of recalcitrant seed appears essential to remove damaging gases and to replenish oxygen lost in respiration.

MELIACEAE

Desiccation tolerance, habitat, mass and shape of seed

The seeds in both of the subfamilies which were studied contain both orthodox and recalcitrant types (Table 1). Various associations have been observed between storage physiology type and other factors. The lighter-weight seeds of the species which were studied in the Swietenieae, the mother trees of which tend to come from more open habitats and from seasonal areas, are orthodox, whereas the often larger seeds of the genera *Guarea* and *Trichilia*, deriving broadly from moister areas, are recalcitrant. Seed of *Carapa procera*, which is found in marshy locations among others, is both large and recalcitrant-seeded. Seed of *Azadirachta indica*, a drought-tolerant tree, is orthodox and small; seed of *Ekebergia senegalensis*, similar in size and appearance to that of *A. indica*, is probably also orthodox.

Seed shape may be correlated with physiology type. The thin seeds of the orthodox-seeded *Khaya* and *Entandrophragma* species are capable of drying quickly because of their high surface to volume ratio. The recalcitrant seeds of *Trichilia* species and of *Carapa procera*, however, are more globular and thus resist desiccation. For orthodox-seeded species in the forest, these characteristics lead to dry 'storage' on the ground, ensuring survival until rain stimulates germination. With recalcitrant seeds, however, desiccation after abscission must obviously be avoided.

Azadirachta indica seed – an intermediate type?

Seed of *A. indica* (neem) has been found by the author to have partial desiccation tolerance (unpublished), as was the case for *Araucaria columnaris* (Tompsett 1984b). Furthermore, neem seed is contained within a drupe, as is coffee, which was the first intermediate seed described by Ellis, Hong and Roberts. (1990, 1991). There are other similarities with coffee, such as the importance of the developmental stage of the fruit in determining desiccation tolerance and hence potential storage life of the extracted seed. In addition, chilling and freezing damage has been found to occur in dry *A. indica* seed (P B Tompsett, unpublished), as was described for coffee. Furthermore, considerable variation in the extent of desiccation tolerance among seedlots has been observed for both neem and coffee seed. However, despite all these physiological parallels, *Azadirachta indica* seed has been stored for 12 years at –20°C and 4% moisture content in the Kew Seed Bank (Table 1). The existence of the intermediate category thus needs further confirmation before it can be accepted as distinct from the orthodox type. The variation in desiccation tolerance observed during development for *A. indica* and *Coffea arabica* suggests a possible explanation for seedlot variation; on different collection occasions, different proportions of the seedlot may have been at desiccation-sensitive stages.

Seed longevity

Orthodox-seeded species in the *Swietenieae* tribe have been stored for several years (Table 1) and *Swietenia humilis* is predicted to survive well for 266 years under the best storage conditions (Table 4). Although the K_E and C_W values for Meliaceae in Table 3 are somewhat low, the ability of the seeds illustrated to be dried to very low moisture contents ensures a lengthy storage life, provided initial viability is high enough. Even the seed of recalcitrant *Trichilia* species has been kept at very high viability for quite long periods (seven months in *T. megalantha*), if kept in inflated polythene bags at 18°C and carefully ventilated (Table 1). All Meliaceae seeds so far studied suffer chilling damage if kept moist and below about 11–16°C.

Table 4. Predicted period (in years) for loss of viability from 99.4% to 85% germination (1.5 probits) for four tree species stored at –13°C and 2°C. Moisture contents selected were those below which further desiccation causes little further increase in longevity, except in *D. alatus* where 7% was chosen to illustrate potential only. Viability constants used are those in Table 3. Equilibrium relative humidity at 21°C is given where known

Temperature	*Swietenia humilis*	*Araucaria cunninghamii*	Ulmus carpinifolia	*Dipterocarpus alatus*
–13°C	266	3295	145	41
2°C	99	1264	52	8
Moisture content (%)	2.0	3.3	3.3	7.0
Equilibrium relative humidity	–	–	c6.0	–

DIPTEROCARPACEAE

Desiccation tolerance, habitat, size and shape of seed

The relationship between moisture content and germination was studied for five *Dipterocarpus* species; two desiccation tolerance groups were identified (Tompsett 1987). In addition, associations between desiccation tolerance and species habitat, seed mass and seed shape were observed (Tompsett 1987). Seed of *D. alatus, D. intricatus* and *D. tuberculatus* could be dried to 10–17% moisture content without damage. Seed of this first group increased in longevity as moisture content was reduced and as temperature was reduced, confirming their orthodox nature. Despite partial desiccation tolerance, there was no evidence that this type should be categorised as intermediate, which would imply fundamental differences from the orthodox type of seed. The species *D. turbinatus* and *D. obtusifolius* could not be dried below 45% moisture content, and were consequently classified as recalcitrant.

In agreement with seed physiology type, the orthodox group is found partly or wholly in seasonal areas, the seed falling on dry ground at the end of the dry season, whereas recalcitrant *D. turbinatus* is found in moister areas. Although *D. obtusifolius* is found in the dry dipterocarp forest, it also possesses recalcitrant seed; this species has an alternative strategy to survive dry conditions, which is to develop a thick and relatively impervious calyx around the embryo. Other habitat relationships for dipterocarps are given in Tompsett (1986b).

The heaviest seed, *D. obtusifolius* (mean mass 6.79 g), was recalcitrant, whereas the lightest seed, *D. intricatus* (mean mass 0.48 g), was orthodox. Seeds of all orthodox species have projections from the calyx (tubercles, lamellae or wings), whereas seeds of both of the recalcitrant species are globular, giving the smallest possible ratio of surface area to volume. These features respectively maximise and minimise desiccation rates, resulting in optimum survival in nature for both quickly dried orthodox seed and desiccation-resistant recalcitrant seed during the period on the ground between abscission and germination. The relationship between size and desiccation tolerance for other dipterocarps is given in Tompsett (1986b). Another association which was observed concerned species habitat and seed longevity; those from the drier habitats had the greatest longevity (Tompsett 1986b). Some of the associations described above were also observed in the genus *Shorea*, although in this case the three species examined were recalcitrant (Tompsett 1985).

All species of dipterocarp examined so far, other than the three described above, have been found to be recalcitrant; many authors have published data, and their results are referred to in a recent review (Tompsett 1992).

Seed longevity

Recalcitrant dipterocarp species vary in longevity, surviving for periods of up to nine months for *Shorea roxburghii* with a final germination of about 50%, when moisture content was 40% and storage temperature was 16°C (Tompsett 1985). Up to one year of storage has been reported for *Hopea hainanensis* with 80% final germination, storage conditions being 37% moisture content and 18°C (Song *et al.* 1984). Among the orthodox-seeded species of *Dipterocarpus*, *D. alatus* and *D. intricatus* have survived without observed loss of viability for 4.5 years at near 0°C with 12% moisture content, whilst recalcitrant *D. zeylanicus* has survived three months with 40% moisture content at 21°C, giving a final 53% germination (P B Tompsett, unpublished). Seed of *D. alatus* is predicted to last 41 years before ageing to the regeneration standard of 85% germination, provided initial viability is 99.4% (Table 4).

FINAL CONSIDERATIONS

Prediction of storage physiology type

The studies described suggest that it may be possible to provide a provisional classification of seed of unknown storage physiology which may aid collection and transport until its true type is known. Characteristics indicating orthodox seed storage physiology are as follows: small size (means of 0.3 and 0.5 g in Tables 1 & 2 respectively); projections from the seed, such as lamellae; and a relatively dry habitat. Conversely, features suggesting a recalcitrant seed type are as follows: large size (means of 2.4 and 4.7 g in Table 1 & 2 respectively); globular shape; and a relatively moist habitat. Dry soil surfaces are associated with the occurrence of orthodox-seeded species, even if water is present below the soil (eg *D. alatus*, which grows by waterways but sheds its seed on to dry ground before the rainy season).

Prediction of longevity from viability constants

The storage life of orthodox seed can be predicted if the four species constants in the above equation are known and if the initial germination (referred to as K_i) is accurately assessed as probability units (see Ellis 1984). To obtain accurate results, however, the seedlot must be homogeneous, having been collected at the same time and at approximately the same maturity. Other factors are important; there is a need to remove all empty seeds, all black-embryo seeds in the case of *Dipterocarpus* species, and all parasitised seeds. The inclusion of such material would distort the normal distribution of seed deaths over time, and so lead to false predictions. If removal is not possible, account must be taken of these factors by adjusting results using estimates of the percentage of empty, black-embryo or parasitised seeds.

Relative longevity of crop and tree seed

A comparison of the mean K_E and C_W values for herbaceous and tree species is presented in Table 5. Although the crop values are based on only five species, they agree well with those for a wider range of less well-determined values for crop species. The values presented show that, if all other factors remain constant, longevity is greater for crop than for tree species. Future research will require consideration of equilibrium relative humidity values (or water potentials, which are related to relative humidity at equilibrium), rather than moisture contents.

Table 5. Mean values for K_E and C_W for the five best-determined herbaceous species compared with mean values for ten tree species

	K_E	C_W	Source
Herbaceous species	8.39 (SE 0.47)	4.72 (SE 0.24)	Dickie *et al.* (1990)
Tree species	5.77 (SE 0.30)	2.80 (SE 0.22)	Table 3

Strategies for conservation

Despite the shorter storage life of tree seed compared with that of crop seed, it is evident from data in the present paper (Table 4) that certain orthodox-seeded species, such as *Araucaria cunninghamii*, could be safely conserved in seed form, as currently practised for crop species. Provided seed is harvested with high initial viability (K_i), survival to the regeneration standard of 85% germination may be over 3000 years for seed kept at −13°C and 3.3% moisture content. For the other species considered, a shorter storage life is predicted (Table 4). For *Dipterocarpus alatus*, the predicted seed survival at −13°C and 7% moisture content is 41 years. This period is adequate to justify conservation as seed, as it is longer than the juvenile stage of development, a criterion suggested by Bonner (1990). However, for certain species, 2°C would appear unacceptable as a conservation temperature. If there is doubt concerning the ability to attain a high initial viability (K_i) for this species, a dual strategy of seed conservation combined with *ex situ* tree stand establishment may be advisable. Orthodox seed exhibiting partial desiccation tolerance (when present harvesting and processing techniques are employed) may require further research, but should eventually be capable of storage for very long periods, as evidenced by the storage of *Azadirachta indica* seed for 12 years (see above).

In the case of recalcitrant-seeded species, whole seed is probably not an option for long-term conservation; *ex situ* tree stands and *in situ* protection are the only possibilities currently practised. Current studies, such as those using abscisic acid and lowered water potential to slow germination, have not yet extended storage life by substantial amounts. Further research is needed to develop new *ex situ* techniques, such as cryopreservation, in order to conserve recalcitrant-seeded species. Whole seeds of recalcitrant species can, however, be used for transport and short-term storage if they are properly handled.

Regeneration requirements of material stored as seed will need attention, but the problems involved should not be insuperable.

Practical transport and storage conditions

If seed is harvested at the highest possible initial germinability (K_i), the greatest possible longevity in storage is ensured. For long-term conservation, orthodox seed should be kept at the moisture content below which desiccation produces no further increase in longevity (about 2–7%, according to species) and at −13°C or lower. Hermetic storage containers are essential and will need to be larger than those employed for crop seed in many cases.

Storage of orthodox seed of the partly desiccation-tolerant type should at present be at slightly higher moisture contents (12% is often suitable) in order to avoid the loss of a proportion of the seedlot by desiccation damage. When further research has resolved the particular harvesting and processing techniques required for each species, it will probably be better to dry to 2–7% moisture content.

Recalcitrant seed can be transported and stored in the short to medium term at above the lowest safe moisture contents; seed of Araucariaceae can be kept at 2°C, but seed of Meliaceae and Dipterocarpaceae must be retained at about 18°C to avoid chilling damage. Ventilation is essential. Seed should be quickly transported in boxes with small holes and packed into containers with a high ratio of air to seed in order to ensure maximum viability on arrival; this procedure minimises the dual dangers of anoxia on the one hand and desiccation due to over-ventilation on the other. For long-term storage, the possibility of storing excised seed parts must be further examined, building on initial findings for dried *A. hunsteinii* embryos, which can retain the ability to produce callus after storage at −20°C for over four years (H W Pritchard, P B Tompsett & K Manger, unpublished).

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Capture of genetic variation by vegetative propagation: processes determining success

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ABSTRACT

Vegetative propagation offers the opportunity to rapidly overcome the limitations to domestication imposed by long generation times, irregular fruiting/flowering and outbreeding. Vegetative propagation techniques are increasingly being applied to a wide range of tree species, of both moist and dry tropics. Identification of the critical factors determining adventitious root development is crucial to sustained, cost-effective propagation, even in species in which these factors are not currently limiting.

Over the past ten years, research at ITE has identified a wide range of factors which influence rooting, including the stockplant growth environment, cutting origin, post-severance treatments applied to cuttings, and the propagation environment. In order to understand the influence of these different factors and their interactions, an appreciation of the physiological, biochemical and cytological processes involved in rooting is required. The primary processes occurring in the leaf are net photosynthesis and transpiration, while those in the stem are starch hydrolysis, translocation of sugars, water and nutrients, respiration, mitosis and cell differentiation. Each of these processes is influenced by a number of environmental, morphological and physiological variables, such as leaf area and thickness, internode length, chlorophyll content, stomatal density, stem lignification, etc.

Suggestions are made for experimental approaches to improve further the understanding of the mechanisms of rooting of leafy stem cuttings. These approaches include the development of a mechanistic model of adventitious root development. The practical implications arising from a process-based approach to propagation are also discussed.

INTRODUCTION

In agricultural crops, substantial increases in productivity and quality of produce have been obtained by breeding and selection over many generations. In contrast, less progress has been made in the domestication of trees because of their (i) relatively long generation times, (ii) irregularity in flowering and fruiting, and (iii) high incidence of outbreeding, with consequent loss of genetic gain in subsequent generations. Vegetative propagation offers the opportunity rapidly to overcome these limitations, by circumventing the need for sexual reproduction and facilitating the capture of individual genotypes.

Vegetative propagation techniques are increasingly being applied to the domestication of tropical tree species (Leakey *et al.* 1990; Mesén, Boshier & Cornelius, pp249–255; Ladipo *et al.*, pp239–248). A range of approaches can be utilised (see Hartmann & Kester 1983; Leakey 1985), including grafting, stem cuttings (Table 1), hardwood cuttings, marcotting (air-layering), suckering, and *in vitro* techniques such as meristem proliferation, organogenesis and embryogenesis. Several of these techniques have the disadvantages of a low rate of multiplication, a high requirement for skilled labour, or the need for high capital investment. These problems have been overcome by recent advances in the development of a low-technology propagation system (Leakey *et al.* 1990; Newton *et al.* 1992; Newton & Jones 1993a), which has enabled the successful propagation of a wide range of species by leafy stem cuttings (see Table 1). This system utilises non-mist propagators constructed out of cheap and readily available materials, with no requirement for a piped water and electrical supply (Leakey 1991; see also Ladipo *et al.*, pp239–248).

Although many species can be propagated easily by leafy stem cuttings, some species are recalcitrant. For example, early attempts at the propagation of *Albizia falcataria* resulted in leaflet shedding and death of all the cuttings within ten days. Pre-conditioning the cuttings by intermittent droughting of the stockplants resulted in leaf retention and high rooting percentages, with more than 100 roots per cutting in some cases (R R B Leakey, unpublished data). In such situations, identification of the factors limiting rooting is critical to successful propagation. Enhanced rooting is important even in species which are propagated easily, as small gains in rooting percentage may be of considerable economic value when the species is mass propagated on a commercial scale. In some circumstances, the rooting ability of cuttings may decline with successive harvests of cuttings from a set of stockplants. This phenomenon can arise when over-frequent harvesting of cuttings causes the depletion of the endogenous reserves of the stump, the death of the stockplant's fine root system, or a reduction in soil fertility. For all these reasons, an understanding of the factors which influence rooting is fundamental to successful and sustained vegetative propagation.

Another key reason for a better understanding of the rooting process is the accumulation of a body of apparently contradictory data in the scientific literature. For example, the role of carbohydrates in the rooting process is still the matter of great debate (see review by Veirskov 1988). Highly contrasting results have been obtained from the same species in different situations. Most propagation experiments usually consider only one or two of the many factors known to influence rooting, and fail to recognise their interactions. Many investigations also fail to measure and record sources of variation in rooting ability which can differ between experiments, such as propagation environment and stockplant growth conditions. Consequently, the mechanisms of root formation remain unclear.

In order to understand the interactions between the different factors influencing rooting, an appreciation of the physiological processes involved is required. In recent years, there have been a number of literature reviews on this topic (eg Leakey 1985; Andersen 1986; Haissig 1986; Davis, Haissig & Sankhla 1988; Thompson 1992). Consequently, this paper attempts to pull together data on these processes in leafy softwood cuttings obtained from a limited number of experiments with tropical tree species. In particular, it suggests how these processes may be influenced by the following factors: (i) the stockplant's growing environment; (ii) the cutting's position of origin within a shoot and the shoot's position within the canopy of the stockplant; (iii) the post-severance treatments applied to cuttings; and (iv) the environment of the propagating system. The implications of these conclusions for both research and the practical application of vegetative propagation techniques are discussed.

PROCESSES INVOLVED IN ADVENTITIOUS ROOT DEVELOPMENT

The key physiological, biochemical and cytological processes influencing adventitious root development in a leafy cutting are

Table 1. Tropical tree species vegetatively propagated at the Institute of Terrestrial Ecology, Edinburgh

West Africa	Central and South America	East and Central Africa	South Africa	SE Asia and Australasia
Afzelia africana	*Albizia caribaea*	*Acacia nilotica*	*Acacia karoo*	*Acacia mangium*
Afrostyrax lepidophyllus	*Albizia guachapele*	*Acacia senegal*	*Colophospermum mopane*	*Agathis australis*
Baillonella toxisperma	*Alnus acuminata*	*Acacia tortilis*	*Triplochiton zambesiacus*	*Agathis dammara*
Carapa procera	*Annona muricata*	*Dalbergia melanoxylon*	*Vangueria infausta*	*Agathis macrophylla*
Ceiba pentandra	*Caesalpina spinosa*	*Faidherbia albida*		*Agathis obtusa*
Milicia (syn. *Chlorophora*) *excelsa*	*Casimiroa edulis*	*Maesopsis eminii*		*Agathis robusta*
Entandrophragma angolense	*Cedrela odorata*	*Melia volkensii*		*Agathis vitiensis*
Khaya ivorensis	*Chrysophyllum cainito*	*Sesbania sesban* var. *sesban*		*Albizia falcataria*
Khaya senegalensis	*Cordia alliodora*	*Sesbania sesban* var. *nubica*		*Anthocephalus chinensis*
Lovoa trichilioides	*Eugenia jambos*	*Terminalia brownii*		*Araucaria hunsteinii*
Nauclea diderrichii	*Ochroma pyramidale*	*Terminalia prunioides*		*Camposperma brevipetiolata*
Ricinodendron heudelottii	*Prosopis cineraria*	*Terminalia spinosa*		*Citrus halimi*
Teclea verdoorniana	*Prosopis juliflora*	*Vateria seychellarum*		*Dipterocarpus turbinatus*
Terminalia ivorensis	*Psidium guajava*	*Vitex keniensis*		*Durio zibe thinus*
Terminalia superba	*Swietenia macrophylla*			*Gmelina arborea*
Tetrapleura tetraptera	*Swietenia mahagoni*			*Shorea albida*
Treculia africana	*Tipuana tipu*			*Shorea contorta*
Triplochiton scleroxylon	*Vochysia hondurensis*			*Shorea curtisii*
				Shorea leprosula
				Shorea macrophylla
				Tamarindus indica
				Terminalia calamansanii
				Terminalia brassii
				Toona ciliata

photosynthesis, transpiration, respiration, starch hydrolysis, translocation of sugars, water and nutrients, mitosis, cell differentiation and elongation. While all of these processes may operate in different parts of leafy softwood cuttings, photosynthesis and transpiration primarily occur in the leaf, and mitosis and cell differentiation are generally of greatest importance in the cutting base. The stem is the primary organ of translocation for nutrients, carbohydrates and water between the leaf and the cutting base.

The interactions between these processes and the factors affecting rooting, mentioned earlier, are considered separately below, although, in reality, they are interlinked.

FACTORS INFLUENCING THE PROCESSES THAT DETERMINE ROOTING

Stockplant growth environment

The physiology and morphology of stockplants are influenced by the growth environment, which may include nutrients, water, temperature and light (both irradiance and spectral composition). In addition, the individual cuttings are influenced by the variation in microclimate within the canopy of the stockplant. The characteristics of the cutting (Figure 1) that are influenced by these environmental factors include:

- the area and thickness of the leaf;
- leaf photosynthetic capacity as affected by stomatal density, chlorophyll content, etc;
- internode length and stem diameter;
- leaf and stem starch, soluble carbohydrate and nutrient contents;
- pre-severance leaf and stem water potentials; and, probably,
- concentrations of endogenous growth substances.

Some influences of stockplant growth environment are illustrated by results from experiments with *Triplochiton scleroxylon*, in which rooting ability was found to be correlated with pre-severance net photosynthetic rate, which in turn was determined by irradiance and nutrient application treatments during growth. In stockplants grown under artificial lighting (6.3 red/far-red (R:FR) ratio) with an irradiance of 250 µmol m^{-2} s^{-1} and nutrient addition, photosynthetic rate varied between 0.003 and 0.009 mg CO_2 s^{-1} leaf^{-1}, and a mean rooting percentage of 33.3±5% was obtained. These figures compared with photosynthetic rates of 0.0005–0.002 mg CO_2 s^{-1} leaf^{-1} and an associated mean rooting percentage of 9.3±3.1% when stockplants were grown under an irradiance treatment of 650 µmol m^{-2} s^{-1} and without added nutrients. The low rooting percentages obtained under this high irradiance/low nutrient treatment were attributed to the accumulation of starch in the cuttings pre-severance (Leakey & Storeton-West 1992).

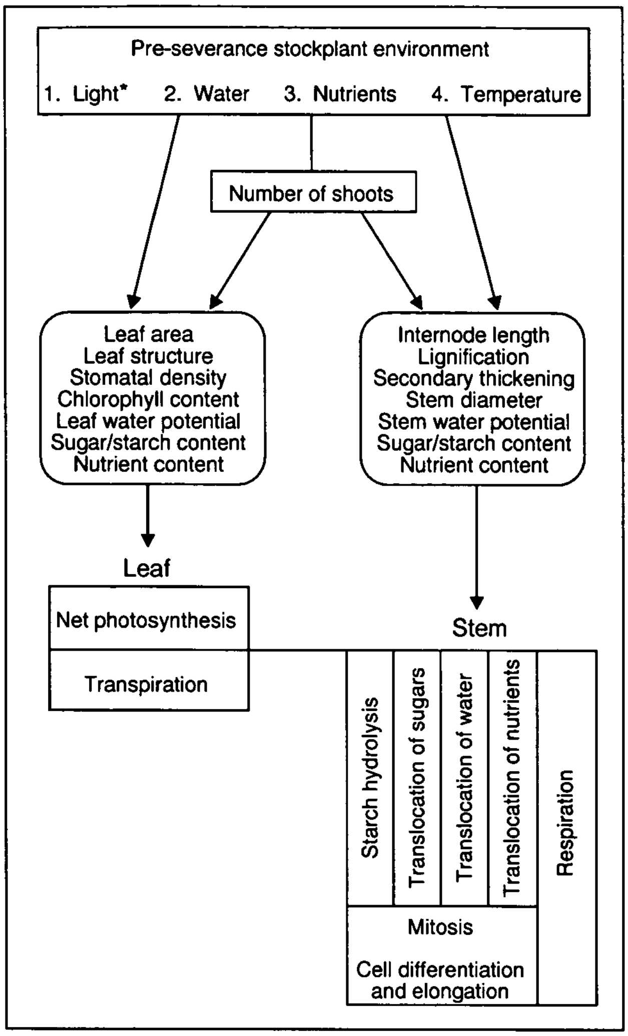

Figure 1. Schematic diagram of the effects of the pre-severance stockplant environment on the morphological and physiological factors affecting rooting ability in single-node, leafy cuttings *via* their influences on the biochemical processes of their leaf and stem (*irradiance and quality)

The importance of stockplant illumination is further illustrated by other experiments with constant irradiance but varying light quality. In *T. scleroxylon* under artificial lighting, higher rooting percentages (92%) were obtained at a R:FR ratio of 1.6, while lower rooting percentages (53%) were obtained at a R:FR ratio of 6.3 (Leakey & Storeton-West 1992). These results, together with those on the effects of irradiance, concur with results examining the varying rooting ability of cuttings from different shoots within the stockplant canopy (Leakey 1983). However, in common with many other vegetative propagation experiments in the scientific literature, no data were collected on the physiological activity of these various shoots. To hypothesise how these treatments affected the physiological processes and morphological condition of these shoots, it is necessary to examine a more extensive data set from similar experiments with *Eucalyptus grandis* (Hoad & Leakey 1992) testing a wider range of R:FR ratios (including more natural ratios of R:FR, eg 0.4–1.3). In this more recent study, rooting ability was related to treatment-induced changes in leaf and stem morphology and to pre- and post-severance gas exchange and carbohydrate dynamics. In addition, pre-severance photosynthetic rate per unit leaf area, chlorophyll concentration, stomatal conductance and water use efficiency increased with an increase in the R:FR ratio. The photosynthetic rate per unit of chlorophyll was, however, greater at low R:FR ratios, and there was a positive linear relationship between the percentage of cuttings rooted and the pre-severance photosynthetic rate per leaf.

As mentioned above, there are important interactions between the light environment of the stockplant and its nutrient regime. These interactions have been demonstrated in *T. scleroxylon* as stockplant environment effects, using controlled conditions and shade trees above rows of stockplants in the field (Leakey & Storeton-West 1992). Similar interactions have also been demonstrated between the shoots of stockplants with and without fertilizers (Leakey 1983). In both instances, the highest rooting percentages occurred in shaded shoots from plants with added fertilizers. The unrestricted application of fertilizers is, however, not recommended as, at very high fertilizer applications, plants of *Khaya ivorensis* yielded cuttings which suffered high mortalities. In this case, mortalities due to rotting were associated with increasing reducing sugar and declining starch contents of the leaves, during the period of propagation (Tchoundjeu 1989).

Cutting origin

The physiology, morphology and subsequent rooting potential of a cutting are also influenced by:

- the position within a stem from which the cutting originates (Leakey & Coutts 1989; Figure 2); and
- the position of the shoot within the stockplant canopy (Leakey 1983, 1985; Tchoundjeu 1989; Figure 3).

Cutting mortality can also be related to node position in the shoot (Leakey 1983), suggesting that the factors determining rooting and mortality are inversely related and form some kind of continuum.

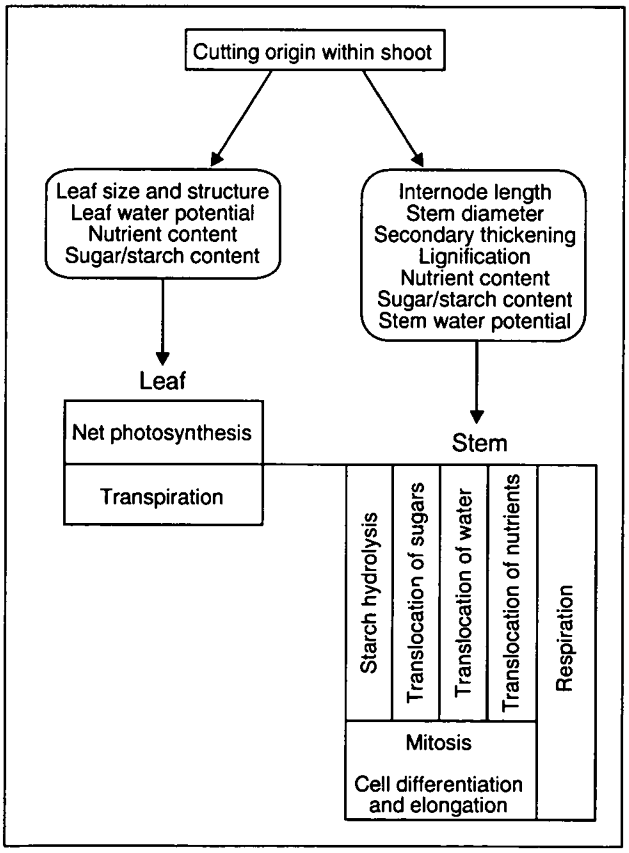

Figure 2. Schematic diagram of the effects of cutting origin within shoot on the factors affecting rooting ability in single-node, leafy cuttings *via* their influences on the biochemical processes of leaf and stem

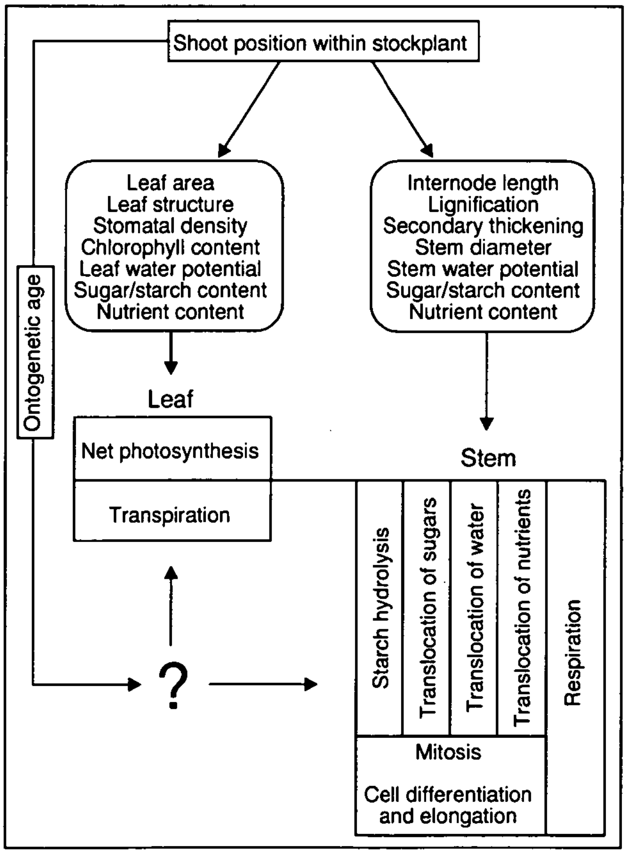

Figure 3. Schematic diagram of the effects of the shoot position within stockplant on the morphological and physiological factors affecting rooting ability in single-node, leafy cuttings *via* their influences on the biochemical processes of leaf and stem

Within a stem, there are gradients in:

- succulence,
- leaf size, age and morphology,
- leaf water potential (Leakey 1983), and
- mutual leaf shading

which affect both the amount and quality of light received by the leaves (Leakey & Storeton-West 1992), and consequently net photosynthetic rate and stomatal conductance. In addition, there are gradients in:

- stem morphology, such as the extent of secondary thickening and lignification, and internode length (Leakey & Mohammed 1985), stem diameter and, consequently, stem volume (Leakey, Dick & Newton 1992);
- starch and sugar content (Leakey & Coutts 1989);
- nutrient content (Tchoundjeu & Leakey 1993); and, almost certainly,
- the content of plant growth regulators and rooting co-factors.

The most important of all these factors in *T. scleroxylon* seems to be the effect of cutting position on the internode length and diameter. Together, these two variables result in variation in cutting volume. From these results and those of other species (see, for example, Hoad & Leakey 1992; Dick, East & Leakey 1991), we have developed the hypothesis that cutting volume determines the capacity of a cutting to store assimilates produced both pre- and post-severance (cf Leakey & Storeton-West 1992). Cuttings with a small stem volume may become saturated with starch, which can inhibit photosynthesis and consequently rooting. However, an often overlooked aspect of the carbon budget is the stem respiration rate, which is influenced by the cutting's size and its environment (pre- and post-severance). To examine the mean respiration rate of internode tissue, a one cm section was taken from the base of *Prosopis juliflora* cuttings with a range of basal diameters (Dick, Blackburn & McBeath 1993). Using an oxygen electrode, the respiration rate per gram dry mass of tissue was found to decrease within sequentially more basal cuttings, possibly as a result of the increased lignification of older tissues. However, because of the larger mass of these basal cuttings, the total respiration for the whole 1 cm section of tissue (Figure 4) was greatest in the cuttings with the largest basal diameter. Thus, the larger mass of tissue in the larger cuttings more than compensated for their smaller respiration rate per unit mass. In addition, the larger diameter cuttings had a larger area of wound tissue which may also have contributed to their increased respiration. These results show that, compared with smaller diameter cuttings, larger diameter cuttings have greater total respiratory/metabolic activity at their basal (wounded) end. This feature may contribute to the increased rooting potential of large diameter cuttings (Dick, Dewar & Leakey 1992).

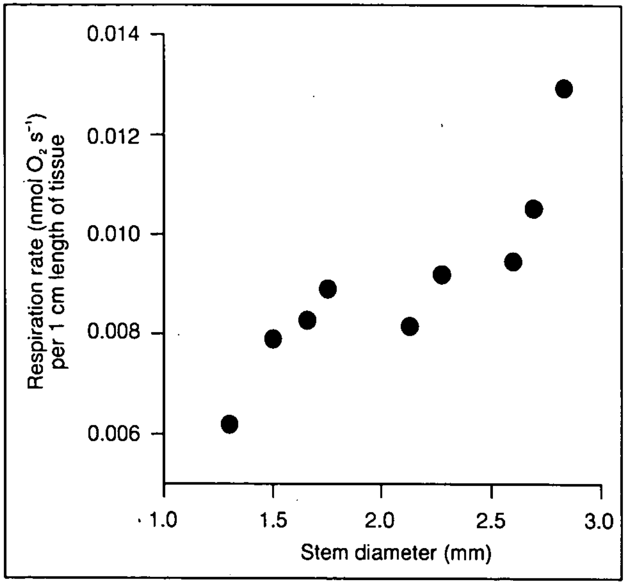

Figure 4. Total respiration rate of the basal 1 cm section of *Prosopis juliflora* cuttings measured at the time of severance, using an oxygen electrode (source: Dick *et al.* 1993)

Between shoots there are variables that affect rooting which are similar to those environmental factors affecting the whole stockplant, except that they are associated with the microclimatic environment of the individual shoot. As in the whole plant, the interactions between light (quality and quantity) and nutrient availability seem to be particularly important (Leakey 1983), presumably mediated by effects on shoot morphology and gas exchange. Cuttings from basal shaded shoots of *T. scleroxylon* stockplants given added nutrients have a high rooting ability. In addition to these microclimatic effects, there is also inter-shoot competition, which is related to the number of shoots on the stockplant and to their position within the dominance hierarchy between shoots (Leakey 1983). In small *T. scleroxylon* stockplants (height 0.5 m), higher rooting percentages were associated with cuttings from the top shoot, and progressively declined with each shoot down the plant. In larger plants (ie 1.5 m), rooting percentages of cuttings from the upper shoots were low and those from basal shaded shoots were relatively high. In *Lovoa trichilioides*, another West African hardwood species, rooting percentages of cuttings from basal shoots were highest, even in small stockplants (Tchoundjeu 1989). The rooting ability of these cuttings from different shoots also depended on how many shoots there were per stockplant.

From this examination of the effects of cutting origin and stockplant environment, it is clear that the physiological and morphological condition of the cuttings at the time of severance from the stockplant is very important, and that, even in small, 'juvenile' plants, rooting ability can range from 0–20% in unsuitable material to 80–100% in suitable material. It is also clear that, as stockplants get bigger and more complex, it becomes more difficult to obtain shoots in a physiological/morphological condition that confers good rooting ability. This loss of rooting ability is frequently attributed to the loss of juvenility (ie attainment of sexual maturity or ontogenetic ageing). Numerous experiments have demonstrated this loss of rooting ability, but they have all been confounded by the many other changes that occur as plants grow bigger and more complex (Leakey 1985). There is, therefore, no good evidence from in vivo studies that sexual maturation per se affects rooting ability, although there are currently some studies from in vitro culture that suggest that there are events in vitro which apparently 'rejuvenate' plant tissues (Jones & Webster 1989). As yet, there is no understanding of what these events are or how they are mediated. For the moment, therefore, it seems most appropriate to indicate (see Figure 3) that the effects of ontogenetic ageing on the rooting process are not known. What is clear is that physiological ageing, as manifested by the physiological and morphological condition of the cutting, does have major effects on the success of vegetative propagation programmes (Leakey et al. 1992).

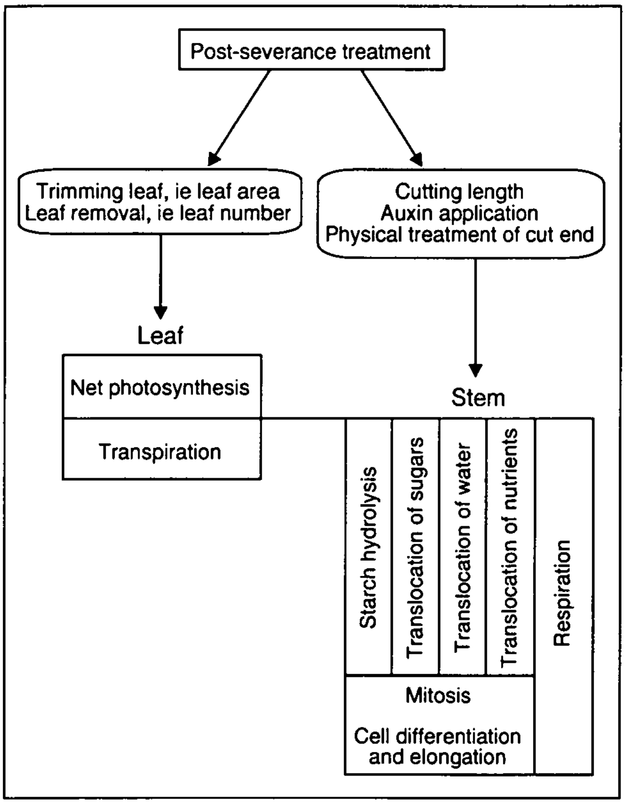

Figure 5. Schematic diagram of the effects of post-severance treatment on the morphological and physiological factors affecting rooting ability in single-node, leafy cuttings *via* their influences on the biochemical processes of leaf and stem

Post-severance treatments applied to the cuttings

The rooting of cuttings is influenced by the application of a number of post-severance treatments (Figure 5). The most common treatment is application of an auxin 'rooting hormone'. Auxins often hasten rooting, increase the percentage of cuttings rooted, and increase the number of roots formed. However, the results of even this most commonly applied treatment are subject to considerable variation, because of the interactions with the factors listed previously (Newton *et al.* 1992). Other post-severance factors which influence rooting include leaf area, which is often reduced to minimise water deficits. Evidence from a number of species suggests that there is an optimum leaf area, as a compromise between having a large enough leaf to produce assimilates and a small enough leaf to minimise water loss (Leakey & Coutts 1989). In *T. scleroxylon* and several other species, the optimal leaf area is about 50 cm^2 (Leakey 1985). However, in *L. trichilioides* and *Khaya ivorensis*, about 200 cm^2 and 20 cm^2 respectively have been shown to be optimal, under the conditions tested (Tchoundjeu 1989). In contrast, other species which root easily have displayed no tendency towards an optimum leaf area (Leakey 1990; Newton, Muthoka & Dick 1992). In small-leaved species, the optimal leaf area can perhaps only be achieved by retaining more than one leaf per cutting and thus more than one node, but there is some evidence that there are interactions between cutting length and the numbers of leaves and nodes.

Cutting length is another variable that can be manipulated at the time of severance. The effect of stockplant/shoot environment on cutting length and volume has already been discussed. However, it is not often realised how trimming a cutting to a standard length rather than accepting natural variation in internode length affects the cutting volume (Leakey *et al.* 1992). Standardising cutting length has the advantage that all cuttings can be inserted into the medium to the same depth and also have their leaf held at the same height above the cutting medium, which can be important for cutting survival (S P Hoad & R R B Leakey, unpublished). As cutting diameter usually increases down a shoot, taking constant-length cuttings usually confers an advantage on more basal cuttings as their stem volume is greater. In contrast, taking cuttings of a constant number of nodes may result in an advantage to apical cuttings, if their greater length exceeds the effect of cutting diameter on cutting volume (Leakey *et al.* 1992).

It may sometimes be necessary to store cuttings prior to insertion in the propagator, particularly if they are collected from the field at some distance from the propagation unit. Rooting ability declines with increased storage time, and may also be influenced by storage temperature. In *T. scleroxylon*, storage for 24 hours in an insulated box (18–23°C) had no effect on rooting, but, after 72 hours' storage, rooting percentages were significantly decreased (Njoya 1991).

The propagation environment

Successful propagation of leafy cuttings is dependent on the maintenance of suitable air and leaf temperatures, irradiances and leaf/air vapour pressure deficits (VPDs) during propagation (see review by Loach 1988b). Leafy cuttings are vulnerable to desiccation during propagation, particularly prior to root development and when VPD is high. The primary effects of water deficits are lower leaf and stem water potentials and the consequent inhibition of physiological activity, and of photosynthetic rate in particular. The association of low leaf water potentials with low rooting percentages has been illustrated by Loach (1988a) and Newton and Jones (1993b).

Although many authors have suggested that current assimilates are important for rooting, there have been relatively few studies that have actually measured photosynthesis and transpiration during the rooting process (see review by Davis 1988). Recent studies have shown that many tropical tree species actively photosynthesise and transpire prior to root formation, supporting the suggestion that gas exchange during propagation is one of the critical factors influencing rooting (Leakey & Storeton-West 1992; Newton, Muthoka & Dick 1992; Newton *et al.* 1992; Newton & Jones 1993b; Hoad & Leakey 1992; Mesén, Leakey & Newton 1992; Mesén 1993). In *Terminalia spinosa*, mean photosynthetic rates of 2 μmol m^{-2} s^{-1} and a maximum rate of over 6 μmol m^{-2} s^{-1} were recorded in a non-mist propagator prior to root development. These photosynthetic rates were associated with rooting percentages of over 80%; the rate at any given time was found to be strongly dependent on stomatal conductance and irradiance (Newton *et al.* 1992b). Transpiration rates of 0.002–0.007 g H_2O cm^{-2} h^{-1} were recorded in cuttings of *Cordia alliodora*, depending on the rooting medium (Newton, Muthoka & Dick 1992; Newton *et al.* 1992), and stomatal conductances in the range 0.1–1.4 cm s^{-1} were recorded for four species in both mist and non-mist propagation systems (Newton & Jones 1993b). The contrasting effects of irradiance on VPD, photosynthetic activity and cutting water relations will determine the optimum leaf area of the cutting, and the shading regime to be employed during propagation (Newton & Jones 1993a, b).

Apart from influencing VPD, air and bed temperatures in the propagator also influence the rates of all the processes directly (Figure 6), particularly in metabolic processes such as starch mobilisation, respiration, mitosis and cell differentiation. Some species display clear temperature optima in terms of rooting. For example, from a range of 20–38°C, an optimum bed temperature of 29–31°C was identified in *T. scleroxylon*, at an air temperature of 25–30°C (Leakey, Chapman & Longman 1982). The relationship between air, leaf and bed temperatures is generally considered to influence the relative activity of the different parts of the cutting, and may account for shoot growth prior to root formation during propagation.

Application of nutrients during propagation may also facilitate root development (see review by Blazich 1988), by influencing photosynthetic rate and other metabolic processes. Nutrient application may be particularly beneficial in slow-rooting species under mist propagation systems, where nutrient leaching from the cutting can be a problem. Foliar nitrogen concentration is particularly influential in determining photosynthetic rate, and nitrogen is also important for starch mobilisation and other metabolic processes.

Variation in ambient CO_2 concentration of the air surrounding the cuttings may also influence rooting, primarily by its effect on photosynthetic rate and dry mass accumulation (Davis & Potter 1983). In non-mist propagators, CO_2 concentrations have been found to vary diurnally

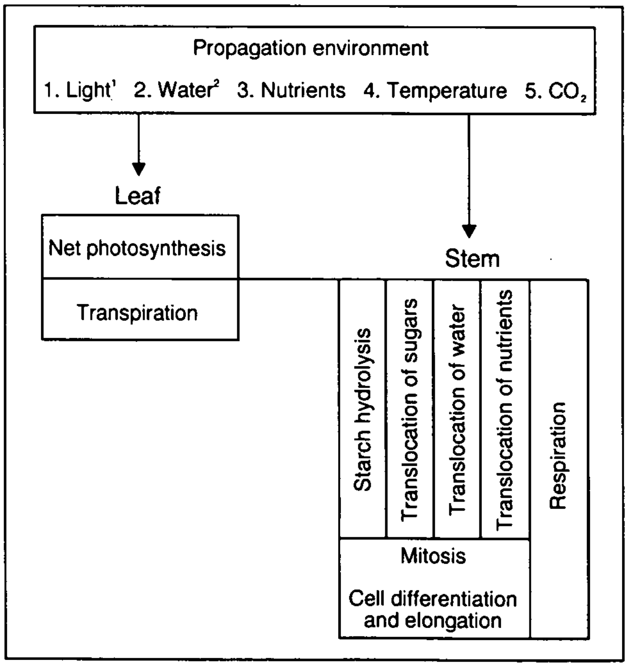

Figure 6. Schematic diagram of the effects of propagation environment on the rooting ability of single-node, leafy cuttings *via* their direct influences on the biochemical processes of leaf and stem ([1]irradiance and quality; [2]VPD, humidity, moisture content of medium, air/water ratio of medium)

between 150 and 550 µmol mol^{-1} (Leakey *et al.* 1990; Matin 1989; Newton & Jones 1993a), which may be expected to have a major effect on photosynthetic activity.

The rooting medium determines the amount of water and air available to the base of the cutting, which will influence the rates of transpiration and respiration respectively, as well as the other metabolic processes in the cutting base. The effect of different concentrations of indole-3-butyric acid (IBA) on rooting of *Bombacopsis quinata* and *Vochysia hondurensis* has been found to interact with the type of rooting medium utilised (Newton *et al.* 1992).

Genetic variation

Different species and clones vary in their physiological and morphological characteristics. It is likely, therefore, that much of the genetic variation in rooting success can be attributed to the interactions between the above processes and factors influencing rooting. In this connection, there is increasing evidence for the role of genes which encode enzymes involved in the biosynthesis and metabolism of the auxin indole-3-acetic acid (Blakesley & Chaldecott 1993).

SUGGESTIONS FOR EXPERIMENTAL APPROACHES TO UNDERSTAND THE MECHANISMS OF ROOTING

For research projects aimed at optimising rooting for a given species, it is necessary to conduct an experimental programme. Ideally, this programme should involve the following strategies, although it is recognised that the ideal situation is rarely achieved in practice.

Experimental analysis and design

All experiments should obviously follow standard experimental design practices and be well replicated. The minimum number of cuttings per treatment or clone/treatment interaction should be 40–60. The major difficulty with analysis is that either a cutting roots or it does not, and thus there are only two possible outcomes, giving a binomial distribution. With moderate numbers of replicates, it may be possible to use standard ANOVA or regression procedures on either the raw data or a transformed data set, but care is needed and the validity of various assumptions must be tested. Alternative approaches involve either the contingency table approach using χ^2 tests, although these results can be difficult to interpret, or use of a generalised linear model with its associated analysis of deviance, which requires more specialised computing software.

Depending on the chosen technique of analysis, an appropriate experimental design should be adopted. Ideally, cuttings should be blocked in the propagator according to the spatial variation in the propagation environment, which may be pronounced (Newton & Jones 1993a). Treatments should be replicated across all blocks and randomised within a block, following standard practice. Other sources of variation should ideally also be randomised within each block, but frequently this is impracticable. For example, cuttings from a single shoot may be most easily laid out in node order rather than fully randomised with respect to node position.

A number of recent studies (Leakey & Storeton-West 1992; Hoad & Leakey 1992) have demonstrated that, if the experimental analysis is limited to the overall effect of treatments, a great deal of the variation in rooting may remain unexplained. By accounting for the variation attributable to node position, for example, more information on different processes is often obtained (Dick *et al.* 1991; Dick & East 1992). If the experiment also includes destructive harvests taken at different times during propagation, additional information on the dynamics of different processes may be obtained. For example, studies of the carbohydrate dynamics in *T. scleroxylon* have demonstrated that there is no relationship between soluble carbohydrate content at insertion (day 0) and subsequent rooting, but a strong relationship between soluble carbohydrate content at day 28 and rooting at day 42 (Leakey & Coutts 1989). Destructive harvests of this sort obviously increase the numbers of cuttings required per treatment. These harvests can and should ideally be associated with non-destructive assessments of physiological variables (gas exchange, respiration, chlorophyll fluorescence, etc), as an understanding of the dynamics of these processes is fundamental to understanding the achievement of successful rooting.

Control of variation

In any given experiment, some variables will be manipulated, whereas others will either be controlled or simply measured. Any variables which cannot be controlled should be measured and reported. The variables which should be noted include all the factors which may influence rooting ability as outlined above, eg leaf area, stem length and diameter, node position, number of nodes, number of leaves, leaf shedding, changes in leaf colour, genotype, propagation environment, pre-severance environment, physiological age, chronological age, ontogenetic age, shoot number and position, nutritional status, etc. Although it is recognised that practical limitations will restrict which variables can be measured, experimenters should be aware of all the potential sources of variation in rooting ability, and should seek to control or record them as far as possible.

Modelling adventitious root development

As rooting is influenced by so many interacting factors, there is a need for process-based models as a tool to understanding. To date, a model has been constructed which describes the development of root structural dry matter from pre-formed initials, as well as the dynamics of sugar and starch pools within the cutting during the rooting process. This model (Dick & Dewar 1992) was constructed on the basis that the following previously mentioned factors were positively correlated with rooting: (i) respiration rate at the base of the cutting; (ii) labile sugar content, rather than total carbohydrates; and (iii) post-severance photosynthetic rate of the cutting.

The leafy softwood cutting is considered to have three structural compartments: leaf, internode and root, but can easily be adapted to include a growing shoot or to be a leafless hardwood cutting. A leafy softwood cutting is represented (see Figure 7) by boxes (i) and (ii) and defined by six dynamic variables: the soluble sugar pools (mg sugar) in the leaf (L_{sg}), internode (I_{sg}), and root (R_{sg}); the starch pools (mg starch) in the leaf (L_{st}) and internode (I_{st}); and the structural dry matter pool (mg structural dm)$^{-1}$ in the root (R_x). If, as in *Cordia alliodora* (Mesén 1993) or *Prosopis juliflora* (Dick *et al.* 1991), the cutting produces a new axillary shoot during propagation, this can be represented by the addition of an additional box (iii). In this case, the bud has a dry matter pool (B_x) which competes for sugars with the new root (R_x). In both these cases, the leaf and internode structural dry matter pools (L_x and I_x respectively) are held constant in the model. In the case of hardwood cuttings (which can be represented by box ii, with or without box iii; see Figure 7), the dynamic variables are the same as for the softwood cutting with a growing shoot, except that the leaf sugar and starch pools are omitted. Given the initial values of the dynamic variables at severance (t=0), the model simulates the development of root initials, and rooting is said to have occurred when the root structural dry mass reaches a threshold (x mg).

As explained earlier in this paper, many factors influence the processes that determine rooting. As an example of the situation when structural root growth is limited by the amount of sugar reaching the cutting base, the output of the model has been parameterised with published data for single-node cuttings of *Triplochiton scleroxylon* (Leakey & Coutts 1989), with leaf areas of 10, 50 or 100 cm^2.

To calibrate the model in the absence of measured rates of photosynthesis, respiration and sugar transport, physiologically reasonable parameter values were assumed (Table 2). These values were taken to be the same for cuttings

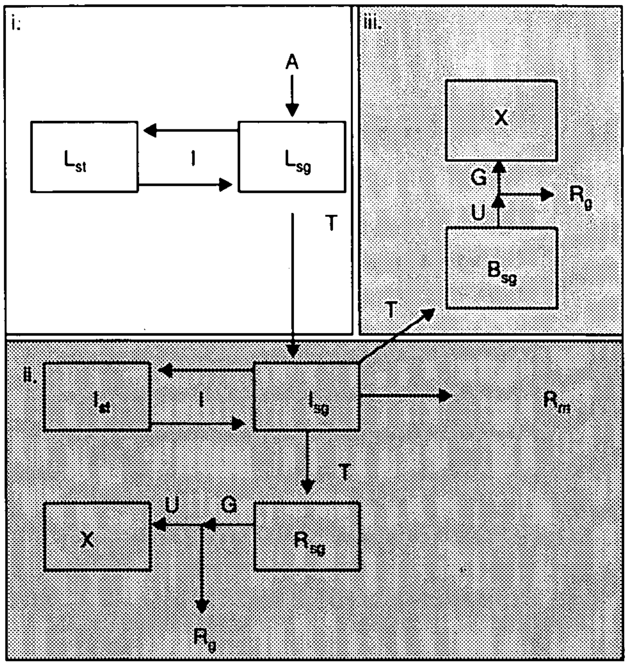

Figure 7. Schematic diagram of the rooting model. Box (i) represents the leaf, (ii) the internode and rooting zone, and (iii) a growing bud or shoot. Solid boxes represent the dynamic starch (st), sugar (sg) and structural dry matter (x) pools. Arrows represent fluxes of sugar assimilation (A), starch/sugar interconversion (I), sugar transport (T), root sugar utilisation (U), root structural growth (G), internode maintenance respiration (R_m) and root growth respiration (R_g)

Table 2. Parameter values and initial values of state variables used to simulate the root development of single-node leafy cuttings of T. scleroxylon, for three different leaf areas (source: Dick & Dewar 1992)

		Leaf area (cm^2)		
		10	50	100
Parameters				
g_{li}	Leaf/internode conductance (mg structural dm d^{-1})	150	150	150
g_{ir}	Internode-root conductance	150	150	150
i_x	Internode structural dm (mg)	300	300	300
k_1	Starch/sugar conversion coefficients (d^{-1})	0.0001	0.0001	0.0001
k_2	" "	0.03	0.03	0.03
k_3	" "	0.0001	0.0001	0.0001
k_4	" "	0.05	0.05	0.05
Y	Root growth efficiency	0.5	0.5	0.5
μ	Utilisation constant (d^{-1})	10.0	10.0	10.0
σ_i	Specific internode respiration rate [10^{-3} mg sugar d^{-1} (mg structural dm)$^{-1}$]	0.0	0.0	0.0
σ_l	Specific leaf photosynthetic activity [10^{-3} mg sugar d^{-1}(mg structural dm)$^{-1}$]	8.0	9.4	4.1
lx	Leaf structural dry matter (mg)	300	500	700
Initial values of state variables (mg)				
i_{sg}	Internode sugar	9.9	9.9	9.9
i_{st}	Internode starch	10.8	0.8	10.8
l_{sg}	Leaf sugar	3.9	6.5	9.1
l_{st}	Leaf starch	0.3	0.5	0.7
r_{sg}	Root sugar	0.033	0.033	0.033
r_x	Root structural dry matter	1.0	1.0	1.0

with 10, 50 and 100 cm^2, except for the specific leaf photosynthetic activity (σ_l) which was derived, such that 50% rooting occurred after 24, 19 and 28 days for cuttings with 10, 50 and 100 cm^2 leaf areas respectively, as in Leakey and Coutts (1989). The results of this simulation suggest that the 10 cm^2 leaves were predominantly area-limited, while the 100 cm^2 leaves were predominantly limited by photosynthetic rate per unit area. This finding is consistent with the observation by Leakey and Coutts (1989) that 50 cm^2 was optimal for rooting and that assimilation rates were limited by low leaf water potential in cuttings with leaf areas of 100 cm^2.

This example serves to show that the model provides a framework for examining the role of factors known to affect rooting. As a further illustration, if an increasing range of specific internode respiration rates is used in the model, rooting in a cutting with a leaf area of 50 cm^2 is progressively delayed until the root sugar pool declines to zero, at which point further increases in respiration rate result in cutting mortality (Table 3).

Table 3. Predicted time of rooting or death of *T. scleroxylon* cuttings with leaf area 50 cm^2, for various values of the internode respiration constant, σ_i. All other parameters and initial values of state variables are as given in Table 2 (source: Dick & Dewar 1992)

Internode respiration constant [10^{-3} mg sugar d^{-1} (mg structural dm)$^{-1}$]	Days to rooting	Days to death
0	19	–
5	26	–
10	46	–
13	137	–
14	576	–
14.3	–	35
14.4	–	19
14.5	–	13
15	–	5
20	–	2

As already mentioned, the model, like all mechanistic models, makes various assumptions. So far, the only assumption tested is that the rate of respiration at the base of the cutting (rooting zone) is higher than that of the stem above it (Dick *et al.* 1993) This study confirmed this assumption and suggests that a concentration gradient is created which drives sugar transport basipetally. The measurements also supported one of the predictions of the model: during the formation of callus and new roots, the respiration rate at the base of the cutting increases with time (Dick *et al.* 1993).

In summary, the model provides a potentially useful framework for: (i) the design and interpretation of rooting experiments on a whole-cutting basis, and (ii) understanding the mechanistic control of adventitious rooting. With further development and a better understanding of the interactions between carbon, nutrients and water, we hope that it will be possible to use the model to improve stockplant management and achieve more predictable and sustained rooting during mass propagation. However, it is already clear, from the experience of developing the model, that there may be several contrasting sets of conditions that will give acceptable protocols for commercial vegetative propagation, depending on whether the stockplants and cuttings are managed in a way that makes them dependent on stored reserves or current assimilates.

PRACTICAL IMPLICATIONS

In situations where a full-scale research programme is inappropriate, the propagation of an undomesticated species may be approached by considering a limited number of key factors. These include leaf area, cutting length, auxin and propagating conditions (eg Tchoundjeu & Leakey 1993). As a starting point, cuttings should be 5–10 cm in length, with a leaf area reduced by 50% and an applied auxin concentration of 0.2–0.4% IBA in a solution of alcohol, or in the form of a commercial rooting powder. Cuttings should be inserted to a depth of 15–25 mm in the rooting medium, ensuring that the leaf does not touch the medium surface, and that the medium at the cutting base is not waterlogged. The rooting medium should consist of an inert, well-aerated moisture-retaining substrate, such as mixtures of fine gravel, sand or rotted sawdust. The propagator should be shaded to about 25% of full sunlight in order to keep the propagators as cool and as humid as possible and yet provide enough light for the promotion of physiological activity.

In any propagation programme, the reasons for lack of success may be difficult to ascertain, as so many factors influence rooting. From the above, it should be clear that the provision of a good rooting environment and the application of standard post-severance treatments are relatively easy and likely to result in a good measure of success. However, the commonest problems associated with vegetative propagation are those caused by inappropriate stockplant management or the unsuitable physiological state of the material to be propagated. To sustain good rooting over many cutting harvests and several years will require (i) much greater understanding of stockplant management in order to maintain stockplants in a good physiological condition, and (ii) a knowledge of how to manipulate rooting ability by pre-severance conditioning. We hope that, in due course, the mechanistic model will be of practical use for this task. This need to sustain physiological youth, which is often confused with the retention of juvenility, is perhaps the most difficult aspect of vegetative propagation. It is important to improve our understanding of these ageing phenomena (Leakey *et al.* 1992).

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Selection and breeding to conserve and utilise tropical tree germplasm

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ABSTRACT

The breeding of non-industrial trees is a relatively new science involving many species and multiple traits, sites and management practices. Most tree improvement programmes, especially in the tropics, will therefore have to deal with large arrays of germplasm which cannot be managed efficiently with traditional breeding approaches. To conserve and utilise genetic resources, strategies are needed to ensure efficient sampling, avoid inbreeding depression, exploit heterosis, develop the potential of cloning, manage the large arrays of taxa and accessions, and use genotype/environment interaction in a framework that does not restrict future options.

Efficient sampling, proficient breeding and cumulative gains can only be achieved if there is a good understanding of natural breeding systems and reproductive biology, yet these remain undetermined for many multipurpose trees. Estimates of inbreeding depression have also been lacking, and this has prevented breeders from risking high selection intensities to capture maximum genetic gain in advanced generations. The consequences of severe inbreeding depression for industrial and non-industrial species are disparate, and considerable discernment is required to balance risks *versus* gains.

Spectacular improvements in growth rate have come from the heterosis expressed by species hybrids. These advances have been translated into increases in productivity of plantations through the development of operational cloning techniques. Breeding to capitalise on these often unpredictable advances must be accomplished by adopting strategies to manage the large arrays of taxa and accessions that hold further potential and, at the same time, avoid reliance on too few clones.

For species where recurrent selection is operative, multiple population breeding strategies are described which assist in the utilisation and conservation of tropical tree germplasm. Analogous concepts apply to improved material of non-industrial species that is released to small-scale farmers, given the likelihood that they will collect their own seed in the future, thus developing local landraces.

INTRODUCTION

Breeding of industrial forest trees began in earnest in the 1950s with *Pinus* species. Pines are analogous to maize in that they are both outcrossing, wind-pollinated species in which the traits of greatest economic importance are quantitative and under multigenic control. Therefore, it was a logical progression for traditional strategies developed for cross-pollinating agricultural crops to be used for their genetic improvement, albeit for species with largely inflated generation intervals and contrasting population structures. Through a strategy of recurrent selection for general combining ability (*gca*) and seed production from progeny-tested clonal orchards, average gains of around 20% in volume production alone were accomplished in the first generation of selection in many programmes.

The potential to increase productivity of plantation trees by selection among natural populations was also firmly realised in the 1950s. A profusion of provenance trials has subsequently been established which demonstrated for a number of species that improved adaptability and even greater increases in productivity may be available from reselection in the natural range (Mullin, Barnes & Prevost 1978). This development has resulted in a crucial need for strategies to manage a plethora of potentially valuable material and to retain the option to include that material in the initial breeding populations.

The improvement of non-industrial trees is a newer science involving many more species (see Simons, MacQueen & Stewart, pp91–102). The taxonomy, distribution, genetic variation and reproductive biology are unknown for many of them. The demands of beneficiaries of improvement programmes of non-industrial trees will be far more diverse than those of industrial species in terms of the traits of interest, the sites for planting and the flexibility of management.

Most tropical tree improvement programmes, both for industrial and for non-industrial tree species, will therefore have to deal with large arrays of germplasm of several species. This is quite a different situation from agricultural crops, where one breeder or a single organisation usually deals with better characterised material of far fewer species. It has become clear that, in many cases, forest tree germplasm cannot be managed efficiently with traditional breeding approaches to produce the genetically improved material required by a wide range of clients. To conserve and utilise this resource, strategies are needed to ensure efficient sampling, avoid inbreeding depression, exploit heterosis, develop the potential of cloning and use genotype/environment interaction in a framework that does not restrict future options.

SAMPLING

Experience with industrial trees has shown that there can be economically significant intraspecific population differences in the natural range of a species. In some cases, this knowledge has come from provenance trials planted long after the breeding programme has started. For example, *Pinus taeda* was introduced into southern Africa at the beginning of the century, probably from a Georgia Piedmont source, and breeding of the resulting landrace has produced substantial increases in productivity. Rangewide provenance trials, however, have subsequently shown that some of the southernmost provenances from Florida have the ability to outproduce the bred material in volume, although stem form is unacceptable (Mullin *et al.* 1978). International provenance trials of *P. caribaea* var. *hondurensis* have revealed the Guanaja Island population not only to be among the highest volume producers, but also to have a wood density approximately 10% higher than the mainland provenances (Barnes, Gibson & Bardey 1983). In addition, these trials have demonstrated the superior wind-firmness of the coastal sources (Birks & Barnes 1990).

International provenance trials also identified a subspecies of *P. patula*, previously unrecognised and untested, that will have a profound effect on the productivity and exotic range of that species in the tropics and subtropics (Barnes & Styles 1983). Moreover, in *P. patula*, provenance trials in southern and eastern Africa have shown the Zimbabwean landrace to have superiority over native provenances in its tolerance of the pine woolly aphid (*Pineus pini*) after the latter's inadvertent introduction from Australia (Barnes *et al.* 1976). Such provenance differences, however, are not restricted to the pines. For example, *Eucalyptus camaldulensis* was used for nearly 100 years in southern Africa before provenance trials showed the great superiority in productivity, stem form and drought tolerance of some of the hitherto untested natural populations from northern Australia, such as Petford and Katherine (Barrett & Carter 1976).

These examples highlight the need to ensure that provenances over the full natural and exotic range of a species are effectively sampled before the breeding populations are closed by the gap created by a number of generations of selection. They show that a strategy is required to maintain and develop new material to a point where it can contribute its potential to the propagules for operational use, and that variation should be conserved in the breeding population to meet unpredictable events.

Trees for non-industrial use will often include species that are not naturally gregarious. They are likely to have much more variable population structures than the traditional plantation species, which normally occur naturally as dense stands, and this variability will affect sampling, domestication, breeding and conservation strategies profoundly. Logically, therefore, classic breeding should not be started before the natural breeding systems are properly understood. For instance, several legumes disperse their pollen in aggregates of 8, 16 or even 32 monads; thus, seed from individual pods are likely to be full-sibs (eg *Calliandra calothyrsus*).

If it is accepted that for most non-industrial tree species there will be little advanced generation breeding and that farmers will ultimately derive their seed requirements from their own or neighbours' fields (see Simons *et al.*, pp91–102), then the correct choice of base population becomes even more critical. Consider the scenario where population A produces a yield of 130 units relative to the mean of all other populations (100), and is chosen for multiplication and release. When it is grown in a seed production area with moderate selection, the seed produced will feasibly have the potential of 145 units of production. When released, this material would spread throughout rural communities, largely by farmer-to-farmer diffusion mechanisms (Cromwell 1990). Meanwhile, further exploration of the native range reveals a new population (B) with a 170 unit production. Even if population A underwent recurrent selection, it would take three or four generations to attain the production of population B at the expense of a narrowing of the genetic base. Depending upon the rate of uptake of population A (in terms of numbers of farmers and proportion of their land cultivated), and the saturation level for the species in an area, the release of population B (even immediately in an unimproved state) may have little effect. This situation would occur even if farmers later collected seed from trees of population B only, because of contamination by pollen of population A. Furthermore, there may even be reduced yields, owing to the negative effects of creating population hybrids.

INBREEDING

Inbreeding in cross-pollinated species almost invariably leads to a loss of vigour and fecundity. As most of the industrial tree species under genetic improvement are outcrossing and single undifferentiated breeding populations have been the norm, breeders have been concerned to keep co-ancestry to low levels, not only in the seed orchards but also in the breeding populations themselves. This fact may have prevented the full potential genetic gain being passed on to operational clients; the gain achieved through higher selection differentials in the early generations is unlikely to have been nullified by inbreeding depression. The materials and mating designs to estimate inbreeding effects independently from *gca* are readily available in many programmes, but, surprisingly, the experimental work has rarely been done.

Selfing is the most extreme form of inbreeding. There are advantages in using selfing both to test and to recombine genotypes. It conserves the effective population size, does not increase co-ancestry, does not dilute valuable gene complexes, can be used for recombination, and, theoretically, can rank parents precisely (Lindgren 1991). The problems are that it is common for self-fertility, seed yield and seedling survival to be low when outcrossing industrial tree species are inbred. For these reasons, selfing has rarely been used by tree breeders, although there are instances of self-fertility and outstanding performance of selfs and of the latter being positively correlated with *gca,* eg with *Pinus elliottii* in Zimbabwe (Mullin *et al.* 1978).

There is clearly a need for tree breeders of industrial species both to be released from the fear of the consequences of inbreeding depression, so that they can be more adventurous in using high selection differentials, and to explore the possibility of developing inbred lines through selfing and establishing homozygous balance in subpopulations, so that they can enhance the prospects of achieving large heterotic effects.

HETEROSIS

Heterosis at the species hybrid level has been responsible for the greatest genetic increases in the productivity of plantations. They have been most spectacular among the *Eucalyptus.* Most hybrids have initially been produced by chance when plots of two species whose natural distributions do not overlap have been grown close to each other as exotics, eg *E. grandis* and *E. urophylla* in Brazil (Campinhos & Ikemori 1989). An added condition is almost invariably that the hybrid exhibits heterosis only in a 'hybrid habitat' (ie in an environment where neither of the parent species is generally well adapted), eg *E. grandis* x *E. tereticornis* in the Congo (Delwaulle, Laplace & Quillet 1980), or where the hybrid tolerates a single factor in the environment that is limiting for both parent species, eg cyclone in the case of *P. caribaea* var. *hondurensis* x *P. patula* ssp. *tecunumanii* (Nikles 1989; Nikles & Robinson 1989).

The potential to increase productivity with other species hybrids is enormous in *Eucalyptus* (eg to introduce cold tolerance into some of the fast-growing tropical species), *Pinus* (eg within the closed-cone pine group to extend the range at present covered by *P. patula*), and in many other genera, particularly those of some non-industrial trees such as *Leucaena* and *Acacia.* There is evidence that those individuals with highest *gca* within species combine to give the best hybrid families. There is, therefore, an advantage in selecting to improve the breeding population genotypes of potential hybrid parent species. One current constraint to hybrid breeding is the labour-intensive controlled crossing required, although, with recent advances in identifying male sterility genes which function in heterologous species, there exists the potential to render one of the parental species male sterile, and thus form an ideal seed parent for natural hybrid crosses.

The potential of interspecific hybrids for non-industrial species is compromised by the likely collection of seed by farmers for their own use, and the need for broadly based planting stock. Hybrids are being promoted in the genus *Leucaena* to combine growth vigour of *L. leucocephala* with the acid tolerance or insect resistance of *L. diversifolia* (see Brewbaker & Sorensson, pp195–204). To fix gene frequencies for desirable traits and to prevent segregation in later generations, breeding populations are having to be taken to the F4 and beyond. The high selection intensities being employed, however, are narrowing genetic diversity in this hybrid, thus making the material more vulnerable to environmental disasters and perhaps restricting its management and environmental flexibility. Without complementary mating tests to determine genetic correlations, there also remains the possibility that other characters are being selected against. The occurrence of sterile triploid interspecific hybrids in *Leucaena* circumvents problems of segregation or fixation, but would tie the resource-poor farmer to returning to the releasing agency each time for new seed.

Although the value of interspecific hybrids has been confirmed for many species, there are conflicting results on the performance of inter-provenance 'hybrids'. In *Pinus radiata*, a population composited from two provenances outperformed the parental provenances by 20% in volume at seven years of age (Shelbourne *et al.* 1979). Several authors conclude that hybrid provenances are usually intermediate between parents, as found in *Picea abies* (Huhn & Muhs 1981), *Pinus sylvestris* (Parks & Gerhold 1986) and *Pinus banksiana* (Magnussen & Yeatman 1988). Such results have led workers to consider hybrid provenances as a way of combining desirable traits uniquely present in only one of the parental provenances. Ericsson (1975) related the character-specific nature of heterosis in *Picea abies*, where positive effects were seen for volume, yet negative effects were seen for insect resistance.

Whether or not it is possible to predict a heterotic response when combining two or more provenances, the compositing of provenances of non-industrial species may be inevitable, given the multiplicity of organisations involved in the testing, promotion and release of these species. Compositing of provenances could arise because farmers will collect future seed from trees in their own or their neighbours' fields. The question arises as to how much provenance compositing should be actively discouraged, or, alternatively, how much it should be promoted. Despite the label 'multipurpose', most non-industrial trees are grown for a single purpose, and the additional products or benefits are viewed as bonuses. Therefore, a wood-producing provenance may not be compatible to composite with a leaf-producing provenance, as the benefits of either may be compromised. Alternatively, it may be possible to combine characteristics such as tolerance of soil acidity with high growth rates by mixing provenances with these attributes.

When improved germplasm is to be released where the material already occurs naturally, further thought must be given as to whether the improvements will survive many generations before the mixing with wild germplasm makes the improvements redundant. One such case is with *Sesbania sesban*, where the International Centre for Research in Agroforestry (ICRAF) is planning to test and release new provenances in Africa (D Boland, ICRAF, Kenya, personal communication; see also Owino, Oduol & Esegu, pp205–209). The success of these efforts will rely upon being able to monitor the dilution of improved material. For instance, it may be that farmers can carry the improved germplasm through three or four generations before needing to resort back to pure stocks. A current study to investigate the breeding system and floral phenology is underway to resolve these issues. For species where vegetative propagation is a possibility, such concerns do not arise.

CLONING

The huge increases in plantation productivity offered by species hybrids have been made operationally possible through the development of new techniques of vegetative propagation by cuttings both in pines and in eucalypts. In fact, it has been the development of this facility for species that were hitherto considered not to be clonable that has been the significant technological breakthrough, not breeding. Many hybrid clones in use, particularly among the eucalypts, remain those that have been produced, often by chance, between unselected parents. Breeding for yield within the parent species populations should bring with it the potential for cumulative increases in yield from the hybrids. There are, however, indications that the correlations between yield of the ortet and that of its ramets are poor (eg in *Eucalyptus grandis*, P A Clegg, SAPPI Research, South Africa, personal communication). Is it possible that yield in the ramets may be more dependent on the genetic capacity of the individual to produce an efficient root architecture in its clone? Better correlations may be found between yield and some rooting trait, or between juvenile and mature characteristics (see Ladipo *et al.*, pp239–248). If such correlations are found, then some form of reciprocal recurrent selection will offer the prospect of cumulative genetic gains in yields from hybrids in the future. If such correlations are not found, identifying a sufficient number of good clones will rely upon the continuous screening of large numbers, gains will not be cumulative, and a point may be reached where it is no longer profitable to look for further increases in yield.

Foresters continue to debate the wisdom of releasing few *versus* many clones to capture optimal gains for industrial tree species. The arguments about susceptibility to environmental (biotic or abiotic) disasters with few clones apply more rigorously to non-industrial trees, given the risk averseness of small-scale farmers and their desire to maximise stability of production rather than production *per se*. The consequences of clonal effects on number of cuttings produced per year may be a climax clonal population based on a few clones. In *Gliricidia sepium*, number of stems is under strong genetic control and, after coppicing, there is a high correlation with number of resprouts. Similarly, the number of resprouts in each successive coppice is highly correlated with original stem numbers. Therefore, after ten generations of vegetative propagation of clones which produced two, three, four and five resprouts per generation, the population would consist of 1024, 59 049, 1 048 576 and 9 765 625 cuttings per clone, respectively. These figures correspond to 0.01%, 0.5%, 10% and 89% representation of the population, respectively. To mitigate against these effects, it would be necessary to release hundreds or thousands of clones rather than the tens being released for industrial trees.

Cloning is and will continue to be used for non-industrial trees for a great variety of reasons. Foremost is the ability to capture and fix desirable traits. Sexual reproduction may not be favoured on genetic grounds because:

- the traits are difficult to breed for (low heritability);
- there is a negative association between desirable traits (negative genetic correlation);
- the traits are not controlled by additive genes (non-additive).

In addition, seed propagation may be disadvantageous for biological reasons, such as poor seed set (eg *Calliandra calothyrsus* in Cameroon), recalcitrant seed (eg *Simarouba glauca*) or difficulties with seedling establishment.

There may also be other consequences of using vegetative propagation. For instance, cuttings may have a different root architecture and compete with crops differently (Liyanage & Jayasundera 1988). For *Gliricidia sepium* in West Africa, hedgerows derived from cuttings last approximately six years, in contrast to ten years for those derived from seedlings (J Cobbinah, International Institute of Tropical Agriculture, Ibadan, Nigeria, personal communication).

GENOTYPE/ENVIRONMENT INTERACTION

Genotype/environment interaction (*gei*) can occur at the species, subspecies, variety, provenance, family and clonal levels. It can be caused by climatic, edaphic, biotic and management variables in the growing environment. Some can, and some cannot, be controlled, and some may not even be predictable. Those that are predictable may interact with those that are unpredictable, thus rendering inconclusive the results of experiments established to test the effects of predictable factors. Climatic factors tend to be responsible for most interactions higher up in the species-to-clone hierarchy, physical and biotic factors in the middle, and edaphic factors at the lowest levels. These interactions have been clearly illustrated by plantation species (Matheson & Cotterill 1990).

Among the tropical and subtropical pine species, mean, minimum and maximum temperatures are the most significant factors in the environment governing a species' performance. For example, *Pinus patula* is at its optimum at a mean annual temperature of about 14°C, *P. taeda* at about 16°C, *P. elliottii* at about 18°C, and *P. caribaea* at about 22°C. As temperatures get too high for *P. patula*, productivity falls off progressively, until male and female flowering becomes asynchronous and no seed is produced. In contrast, as it gets too cold for *P. elliottii* and *P. caribaea*, wood density becomes unacceptably low, and no pollen or no seed are produced (Barnes & Mullin 1976). Within climatic zones, there may or may not be cyclonic winds. In *P. caribaea*, there are very distinct provenance differences in resistance to wind damage; the coastal populations are much more wind-firm than the inland populations (Eisemann, Nikles & Newton 1984). At the family level, heritability of resistance to aphid (eg *Pineus pini*) and rust (eg *Cronartium fusiformis*) are high in *P. elliottii*; if the disease is present in one site and the insect in another, a complete reversal in the ranking of families can occur. At the individual tree level, it is known that certain clones of *P. radiata* rank at the top where there are high phosphorus levels in the soil, but rank lowest where there is a deficiency of this element (Wilcox 1982).

Clear evidence of *gei* at all levels has led tree researchers and breeders to expect it to have important consequences for both conservation and genetic improvement. Many provenance, progeny and, more recently, clonal trials have been replicated over a range of sites in the expectation of observing *gei* and being able to explain and predict it through statistical analysis to establish the causal factors in the environment. This has not happened, and there seems to be little prospect even now of being able to gain more than empirical indications of interaction, except where there is one over-riding effect in the environment, eg frost, cyclone, disease, predators or elemental deficiency. The failure to do more is largely attributable to the difficulty of measuring the variables required to characterise an environment and the inherent microsite variability. Climatic data are the easiest to record, yet at many trial sites it is necessary to interpolate statistics from distant meteorological stations with attendant inaccuracies. Soils are notoriously difficult and expensive to characterise, especially in the case of forestry experiments which tend to cover large and variable areas. Most biotic effects are by nature unpredictable; however, striking examples of the effects of microsymbionts on performance have been recorded (see papers by Mason & Wilson, pp165–175; Lapeyrie & Högberg, pp158–164; Sprent, pp176–182). The interaction of all these factors with management, which inevitably varies from site to site, further confounds the effects.

Replicated progeny tests within a species' range have regularly shown, for many industrial trees, that *gei* for productivity at the family level is present. The interaction variance is usually caused by a few families that perform outstandingly well at a specific site. There are usually, however, also some families that are good overall performers. Because of the empirical nature of these results, the expense of testing over a large number of sites, and the impracticality of running a large number of breeding programmes for different site types, breeders have tended to select the good all-rounders and confine themselves to a single breeding programme to cover all sites. There is no doubt that potential to increase productivity and maintain variation is forfeited with this strategy, both because adding stability to the list of selection criteria will reduce gain for other traits, and because the specific high-performers are lost. Further, wide testing to identify the good all-rounders is costly, if it is to be effective.

The situation of *gei* with respect to non-industrial trees is important and relates largely to performance. Following testing of provenances or clones at experimental sites, material will be released to resource-poor farmers who will manage it in a wide range of ways and physical environments. The crucial issue is one of reliability of performance, as farmers seek to maximise stability of production rather than production *per se*. Therefore, provenances or clones should be sought that show stability of performance across differing site types or management regimes, rather than tailoring specific provenances or clones to restricted geographic areas.

A STRATEGY

A breeding strategy has been developed at the Oxford Forestry Institute which accommodates most of the above requirements (Namkoong, Barnes & Burley 1980; Barnes 1986). It has been called the Multiple Population Breeding Strategy (MPBS). In it, the breeding population for a single species consists of a variable number of subpopulations, which are kept separate so as to produce trees with different gene complexes. The objective is to maintain or create diversity between them, while practising various intensities of selection within them. Diversity will occur between the subpopulations even if the selection criteria, the selection pressure and the breeding environment are the same, because most traits of interest are under *gca* control and different sets will be brought together in different populations. Currently, neutral alleles will not be lost in the same frequencies. Variation can be reinstated, inbreeding depression overcome, and new populations with specific attributes created by crossing between the subpopulations. Undesirable or superfluous populations can be dropped at any time.

There are three types of multiple population in this breeding strategy:

i. *replicate populations,* where independent subpopulations are bred for the same trait and elements from each are brought together for operational seed production to ensure outcrossing;

ii. *diversified populations,* where existing differences are used or new differences created by selecting for different traits and/or environments, and commercial seed production occurs within subpopulations for special products and/or environments;

iii. *heterotic populations,* where both additive and heterotic gene effects are used through hybrid or reciprocal recurrent selection in the different subpopulations, and heterosis is exploited in operational seed production by crossing between specific subpopulations.

Experience with industrial plantation species has shown that there are subspecific differences at the provenance (natural and exotic) level that have a lasting operational significance. Knowledge of these differences and the materials to represent them rarely become accessible together; in fact, both characteristically become available over an extended period of time. With non-industrial species, the situation is complicated further because domestication may start before there is sufficient knowledge on reproductive biology to permit an informed sampling of the genetic range of the species. The MPBS provides pedigree structure at the population level that permits the management and conservation of this variation.

By providing structure at the population level, the MPBS ensures a backstop of pedigree control and escape routes from inbreeding depression, which gives the breeder confidence to be more adventurous and pursue potentially fertile avenues of research, including those into the production of inbred lines or high-performance clones, in order to increase genetic gain.

The MPBS is also a suitable framework in which to breed and conserve parent populations for creating species hybrids and high-performance clones. The ways in which traits can be combined and heterosis used are not predictable. Selection within carefully defined provenance and species breeding populations will preserve the potential to make successful hybrids for possible subsequent cloning, as needs unfold.

There is an argument for using the MPBS to retain the potential to use *gei* and, at the same time, to benefit from it by default. Rather than testing the same population over a large number of sites, replicate populations can be established in very different environments with different sets of families in each. When the best families are selected, both the best all-rounders and the best performers in specific environments can be saved. The average operational performance of progeny of the combined top performers is not likely to be below that of the good all-rounders alone. If routine seed source tests showed that one particular breeding population were doing better than seed from the combined seed production orchard, this would be an indication that a separate seed orchard should be established for that area, thus taking advantage of any substantial *gei*. An additional advantage of this strategy over the conventional single breeding population is that the selection differential for the seed production population could be much higher because of the larger number of families constantly kept under test. A breeding population with a much broader genetic base could be maintained for the equivalent cost of a conventional programme, and would serve as a buffer against unpredictable environmental events.

Finally, the MPBS is seen as an effective framework in which to conserve genetic variation, not only as a safeguard against inbreeding and as a source of variation for breeding, but also to conserve genes for an uncertain future in which environmental change and material demands are unknown.

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Strategic concepts in the domestication of non-industrial trees

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ABSTRACT

The planting of non-industrial trees has been widely promoted in the tropics to counter the effects of fuelwood shortages, to increase sustainability of agriculture, and to prevent land degradation. Two key components to the success of these endeavours have been identified as (i) the particular species used, and (ii) the source of seed, as these may enhance productivity independently of other inputs. Given that most non-industrial tree species have not undergone organised breeding, there exists a potential for genetic improvement through selection and recombination of desirable individuals from selected seed sources. There is likely to be some disparity, however, between what is technically feasible and what is practically appropriate. In the absence of theory and strategies for breeding non-industrial trees, an adoption of agricultural and commercial forest methodology seems probable, although the case for advanced generation breeding and cumulative gain through recurrent selection in non-industrial trees is equivocal, and in many cases illusory. In addition, little consideration has been given to the demand-side variables and the distribution mechanisms for improved seed of non-industrial trees. This paper examines the potential and scope for improvement of non-industrial trees, and the likely demand for genetically improved trees.

INTRODUCTION

The importance of non-industrial trees in the farming systems of rural communities in the tropics has recently been elevated by human population increases, accelerated deforestation and the lack of land for agricultural expansion. One reason for the popularity of such trees is the diverse spectrum of products (eg fuelwood, fodder, green manure, food) and benefits (eg shade, erosion control, soil amelioration) that they provide. Although the growing of non-industrial (or 'multipurpose') trees as part of an integrated agricultural system is not a new innovation, its greater frequency of occurrence is a recent phenomenon. Palmberg (1989) reported that 2.6 million hectares (Mha) in the tropics were planted with non-industrial tree species during the period 1981–85, almost matching the area planted with industrial species (2.9 Mha) during the same period. Unlike commercial forestry where a few species dominate plantings, more than 2000 tree species have been planted for non-industrial use (Burley, Hughes & Styles 1986). Consequently, individual non-industrial tree species may not warrant such intensive breeding effort as their industrial counterparts.

With a few exceptions (see Willan, Hughes & Lauridsen 1990), there has been no organised breeding of non-industrial trees, suggesting an untapped potential for genetic selection and improvement (Simons 1992). In the absence of theory and strategies specifically for the breeding of non-industrial trees, an adoption of agricultural and commercial forestry methodology appears likely (eg Ventakesh 1988). The feasibility and appropriateness of such methodology, however, remain untested, and in many cases it may be unsuitable.

STATUS OF NON-INDUSTRIAL TREES

The economic status of non-industrial trees is inherently low. Nonetheless, they may contribute to the income of small- and medium-scale farmers through enhanced crop/livestock production, or may occasionally be sold directly (eg for firewood or construction), although markets for the latter are often not well established. The greatest benefits from cultivating non-industrial trees are likely to accrue outside the cash economy, so efforts to increase their production should be considered primarily as rural development rather than an economic return on investment. Given this situation, questions arise as to who will fund the breeding of non-industrial trees and whether this will be a sustained activity. The recent emergence of two new Consultative Groups on International Agricultural Research (CGIAR) – the Centre for International Forestry Research (CIFOR) and the International Centre for Research in Agroforestry (ICRAF) – to focus on tropical trees suggests that a long-term commitment to non-industrial tree improvement may develop.

An often quoted output from the Green Revolution, in which the CGIAR agricultural centres were prominent, was the breeding of high-yielding crop varieties, albeit with reliance on chemical fertilizers and irrigation. This advance, however, was allied to major outbreaks of pests and diseases leading to disastrous crop failures (Cooper, Vellve & Hobbelink 1992). Agricultural history includes many examples of the imprudence of over-narrowing the genetic base of planting stock (eg the susceptibility to southern leaf blight of Texas male-sterile cytoplasm in maize) (Simmonds 1979). More recently, examples of attacks by pathogens on genetically uniform trees have emerged, such as rust diseases of *Populus* and *Citrus*. Pest epidemics are of equal importance, and the devastation of large areas of *Leucaena leucocephala* by a defoliating psyllid highlights the need to ensure the genetic diversity of planting material of non-industrial trees (Hughes 1989). It may be that outbreaks of insects on early introductions of other non-industrial trees (eg mealybug attack on *Gliricidia sepium* in Uganda in 1914 – Tothill 1940; stem-borer on *Calliandra calothyrsus* in Philippines – Luego 1989) were a result of narrowly based germplasm.

A broad genetic base in non-industrial trees is required not only for biological insurance, but also because of the vagaries of the physical environment where they are grown. Furthermore, farmers who grow these trees operate with low inputs, because of insignificant cash reserves and minimal capacity to withstand high losses (Haugerud & Collinson 1990). Such farmers seek to realise stability of production, rather than to maximise production *per se,* which incurs unacceptably greater risk. Consequently, improved material of non-industrial trees should retain a broad genetic base to cope with current and unforeseen production and environmental variables.

DEMAND FOR NON-INDUSTRIAL TREES

It is evident that natural tropical forests are disappearing and that land for agricultural expansion is often restricted, indicating in general terms a need to plant trees. The demand for trees from people in rural communities, however, remains largely unquantified. Information on the demand for individual species, many of which are largely unknown, is also scant. Yet it is this demand for planting stock of individual species that should drive tree improvement.

Taking an example of demand for an agricultural crop, Griliches (1957) fitted a logistic model to the origin (*a*), slope (*b*) and ceiling level (*c*) for cultivation of hybrid maize when it was introduced in the USA. Despite the clear technical advantage of hybrids, there were marked differences between regions in their rates of acceptance (*b*=0.35–1.02) and ceiling levels (*c*=53–100%) of this new technology. These differences were explained partly by dissimilarities in farm size, isolation of farms and farmer wealth. The point to draw is that even in a relatively resource-rich environment, such as the USA farming community, demand and acceptability varied. For non-industrial trees, it is reasonable to expect even greater differences between different rural communities in their acceptance and uptake of germplasm for what may not only be a new species but also a whole new technology (eg growing trees in alleys between crops).

Clearly, without economic models of the process of adapting and distributing non-industrial tree germplasm, it is difficult to know how much seed to produce or, indeed, by which strategy it should be produced. Figure 1 represents a generalised, hypothetical case for the introduction of a new tree species into an exotic location. Not all farmers would take up the new species (Figure 1i), and farmers who did would not plant all of their available land with it (Figure 1ii). There may, in fact, be a peak acceptance, with a stabilised ceiling level below this peak owing to alternatives becoming available or to dissatisfaction with over-promoted material. Knowledge of the initial uptake, the rate of

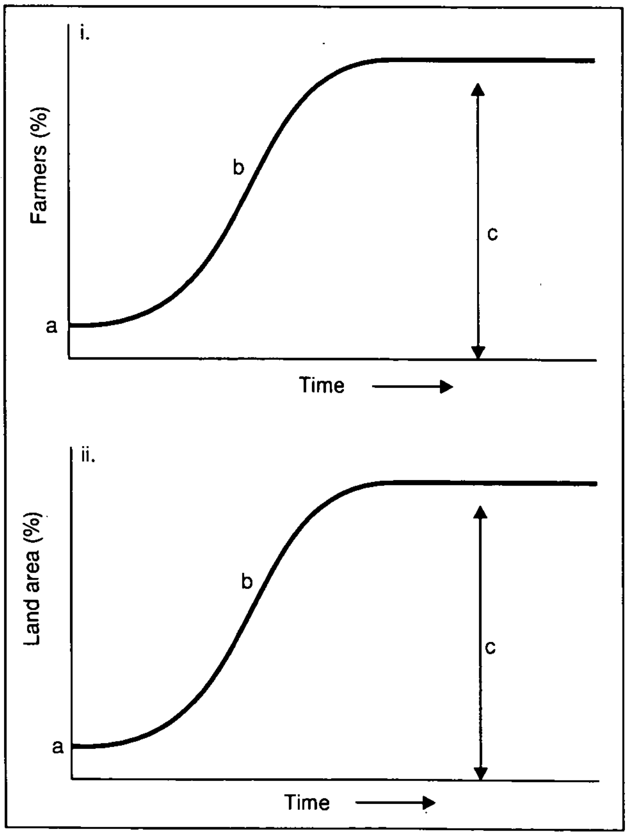

Figure 1. Generalised hypothetical case for uptake of tree planting in terms of (i) number of farmers and (ii) area of land (see text for further explanation)

uptake and the ceiling level would greatly assist in the formulation of breeding strategies and mechanisms for release. The way in which the timescale along the *x* axis in Figure 1 relates to the generation interval for that species is also important. If most farmers have taken up planting the tree (on whatever proportion of land they deem fitting) before one generation interval has elapsed, then the scope for introducing the next generation of material is limited to replacements. The significance of replacements will be high for short-lived species such as *Sesbania sesban*, but for most non-industrial trees, which are longer-lived, it will be minimal.

To convince smallholders of the merits of planting material from an advanced generation, the more genetically advanced material would have to be demonstrably superior. For quantitative characters such as wood yield, a small increase (say 10%) would be difficult for small farmers to perceive, particularly for multistemmed species. This does not mean that a modest gain is not important, but rather that it may be difficult to implement. Conversely, for qualitative characters such as tree form or insect resistance, the superiority of improved material would be readily observable, thus increasing its likely acceptance.

The qualities of a tree species are likely to be as important as the amount of material demanded. For crops, it has been found that farmers have different cultivar preferences, depending upon farm size, family structure, gender, wealth and market opportunities (Haugerud & Collinson 1990). Regional differences will also prevail, such as with the species *Moringa oleifera,* which is used for oil in Central America and leaf in Indonesia (Jahn 1989). Differences can also be seen in trait preferences in one region, such as the case with *Calliandra calothyrsus* in Flores, Indonesia, where certain farmers want single-stemmed aggressive trees for posts, whereas neighbours desire high leaf biomass trees, which display minimal root competition with crops. Therefore, if preferences are ignored, trees may be bred which farmers do not want.

SEED ORIGIN

Exotic species are being used in many cases where non-industrial trees are being promoted. For species where no naturalised populations or landraces already exist, smallholders must derive their material from farmer co-operatives, government extensionists, non-governmental organisations (NGOs) or donor agencies (collectively referred to here as 'seed distributors'). In these cases, however, after the initial planting material has fruited, farmers have the option of collecting seed from their own trees or from those of a neighbour. For *Calliandra calothyrsus* in Java, farmers leave one tree every 10–20 m of hedgerow to act as seed trees. Therefore, as time progresses, the proportion of seed derived from seed distributors will decrease as that from local sources increases (see Figure 2). The relative proportions of the two sources will vary according to region, and perhaps species. The way in which seed origin relates to farmer uptake is also important (cf Figures 1 & 2). One consequence of the majority of seed being derived from a farmer's own fields is that other farmers who do plant improved seed from the seed distributors will obtain increased performance for the life of those trees, but that any seed collected from them will be diluted by pollen from unimproved sources.

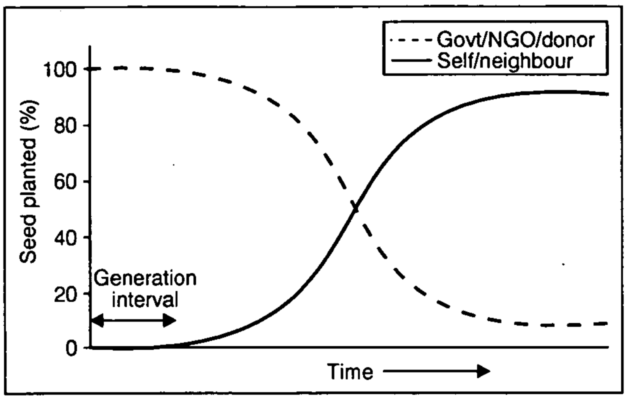

Figure 2. Hypothetical relationship showing change in origin of seed with time

The relative proportions of the two seed sources over time can only be guessed; though, by drawing an analogy to agriculture it could be expected that most seed will ultimately come from farmers or their neighbours' fields (Cromwell 1990). In this way, farmer seed diffusion mechanisms will have more impact than public sector seed organisations. For crop species, Cromwell (1990) described five characteristics for the success of the farmer seed diffusion mechanism, namely:

- its traditional nature;
- the informality of the mechanism;
- the operation at the community level;
- the evidence of a variety of exchange mechanisms; and
- small quantities of seed involved per transaction.

The significance of farmer seed diffusion mechanisms can be seen for many agricultural crops. In the Punjab Region of Pakistan, it was found that 86% of seed replacement of an existing wheat variety came from farmers' own fields or those of neighbours. New varieties entered the system through a few large farmers with later farmer-to-farmer exchange at the village level (Cromwell 1990). For maize, it was found that farmers in Kenya wanted to experiment with new varieties, and would evaluate riskiness, taste, marketability and susceptibility to pests. Interestingly, yield was not measured. They did not feel the need for the formal sector to provide improved seed in large quantities on a regular basis for replacement, and had the capability to multiply tested varieties themselves (Cromwell 1990). With a new rice variety in Nepal, six years after introduction 94% of farmers obtained seed of it from other farmers and not from the research centre (Cromwell 1990). The majority of farmers who received seed did not pass it on; rather, a few key individuals were responsible for passing seed on to other farmers.

A critical point with respect to farmer multiplication of cereal crops is that most cereals are self-pollinating and therefore breed true (Simmonds 1979). Consequently, the quality of newly released material would not be diluted by existing material present. Most tree species, on the other hand, are strongly outcrossing, so such dilution may occur. Another important distinction is that crops are generally annuals so the scope for new introductions is greater because new seed is required each year. Conversely, trees are longer-lived and their rate of replacement is low, so new releases would have less impact.

From the studies conducted on agricultural crops, it appears that farmers procure seed from local and readily available sources. A key element in the success of the release of non-industrial trees will be close liaison of technical scientists with sociologists and extension workers. One key area would be the planning and functioning of community-based nurseries (Scherr 1992); another would be the identification of the seed diffusers in rural communities. It may be that most gain through selection will come about from participatory breeding schemes, as suggested by MacDicken and Bhumibhamon (1990). Certainly, participatory plant breeding approaches have had great success with legume crops in India at the International Crop Research Institute for the Semi-Arid Tropics and with bean breeding in Colombia at the Centro International Agricultura Tropical (CIAT) (Cooper *et al.* 1992).

Greater awareness of the potential risks (eg weediness) of introducing exotic pioneer species (Hughes & Styles 1987) has, in part, led to initiatives to concentrate on native or naturalised species. Concerns over conservation issues have also led to the increasing sensitivity of donor agencies to the promotion of exotic pioneer species, as reflected by the emergence of regional biodiversity programmes (eg the Southern African Development Coordination Conference (SADCC) regional gene bank). With these species, trees may be planted or simply allowed to regenerate naturally. Where trees are planted, local farmers may possess knowledge of seed collection, ripening and treatment, yet may be unaware of the consequences of propagation from a restricted genetic base. In this case, forestry extension efforts could be redoubled to promote more optimal sampling and selection. Naturally regenerated material may also suffer from reduced outcrossing; supplemental planting schemes or recommendations on minimal numbers of trees could be proposed to counteract this effect.

CONTINUITY OF RELEASE

Before breeding of non-industrial trees commences, long-term decisions need to be taken regarding the continuity of release of improved germplasm. If the assumption that farmers will largely collect their own seed in future is correct, then this factor should guide the breeding strategy.

Once particular species have become known or superior provenances have been identified, there will be some demand by innovative farmers or strong supply initiatives by seed distributors to plant that material. The question arises as to whether or not unimproved seed of superior provenances should be released immediately or whether release should be postponed until after one generation of improvement. Following the former course would jeopardise gain from improved material released at a later date, whereas the latter situation requires farmers to wait one to several years. The relative advantages of these options could be evaluated if the information presented in Figure 1 were known. In the absence of such models and in the face of strong demand, it seems prudent to release unimproved material as many farmers are likely to plant what is available rather than wait, which is a luxury available only to non-subsistence farmers. Research workers also sometimes succumb to demand by releasing whatever is available even if this means collecting seed from provenance trials (J Timyan, SECID, Petion-Ville, Haiti, personal communication).

In the absence of strong demand from farmers, restraint in the wide promotion of identified superior sources by research organisations should be practised until sufficient seed is available. Some of the failures in popularisation of superior non-industrial trees in southern India have followed cases of over-promotion of insufficient seed supplies of these species (R Jambulingam, Tamil Nadu Agricultural University, Coimbatore, India, personal communication).

Some control over the amount of the dilution of gain may be possible with the release of unimproved material comprising families of low fecundity. This situation could be further rectified by selecting for high fecundity in the improved material to be released at a later date (providing this is not negatively correlated to desirable traits and there is no weediness potential).

It can be argued that there is a one-off chance for the release of improved material because future seed will largely come from farmers' own fields, which means that this material must be genetically diverse to avoid inbreeding and large founder effects. It does not rule out, however, future smaller releases to ensure a maintenance of genetic diversity. Future releases would ideally comprise different families from the initial releases, in essence being a sublining across time. In fact, the greater the opportunity for secondary releases (not necessarily second generations), the greater the scope for more intense selection, and hence gain, in the first generation. It is important for widely planted species that the genetic diversity of landraces is monitored to permit ameliorative action, if required.

POTENTIAL FOR IMPROVEMENT

Most tropical non-industrial tree species have not been improved beyond their wild state (Simons 1992). From reviews of isoenzymic variation, it is apparent that tropical trees contain pronounced intraspecific variation and show high levels of population differentiation (Hamrick & Godt 1989). Within each species there exists a breadth of variation that has been created and partitioned by evolutionary forces (mutation, migration, selection and drift), and which may also reside within naturalised or landrace populations.

Population differentiation is known to differ in magnitude between different species (Hamrick & Godt 1989), but for many of the tree species investigated there is significant variation at the provenance level, with four-fold differences in productivity not uncommon. For instance, the difference between best and worst provenances of *Eucalyptus* spp. grown in Africa was as much as 800% (Palmberg 1989). In attempting to breed from even an average-performing provenance, such increases would probably not be achievable. Clearly, then, significant improvement can be anticipated from the correct choice of population, suggesting that comprehensive provenance testing should be carried out before breeding begins.

From the large expense associated with rangewide collections (Willan *et al.* 1990), for a particular species to warrant intensive genecological investigation it must have shown some superiority or desirability. For lesser-known species, however, there exists the paradox that, unless they are evidently superior, no rangewide collection will be carried out, yet their superiority may only become manifest once rangewide samples are available for testing. Therefore, particular species may be discounted on the basis of the performance of one or a few provenances. Indeed, Stewart and Dunsdon (1991) found this to be the case where a poor population of *Prosopis juliflora* was included in an international trial series of Central American dry zone species.

The need to test more than one provenance per species, however, raises some difficulties with respect to the size of species elimination trials. If provenance identity is retained, then the large number of treatments may cause large block/treatment interactions. An alternative approach would be to bulk as many seed sources as possible for each species and examine not only mean performance, but also the variation around the mean. In this way, promising species could then be investigated in detail at the provenance level, an activity that would be required even if provenance identity had been maintained, unless a large number of provenances were included.

In commercial forestry, there has been a strong tendency to maintain the fidelity of provenances with an avoidance of provenance mixing, following the assumption that such mixing would cause breakdown of co-adapted gene complexes. Deliberate attempts at provenance hybridisation have had mixed success (see Barnes & Simons, pp84–90). Independent of whether or not there is a heterotic response to combining two or more provenances, the hybridisation (compositing) of provenances of non-industrial species may be inevitable as many organisations are involved in the testing, promotion and release of these species. Provenance hybrids would arise where two organisations released different provenances to the same area and farmers subsequently collected seed from trees in their own fields. In addition, where a landrace or naturalised population already existed (eg *Calliandra calothyrsus* in Indonesia), any new material released would hybridise with the existing population. It is unclear how much provenance compositing should be actively discouraged, or, alternatively, how much it should be promoted. For instance, while it may seem intuitively obvious not to permit compositing of a wood-producing provenance with a leaf-producing provenance because the benefits of each might be compromised, it may be possible to blend characteristics not found in combination in separate provenances (eg acid tolerance, insect resistance, high growth rate). These considerations are currently being examined for *Gliricidia sepium* in collaboration with the conservation and genetic improvement of Honduras forest resources (CONSEFORH) project, where a three-provenance hybrid is being evaluated against each of the parent provenances.

Whilst variation is likely to exist for the multiplicity of traits that farmers seek from trees in general, it may not be present for all traits in one species. Moreover, despite the label 'multipurpose' that is attached to most non-industrial trees, in many cases small-scale farmers cultivate trees for one or a few reasons and accept (but do not demand) the associated benefits. There may even exist negative genetic correlations between characters, making their simultaneous improvement difficult or impossible. Therefore, the concept of the ideotype that can fulfil all functions (ie shade, green manure, wood, fodder) is often illusory. Furthermore, in attempting to breed trees, it is important to be aware of the selection criteria of beneficiaries, as these may not coincide with those of scientists blinkered by mechanised, replicated and straight-line ideologies. Indeed, what will be required are trees which interact in a positive way with farming practices, rather than the most vigorously growing provenances, as these could overly reduce crop production in agroforestry.

A strategic concept in the breeding of non-industrial trees is not whether desirable variation exists for a particular species, but rather what chance there is of incorporating it into the fields of farmers. Figure 3 presents some generalised options for improvement, together with estimated gains. The way in which these relate to the generation interval and to farmer uptake and seed origin (Figures 1 & 2) should contribute to decisions on an improvement strategy.

Recurrent selection is expected to yield greater ultimate gains. However, if most farmers have planted the tree and seed is currently being derived from local sources, then such improvements are redundant. Another problem with recurrent selection is that, in order to achieve cumulative gains, there is a need to modify gene frequencies and thus narrow the genetic base. For some species in certain areas, there may be an opportunity to practise recurrent selection on different base populations of the same provenance, and to release second-generation material comprising different families from earlier releases (unimproved or first generation).

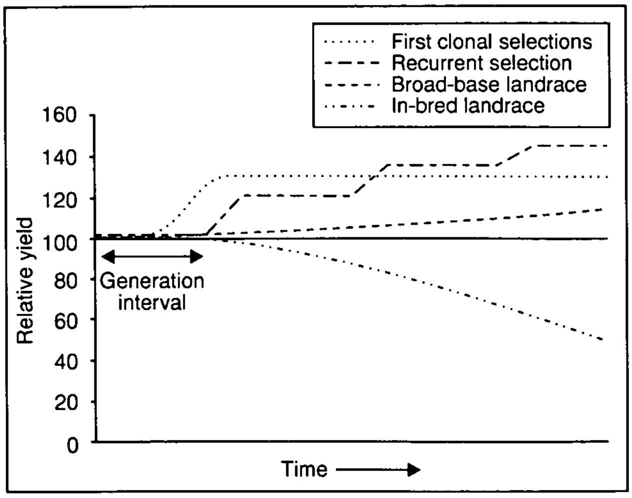

Figure 3. Hypothetical relationship showing genetic gain with time obtained from different breeding strategies

Selection of vegetative propagules has the advantage that it captures non-additive as well as additive gene effects (Simmonds 1979). Some species may not be amenable to vegetative propagation (usually by cuttings); however, for those which can easily be propagated, this method may offer the greatest scope for improvement. In cases where farmers cultivate only a few trees, then they are interested in all of their own trees doing well and not interested in the fact that the mean performance of all trees in their district is high. Accordingly, cuttings could be used to achieve this aim. For *Artocarpus heterophyllus* in Sri Lanka, two predominant varieties exist (with hard and soft flesh) which are used for different purposes, although they do not breed true. The use of cuttings allows hard-fruit trees (most desired) to be guaranteed.

Stakes as vegetative propagules are commonly used to create *'instant' fences or boundaries. For Gliricidia sepium*, stakes 2 m in length are often used, which show excellent survival. It is unclear in some areas whether stakes are used because of the problems of setting seed (eg northern Honduras, upland Sri Lanka) or because they are inherently preferred. Their advantages include that they do not take time to grow up, they compete well with other vegetation, and they require little tending. Unfortunately, this option is not available for all species (eg *Calliandra calothyrsus*).

Physiological differences between seedling- and cutting-derived plants may restrict the use of cuttings in some cases, such as with *Gliricidia sepium* where cuttings can be coppiced for four to eight years before declining whereas seedling-derived trees can be coppiced for over ten years (Liyanage & Jayasundera 1988). In addition, the more lateral root architecture of cuttings may not be suitable where below-ground competition with crops is important (eg in alley cropping). Another difficulty which can be seen with vegetative propagation is that, if few clones are released or come to dominate the clonal population, then seed collected from them may have a narrow genetic base, resulting in inbreeding.

If little organised breeding is operative, then it is hoped that landrace populations will develop that are more productive and relatively well adapted. The performance of the resultant landrace will depend upon the quality and quantity of different seed releases. To ensure sufficient variation to minimise inbreeding, to provide scope for farmers to select, and to exploit genotype/environment interactions, broadly based material must be released (see below, section on genetic gain and diversity).

METHODS FOR PROVISION OF SEED

Assuming that a provenance has been selected or that little population differentiation exists for a species, a range of methods are available to deliver seed to farmers: it may be:

- collected from the native range;
- produced from base populations; or
- bred in seed orchards.

Native range

Seed for distribution to small-scale farmers may be collected from selected or unselected trees in native stands. Some populations, however, may contain too few individuals for phenotypic selection to be practised (eg *Calliandra calothyrsus, Acacia tortilis*). Collection of seed from selected trees is not possible for some other species, because desirable phenotypes are masked as a result of disturbance (eg grazing or lopping for firewood). Even where numbers or disturbance are not restrictions, the efficiency of plus-tree selection from natural stands is debatable (Ledig 1974) so seed should ideally be collected from a representative sample of trees.

Willan *et al.* (1990) comprehensively reviewed the methodology for sampling germplasm from populations of multipurpose trees. These authors stressed the importance of adequate numbers of trees, minimum distance between them, and equal representation. For some species, however, this method may not satisfy the demand. For example, with *Gliricidia sepium*, every seed was collected from native trees of the most desired provenance (Retalhuleu, Guatemala) in 1992; the 10 kg thus collected, however, constituted less than 1% of what was currently requested. Similarly, with *Calliandra calothyrsus,* because of the small amount of seed produced per tree, combined with prolonged ripening and explosive pod dehiscence, the combined yield of a rangewide collection of 31 provenances in the native range in 1991–92 by staff from the Oxford Forestry Institute (OFI) was only 45 kg. During the same period, demand from just two countries (Haiti and Sri Lanka) exceeded this amount three times.

Some logic is contained in the statement 'the best way to conserve is to utilise', and this certainly applies for genetic resources under heavy pressure. Measures to prevent the loss of key genetic resources are fundamental to improvement capability.

Base populations

Seed may also be obtained from base populations for release to farmers. This system can be used when collection from native populations is insufficient or difficult, and is a simple, low-cost and quick option. Although no deliberate selection would be practised, it would be prudent to raise these populations in the target environments in case natural or inadvertent selection were prominent. This is essentially the concept behind the multiple population breeding strategy developed in Zimbabwe, which is designed to exploit genotype/environment interaction (Barnes & Mullin 1989).

A broad genetic base should be ensured through the planting of seed from as many trees as possible (ideally more than 50). The large number of families should mitigate against the effects of non-random mating and the build-up of co-ancestry in future generations.

Seed orchards

Lastly, seed may be produced from seed orchards where deliberate selection is made to enhance desirable traits. Within this format there is a range of options (described below in section on breeding options). The relevance of each of these methods will hinge upon the demand, the mechanism for release, and the available resources. There may even be a mixture of the three mechanisms, although the success of the third will depend on how much previous material has been released (if the assumption that farmers will collect their own seed in future is correct). If one organisation came into an area releasing unimproved germplasm and satisfied most of the demand before another organisation had bred its first generation of material, the overall effect of the latter on mean population performance would be diminished. Some co-ordination of effort between different organisations releasing germplasm is clearly required; the new CGIAR centres could have a role to play in this area. Understanding the role of improved seed and the mechanisms by which seed reaches small farmers has been critical to agricultural development, with the timely availability and physical accessibility of seed being identified as major determinants for planting of individual varieties (Cromwell 1990). For each of the methods used for the release of non-industrial tree germplasm, cognisance should be taken of these points.

For species that are already planted in an area before new (improved?) germplasm is released, the situation will be different. Where vegetative propagation is the mode of reproduction, then it may be easy to introduce new material and capitalise on its benefits (eg with *Gliricidia sepium* in Sri Lanka). It may be harder, however, if material is sexually reproduced, because there would be a mixing of unimproved and improved sources through the self-collection of seed. In some locations, particularly with good extension services and a high appreciation of improved germplasm, it is conceivable that multiple releases could satisfy planting requirements for a period of time until most previous material was replaced or newer material became available. Such situations, however, are likely to be the exception rather than the norm.

BREEDING OPTIONS

Where seed is to be produced in managed seed orchards, there are a number of important considerations which will be largely species- and region-specific. They include:

- seed orchard design;
- intensity of selection; and
- orchard management.

Seed orchard design

Seed orchards can be clone- or seedling-based. The classic clonal seed orchards of commercial tree species contain cloned genotypes selected at high intensities (eg 1/10 000; Zobel & Talbert 1984) following half-sib progeny tests or complex mating designs (eg diallels). This level of activity would be difficult to justify for non-industrial tree species because:

- intense selection reduces the genetic base and incurs risk;
- germplasm is required immediately, thus ruling out sequential testing as gain per year is more important than gain per generation;
- it may be difficult to select plus-trees because of disturbance;
- there are high and recurrent costs involved in this method; and
- the vast array of germplasm with which programmes have to deal makes intense work on any one species difficult to justify.

Seedling seed orchards (SSOs) or breeding seedling orchards (BSOs) are already being used for commercial trees for some of these reasons (eg *Pinus pinaster* – Alazard 1986; *Eucalyptus* spp. – Barnes & Mullin 1989). Reddy, Rockwood and Meskimen (1986) and Franklin (1989) examined the gain after one generation in an SSO of *Eucalyptus grandis* in Florida. Through retention of 117 families from 500 and on average 14 individuals per family from 60, there was a realised gain of 95% in wood volume in the first generation of selection. It is likely, therefore, that SSOs will prevail for non-industrial trees. Design of SSOs is important and includes elements of composition (ie number of families, number of individuals) and layout (spacing, plot type, number of replicates). Each of them should reflect the objectives of the seed orchard, the management of the orchard, and the selection intensity that can be practised.

Composition

Ideally, the larger the number of families included the better because it will ensure a broad genetic base and also allow for some between-family selection. For many species, though, family number will be limited by small population size (eg 25 in some *Acacia tortilis* populations) (Olong'otie 1992). If an objective of the SSO is to provide genetic parameters, then family number should be at least 20–25; otherwise, the standard errors are likely to swamp the parameter estimates (Crockford, Birks & Barnes 1989; A J Dunsdon, OFI, personal communication). To obtain accurate estimates of family means, numbers in the order of 20 per family are required (Cotterill & James 1984). With only 20 trees per family, however, this narrows the scope for within-family selection to 5% at most.

Layout

Assuming that there are fixed numbers of families and individuals per family (half-sibs), it is possible to arrange them differently within and between replicates. If a key objective is to estimate family means accurately, then smaller plots (down to single trees) should be used, particularly if family size is small. Apart from considerations of the statistical validity of single tree plots (Shuie & Pauley 1961; Franklin 1971), they are not always the ultimate arrangement. For example, work with *Picea sitchensis* (Johnstone & Samuel 1974) and *Pinus radiata* (Correll & Cellier 1987) found that four plants per plot were more efficient. If, however, within-family selection is more important, then larger family plots should be used to increase the efficiency of comparisons between individuals (Cotterill & James 1984). There will be a trade-off between these two considerations, depending on the method of selection (individual, family or combined), the relative values of family and individual heritabilities, the significance of final spacing, and the intensity of selection. Ideally, plot size should be equal to or less than 1/*p* (where *p*=proportion selected); otherwise, relatives will occur in the same plot, thus increasing the chances of inbreeding.

Intensity of selection

Intensity of selection comprises two elements: between- and within-family selection. Between-family selection will be most beneficial when number of families is high and when family heritabilities are high or individual heritabilities are low. Conversely, within-family selection is better when number of families is small and individual heritabilities are high. The largest family differences are likely to be evident at good growth sites, but these may not be representative of target environments, and there is the chance of family/environment effects.

The prime objective of a managed seed orchard may be to capture genetic gain (G) through selection. It is possible to calculate this algebraically using the standard equation:

$$G = i \cdot \sigma_p h^2$$

where i = intensity of selection; σ_p = phenotypic standard deviation; and h^2= narrow sense heritability.

It is easy to examine the effect of intensity of selection (i) on gain and to express this in terms of increased production. Increasing selection intensity, however, will reduce the genetic diversity of planting stock. If the proportion of selected individuals (p) is plotted against the intensity of selection (see Figure 4), it is clear that, with an increase in the proportion beyond 10%, there is a near-linear relation. A more rapid increase in (i) comes about if proportions below 10% are selected, when the relation is highly non-linear. Therefore, to obtain the greatest gain requires reduction of the selected population to a very small number of individuals. However, this incurs an exponential decline in diversity.

Lindgren (1986) plotted heritability, h^2, against optimal proportion of parents selected for different numbers of parents, and demonstrated that for h^2 between 0.1 and 0.3 the optimum is between 8% and 4%, respectively, for n=50. Such intense selection, however, would be inappropriate for non-industrial trees where the likelihood of few releases would cause genetic erosion.

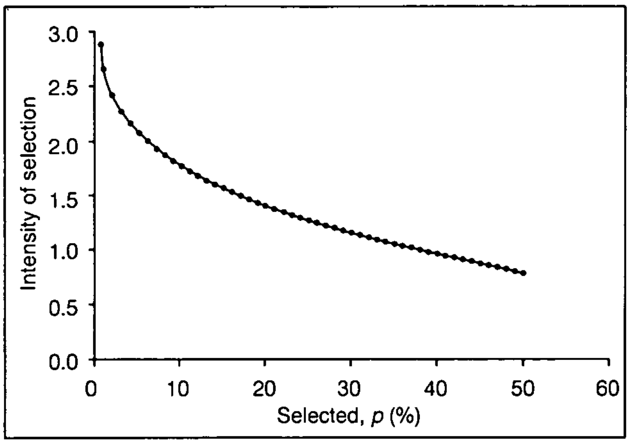

Figure 4. Relationship between percentage of population selected and the intensity of selection (see text for further explanation)

Orchard management

A conflict of purposes may arise in an SSO with respect to thinning. If the orchard is a progeny test, and this is a prime function of it, then selective thinning will bias genetic parameters. Matheson and Raymond (1984) found that h^2 of diameter at 19 years in *Pinus radiata* was inflated from 0.24 (SE 0.059) to 0.56 (SE 0.132) using systematic *versus* selective thinning, even at the mild selection rate of 50%. Other problems may arise with early selective thinning if juvenile/mature correlations are not good. Selective thinning will also cause uneven spacing, with resultant problems in comparing individual or family performance at later dates.

Early systematic thinning overcomes problems of heritability biases, spacing and juvenile/mature correlations, but there is the chance of eliminating useful individuals. If there are large numbers of trees in an SSO beyond those needed to calculate genetic parameters, then a compromise could be struck by having a central core to the trial which was systematically managed with surrounding blocks, where selective thinning was operative. The trees in the central core would provide information on genetic parameters yet could still contribute as seed or pollen parents after parameters were obtained. Meanwhile selection, and possibly early seed collection, could proceed in the surrounding block.

Caution will need to be exercised with selective thinning of dioecious species (eg *Simarouba glauca*). If thinning were carried out before flowering occurred, and morphological characters were sex-linked (eg as in *Fraxinus* spp.), then it is possible that the outcome could be an all-male orchard.

One advantage of the family-based seed orchard over a base population, even if no selection is practised, is that it provides control of pedigree. In this way, inbreeding can be minimised by maintaining sufficient individuals of selected families (or all families if no between-family selection is practised).

GENETIC GAIN AND DIVERSITY

Although calculation of the relative merit of greater genetic gain through intense selection is possible, the value of maintaining genetic diversity remains obscure because it is difficult to estimate. It includes a component of immediate economic value and a component of future potential to adapt to changing conditions (Namkoong 1984). Given that small-scale farmers who will use the trees need genetically diverse material, the numbers of parents retained should be high. Various published estimates of minimum population size are available, although they differ greatly in magnitude (n=25–1000) (Gregorius 1980; Namkoong 1984). There is no reason to suggest, however, that inferior trees within families are more likely than superior trees to contain useful variation for some unforeseen future purpose. Within-family selection, therefore, does not need to be compromised if large numbers of families are available.

With recent advances in molecular biology (eg RFLPs, RAPDs) (Waugh & Powell 1992), there is the opportunity to measure the total genomic diversity of individuals, families or populations free from the restrictions of sampling limited numbers of loci of largely structural genes (ie isoenzymes) (Hamrick & Godt 1989). Consequently, relative measures of diversity between families or individuals could be used to guide selection for seed parents in an orchard. This prospect is currently being studied in collaboration between the Oxford Forestry Institute and the Scottish Crops Research Institute, Dundee.

Associated with the estimation of genetic parameters, and hence gain, are a number of assumptions (eg random mating, no inbreeding, no selfing, additive gene action, etc) which may not necessarily be fulfilled. Although adjustments can be made for inbreeding or selfing (eg Reddy *et al.* 1986), it is important to verify the predicted gains by examining realised gains in genetic check trials. For example, Franklin (1986) found realised gain to be far below expected gain for growth traits in *Eucalyptus grandis.*

Maintaining a large genetic base allows a minimisation of inbreeding but conflicts with the objective of maximising gain. Studying inbreeding in *Pinus radiata*, Griffin, Raymond and Lindgren (1986) found that for each increase of 0.1 in F (inbreeding coefficient) there was a 5% decline in height growth rate after three years. Given the status of non-industrial trees, the avoidance of inbreeding cannot be overstated. When *Gliricidia sepium* was first introduced into Sri Lanka during the last century, it is believed that seed came from only a few trees; this restricted genetic base led to severe inbreeding in the resultant landrace (Hughes 1987). In support of this claim is the inferiority of this landrace when tested against unselected provenances from throughout the native range (Liyanage, Jayasundera & Liyanage 1991).

An often neglected aspect of tree improvement is an understanding of the reproductive biology of the species. This can affect genetic diversity and gain in several ways. For instance, with *Calliandra calothyrsus*, which has been shown to be largely bat-pollinated (D J MacQueen, unpublished data), there may be problems with fruit set in exotic locations (eg parts of Africa) because of a lack of the primary pollinator. In addition, flowering phenology may be significant: El-Kassaby, Davidson and Webber (1986) found more inbreeding in early and late flowering classes in a seed orchard of *Pseudotsuga menziesii.* Tremendous differences often exist between individual trees in their precocity of flowering so, although equal amounts of seed may be collected from trees, the intensity of sampling of individuals as male parents may differ greatly. One approach to this problem would be to collect seed from trees in amounts inversely proportional to the number of fruits they contained (assuming there were no sex-linked characters or that functional dioecy was not operating).

CONCLUSION

Although it is difficult to generalise about the improvement of all non-industrial tree species, similar features and decisions for different species are evident. In the formulation of decision models to guide tree breeding strategy of non-industrial trees, a number of salient concepts emerge, including status, demand, seed origin, continuity of release, potential for improvement, and genetic gain *versus* diversity.

Although no specific methodology for breeding non-industrial trees exists, workers in this field should avoid attempting to emulate work on agricultural crops and commercial forestry as the status of non-industrial trees is more varied. A requirement to ensure sufficient genetic diversity for current and unforeseen needs demands that broadly based material is released and selection intensities are relaxed. Recurrent selection and advanced generation breeding are generally irrelevant for non-industrial trees, except in areas where established extension services exist or appreciation of bred material is high. Gains should largely be seen as improvements to rural development, rather than as economic returns on investment.

Demand for planting materials of non-industrial trees will arise owing to farmer requests and the promotional activities of external organisations. Without knowledge of these demands, the direction that breeding should take is not well defined. Accordingly, some flexibility in approach should be retained, but not at the expense of making bred trees redundant because demand has already been satisfied from unimproved sources. Material from advanced generations will have to be demonstrably superior to make it preferable to previously planted stock, and this material will differ for quantitative and qualitative characters.

It is reasonable to assume that farmers will collect their own seed of non-industrial trees once this option is available. Consequently, there will largely be a one-off chance of release, which has implications for co-ordination of release: separate organisations should not release different populations which will subsequently hybridise and may reduce performance. Liaison between breeders and extension workers in the setting up of community-based nurseries and participatory breeding schemes is essential to ensure that planting material is appropriate and optimally productive.

Despite the undomesticated state of many non-industrial trees, the potential for improvement is tempered by the risk-averse and diverse group of beneficiaries who require stable as opposed to maximal production. In the majority of cases, selection of superior seed sources will provide the largest benefits, and it is of little point to begin breeding inferior populations. Multiplication of limited seed in seedling seed orchards provides some scope for moderate selection and gain.

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Clonal development and deployment: strategies to enhance gain while minimising risk

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ABSTRACT

Clonal tree improvement programmes contain two complementary aspects, clonal development and clonal deployment. Clonal development entails strategies to provide clones which not only express superior growth and yield, but are also buffered genetically against varying environments, including pests. Selection of clones from diverse populations and establishment of a large breeding population enhance the chance of including substantial genetic diversity, especially for developmental (individual tree) homeostasis toward environmental change. A multistage testing programme ensures that the clones in the production population are superior for growth at the forest stand level, as well as being genetically diverse for life history traits and pest resistance. Once clones are assigned to the production population, forest stand composition can be designed by the tree breeder and forester to utilise genetic (population level) homeostasis to take advantage of diverse pest resistance among the clones or diverse competitive strategies to occupy fully the niches within the stand. In addition, production traits which do not affect clone/environment interactions, such as wood properties and tree size, can be structured to be highly uniform within the stand in order to enhance product development.

INTRODUCTION

Clonal reforestation is practised operationally with both temperate (Kleinschmit 1974; Shelbourne, Carson & Wilcox 1989) and tropical (Leakey 1987) species worldwide. Interest among forest managers in clonal reforestation has increased dramatically within the past 15–20 years in response to the development of operational cloning systems (usually rooted cuttings) and to enhanced awareness of the benefits of such systems. To date, clonal technologies have been applied to a limited number of species. This review, therefore, draws primarily from experience with *Eucalyptus, Populus* and temperate-zone conifers.

Some of the most important benefits of clonal reforestation include:

- faster availability of genetically improved planting stock for reforestation compared with a traditional seed orchard/seedling-based tree improvement programme (Matheson & Lindgren 1985);
- higher genetic gains per generation compared with a seed orchard/seedling-based tree improvement programme (Chaperon 1991);
- greater uniformity of the resultant stands and forest products (Campinhos & Claudio-da-Silva 1990; Zobel, Campinhos & Ikemori 1983); and
- greatly reduced dependence on seeds for planting stock production (Leakey 1987).

Clonal tree improvement and reforestation programmes must be designed to optimise realised genetic gain. With any tree improvement programme, there is a risk that realised genetic gain (ie forest stand yield) will be less than predicted genetic gain. The worst-case scenario would be the loss of the stand prior to final harvest. The goal of a tree improvement programme is to develop one or more populations of planting stock which are adapted to the environments in which they are established, including resistance or tolerance to diseases, pests, and other adverse environmental factors, so that the risk of loss of stand growth and yield is minimised.

In a clonal tree improvement programme, the final yield of the forest stand (or other array of trees, ie agroforestry) is strongly influenced by the adaptation of the trees, individually and collectively, to the site. This adaptation has two components: (i) clonal development, and (ii) clonal deployment or stand establishment process. Clonal development approaches, including breeding, testing, and selection, largely affect the genetic quality of the resultant clonal population available for reforestation.

Clones must be developed which are highly selected for growth and productivity traits, but which display substantial developmental (individual basis) homeostasis as well as genetic (population basis) homeostasis. Developmental homeostasis refers to a genotype's ability to alter its physiology, physical development, and growth to adapt to its changing environment (Lerner 1954). Clones with highly stable performance over a range of environments (Burdon 1971; Bentzer *et al.* 1988) exhibit greater developmental homeostasis. Genetic homeostasis is 'the property of a population to equilibrate its genetic composition and to resist sudden changes' (Lerner 1954). Lerner proposed that heterozygosity provides the basis for both types of homeostasis. In a clonal reforestation programme, the fate of a particular ramet of a clone or clone within a stand is not as important as the growth and yield of the entire stand. Some mortality is expected during stand development, and trees have the ability to take advantage of additional growing space and other resources so that the growth of the survivors may compensate for the missing trees. Clonal deployment must strike a balance between the need for efficiency of forest management, harvesting and converting into economic products and the need to deploy populations which are genetically buffered against environmental changes (including pests).

CLONAL DEVELOPMENT

Clonal development relies on three processes: breeding, testing, and selection. Breeding creates new genetic variability; testing exposes the new genotypes to appropriate environments; and selection favours certain genotypes for population development. At least three populations are conceptualised: the gene resource population, the breeding population, and the production population (Libby 1973; Foster 1986; Shelbourne *et al.* 1989). The gene resource population is often the wild or unimproved population from which new selections can be derived. The breeding population is the somewhat improved population of all genotypes which are used to create the next generation of crosses. A wide range of genotypes may be kept in this population as long as each one has at least one characteristic of possible future interest. The production population consists of the highly selected genotypes which are used for reforestation.

Breeding

Breeding is used to create genetic diversity from which new selections can be made. To be functionally useful, genetic diversity is needed in traits which aid survival, growth, and development of genotypes in the population. Functional genetic diversity results in enhanced developmental and genetic homeostasis, and hence in adaptability.

Several breeding methods can be used to breed for enhanced genetic variability, especially for creating extreme genotypes useful for clonal reforestation (Foster 1986, 1993). These methods include the development of multiple populations or sublines; use of specific mating designs; use of positive assortative mating; breeding for non-additive and additive genetic variation; and interspecific hybridisation. A brief summary of each follows.

Multiple populations, nucleus breeding and sublines

Multiple populations differ from sublines in that the former seek to enhance or at least maintain genetic differences among populations, while sublines are random subsets of the population (Burdon & Namkoong 1983). Genetic differences among sublines are due to the effects of initial sampling, 'founder' effects, and random drift over generations of breeding.

Nucleus breeding is a variant of the multiple populations approach in which a small subset of individuals (eg 40) is copied from the main breeding population into a nucleus population (Cotterill *et al.* 1989). One or more nucleus populations can be developed, each with the same or different goals of selection. Breeding efforts continue at a lower level in the main breeding population, while the major breeding effort is concentrated on the nucleus population(s). The goal of multiple or nucleus population development is to enhance genetic differentiation. Interpopulation crosses could be used as terminal crosses to create extreme genotypes for one or more traits. Aracruz Florestal SA has incorporated the multiple population concept in its tree improvement programme with 20 populations (20 genotypes per population) of *Eucalyptus grandis* and 20 populations of *E. urophylla*. Ten crosses will be made inside each population, forming ten full-sib families per population. In the full-sib families, the best tree will be selected and interspecific crosses made to seek 'super hybrids' for the clonal programme (Campinhos & Ikemori 1989).

Mating designs

Once the genetic basis (type of gene action: additive, dominance or epistasis) is known for the superiority of traits in specific genotypes, then mating designs, heretofore unique to animal breeding, can be used. The goal of these designs, such as breed complementation or specific three-breed terminal crosses (Hohenboken 1985), is to develop specific types of individuals in the offspring generation for the production population. The parents are often superior for different traits, which are then combined in the offspring.

Positive assortative mating

Positive assortative mating entails mating 'like' parents in the population rather than random mating. For example, the top-ranked individual is mated to the second-ranked, third-ranked is mated with fourth-ranked, etc. This pattern of mating is known to increase genetic variation in the population while also increasing homozygosity for the selected trait (Crow & Felsenstein 1968). Much of the effect is seen in the first few generations of positive assortative mating. In a simulation study, Mahalovich and Bridgwater (1989) found an increase in genetic gain of 0–6% from positive assortative mating and selection through 14 generations of mating. In addition, they found an increase in the number of extreme genotypes.

Breeding for additive and non-additive genetic variation

Most tree improvement programmes emphasise breeding and selection for additive genetic variation or breeding value (recurrent selection). However, additional gain may be obtained by breeding for both additive and non-additive (dominance and epistasis) genetic variation. Improvement plans such as reciprocal recurrent selection (Comstock, Robinson & Harvey 1949) can be modified for use in forestry (McKeand, Foster & Bridgwater 1986). These types of improvement plans require several generations to develop, and to date remain untested in forestry.

Interspecific hybridisation

Interspecific hybridisation is known to create large amounts of variability in the offspring generations. This genetic variability can then be used within a tree improvement programme, especially with clonal reforestation (eg Teissier du Cros 1984). This process often contains many problems, eg cross-incompatibility and low-vigour offspring, but occasionally some outstanding offspring are produced. Results from such crossing vary tremendously, depending on the species involved. One goal of interspecific crossing is to join the desirable characteristics of two different species. A good example is crosses between *E. grandis* and *E. urophylla*, whose hybrids have shown great stability and high quality of wood for pulp production.

Testing

Tree breeders have expended considerable effort on researching the effects of genetic test design on genetic gain. There is a trade-off between accuracy of genetic value estimation and intensity of selection (ie greater accuracy is at the expense of numbers of families, individuals per family, or clones). The optimum strategy depends on heritability of the trait and available testing resources. For clonal tree improvement programmes, Shaw and Hood (1985) and Russell and Libby (1986) found that, for fixed resources, as many clones as possible should be tested with relatively few (ie 2–6) ramets per clone.

The tree improver must stratify the potential reforestation environments into more or less uniform (non-interactive) subsets. Initially, the entire breeding population must be tested across the potential reforestation environments. The trees in the breeding population are used as a bioassay to delineate these 'breeding zones'. Simultaneously, the breeding population and the environments are subdivided into subsets of genotypes and matching environments. Within a breeding zone, genotypes are expected to express a non-significant interaction (ie rank change) with environments. Trees are matched within but not among breeding zones. Resultant clones are planted within the zone.

The tree improver must also assess the potential environment apparent within the range of reforestation environments, and must establish appropriate genetic tests to assess genotypic performance in the various environments. In most tree improvement programmes, multiple traits (eg survival, volume, height, disease resistance, bole straightness) are being improved simultaneously. Different types of tests may be used to assess each trait. For example, tree growth and yield, bole form, and wood properties may be assessed in field tests, while rapid screening for disease resistance may be accomplished in a greenhouse environment (eg Matthews & Rowan 1972). Disease screening in artificial environments allows collection and use of a wide range of pathogen races to screen simultaneously for host resistance. However, strong correlation must exist between host reaction in the field and in the artificial environment.

Genetic improvement for yield per hectare in forestry will undoubtedly require a series of tests. For clonal forestry, Libby (1987) has proposed four levels of testing. The four levels are: *initial screening* (Level I) with large numbers (eg thousands) of genotypes and only a single seedling or few ramets per clone; *candidacy testing* (Level II) with large numbers of genotypes (fewer than with Level I, hundreds or low thousands) and low numbers (2–6) of ramets per clone; *clonal performance* (Level III) with moderate numbers of genotypes (eg <200) and large numbers (eg 0.1 ha plots) of ramets per clone; and *compatibility trials* (Level IV) with small numbers of genotypes (eg 20–50) with very large plot sizes. This scheme would result in the choice of clones with detailed growth and yield performance. As such a scheme will require a long time period, clonal maturation must not be an insoluble problem.

Selection

Initial selections are made from the gene resource population. Selection intensity may be high, but low heritabilities in natural stands typically result in relatively low genetic gain from this initial step in a selection programme, if the resource population is a natural stand. An important exception may be genetic gain for disease resistance when disease-free individuals are selected from heavily diseased forest stands. Superior select trees should be derived from a wide range of locations within the appropriate portion of the species' range. General tree improvement principles (Zobel & Talbert 1984; Wright 1976) can be used to guide the choice of area to sample within the natural range. A wide dispersion of sample locations within the natural range will enhance the chance of capturing a large range of genetic diversity in the breeding population.

Once initial selections are made, genetic tests, either seedling or clonal, are established. Superior selections for the breeding population and the production population are made from the genetic tests. Selection for the breeding population focuses on superiority for additive genetic value. Because the breeding population is relatively large (hundreds or even thousands of genotypes), a large number of genotypes is selected to reconstitute the population, and hence selection intensity and genetic gain are modest.

Clonal selection

Clonal trials can be established directly (by felling the select trees and rooting cuttings from the stump sprouts, which is feasible with some *Eucalyptus* species, for example), or seedling-based progeny trials can be established with either open-pollinated or controlled-cross seedlings. In a clonal programme, the production population contains relatively few clones (usually fewer than 100; Aracruz Florestal SA currently has 80 clones in operational plantations) which are selected for genotypic value, not breeding value. The exact source of the genetic superiority is unimportant for this population. In fact, if non-additive gene action is important in a population, many of the genotypes in the production population may not be included in the breeding population (Foster 1986, 1993). Genetic gain in the clonal production population is greater, and possibly much greater, than in the breeding population (Foster 1986).

Multiple trait selection

Most tree improvement programmes emphasise selection for multiple traits. Unfortunately, as the number of traits increases, the number of genotypes superior for all traits diminishes rapidly; selection intensity must therefore increase, or genetic gain will plummet. For this reason, only the few most economically important traits (typically growth and productivity traits) should be emphasised. In environments where disease or drought are important, tolerance of these conditions may also be strongly emphasised. Debate rages among pathologists and plant breeders as to the best breeding strategy for disease resistance (Marshall 1977). The use of single major resistance genes (vertical resistance) has proven to be only a brief solution in breeding agronomic crops, as the pathogens can quickly mutate to overcome the host's resistant gene. More promising strategies include breeding multiple single genes for different resistance mechanisms into the same variety, or utilising polygenic resistance genes (horizontal resistance) (Marshall 1977). Multiple resistance mechanisms for the same disease are well known in forest trees; such procedures are therefore also feasible in forestry.

Genetic conservation

Agronomic plant breeders have been somewhat careless about allowing genetic diversity within their crop species to erode as a trade-off for greater genetic gains (Marshall 1977). Tree breeders must be careful to maintain wide genetic variability for all traits that are not being selected during directional selection, because the latter narrows the genetic base for those traits under selection. This is especially true for traits which control adaptation. The breeding population is a good place to maintain this diversity. Traits of interest for developmental homeostasis (adaptability) include: growth rhythm, response to moisture deficits, disease resistance, pest resistance, tolerance of different irradiances, rate of photosynthesis and respiration, live crown dimensions, leaf shape, coppicing ability, etc. It is very important for tree breeders to know genetic correlations among these traits and the traits of more economic interest. This information will help them to monitor the inadvertent effects of indirect selection for the homeostatic traits and even counteract the effects if they are detrimental. Given that the set of genotypes in the production population is dynamic, it is necessary to maintain clone banks as a repository for germplasm. The breeding population will also serve as a repository for genetic variability.

CLONAL DEPLOYMENT

Despite its overwhelming importance, little research has been conducted to investigate the effects of different deployment strategies on the health, growth and yield of forest stands. By nature, this type of research requires a large amount of resources and a long period of assessment. The major questions are as follows.

- How many clones should be in the production population, and how many should be deployed to a single site?
- Should the clones be deployed at a single site as a mixture or as mosaics of monoclonal stands?
- What are the key attributes of the clones themselves that cause them to be used either as mixtures or as monoclonal plots?

Number of clones

The question of number of clones to be deployed contains two aspects: the number of clones within the production population, and the number of clones planted per site. Several research papers have addressed the theoretical aspects of these issues, but few experimental results have been reported.

Number of clones in the production population

Consensus among tree breeders and forest geneticists indicates that production population sizes of 100 genotypes or fewer are acceptable. Seed orchard/seedling-based tree improvement programmes utilise 20–50 parental genotypes in the rogued seed orchard. Owing to genetic recombination in the seed production process, the variety of offspring genotypes from such a programme is very large, especially given the relatively large amount of genetic heterozygosity within most populations of forest trees.

Theoretical studies have sought to assess either the risk of plantation failure or the stability of performance when using varying numbers of clones in the production population. Although the goal of these studies was to examine the effect of varying numbers of clones per site, the results can be extended to gain insight into the minimum number of clones needed in the production population. Libby (1982) proposed a range of between seven and 30 clones as a relatively safe number, while Huehn (1988) found that a safe number of clones in a clonal mix was generally between four and 50, depending on assumptions and the area to be forested.

Actually, the absolute number of clones is less important than the range of genetic diversity among the clones. Ten clones which share the same alleles for a particular trait would express no genetic diversity, as contrasted with five clones each of which had different alleles for the same trait. Hence, the tree breeder must emphasise genetic diversity for traits associated with survival and adaptation, while exercising strong selection pressure on production traits.

Aracruz Florestal SA currently uses 80 *Eucalyptus* clones in its production population, with more in the initial stage of multiplication. The planting area is divided into three regions with 65 clones used in Aracruz, 40 in Sao Mateus, and 29 in the south of Bahia State. Several of the clones are common to all three areas because of their superior developmental homeostasis. Following rigorous multisite testing, new clones are added to the production population each year.

Number of clones planted at each site

The goal of deploying superior clones to reforestation on a site is optimum production (solid wood products, fibre, food, or other forest products) with minimal risk of failure to meet the production potential. Libby (1982) utilised the concept of 'risk to a random genotype' (RRG) in a theoretical study investigating acceptable numbers of clones to be deployed in clonal reforestation. Furthermore, he utilised the concept of 'maximum acceptable loss' (MAL) as the level of stand loss below which a forest manager would be unwilling to accept the loss. Based on probability theory, he found that seven to 30 clones, depending on RRG and MAL, provide reasonable probability of achieving an acceptable final harvest. In their theoretical study, Lindgren, Libby and Bondesson (1989) investigated the interaction between clonal diversity within mixtures and genetic gain. A key, and somewhat controversial, assumption of their analysis was that interactions between ramets of the same clone are negative and, conversely, that interactions between ramets of different clones are positive. Therefore, fewer clones in the population conferred an increasingly greater disadvantage, or reduction in genetic gain. Using this assumption, they developed a model which related effective population size to the truncation point, due to selection, on the normal distribution curve. Their analysis demonstrated that, by varying the frequency of clones in the mixture, rather than using equal proportions, genetic gain could be enhanced by selecting more clones, with the lower ranked clones occurring at increasingly lower frequencies.

For operational plantings with *Eucalyptus* clones, Aracruz Florestal SA utilises at least four different clones for each 150 ha. Also with *Eucalyptus*, the Industrial Afforestation Unit of the Congo (UAIC) operationally plants their clones in 50 ha monoclonal plots around Pointe-Noire, Congo (Leakey 1987).

Well-designed empirical studies are needed to address the question of the number of clones which should be deployed per site, to guide clonal reforestation. Such studies must incorporate a variety of clones with a range of known growth and yield performance, as well as susceptibility to disease, moisture deficits, and other adverse environmental factors. The tests should include a wide diversity of site quality.

Clonal mixtures *versus* mosaics of monoclonal stands

Most tree improvers and forest geneticists agree that single-clone plantations do not offer any chance for genetic homeostasis, and so the risk of plantation failure owing to the failure of a single clone is too high. If more than one clone is deployed on a site, then the two extreme alternatives are a complete mixture of all clones at the site, termed 'widespread intimately mixed plantations', or 'mosaics of monoclonal stands' (Libby 1987). A large body of research results on this issue with agronomic crops has been published (Trenbath 1974; Harper 1977). Unfortunately, the results have been mixed, with some reports showing superiority of the pure varieties over the mixtures, while others have indicated that the mixtures have significantly outperformed the average of the pure plots. On occasion, the mixtures have even outperformed the best pure variety. In his review on non-woody plant biomass yields, Trenbath (1974) found that, of 344 mixture comparisons reviewed, the mixtures over-yielded the best pure component 24% of the time, and under-yielded the worst component 13% of the time, with the remainder being intermediate between the two pure components. In his review, Marshall (1977) showed only two out of 328 mixtures which over-yielded the best pure component plot.

The only published study with forest trees comparing pure *versus* mixed-clone plots of which we are aware was published by Markovic and Herpka (1986). The authors reported fourth-year field results with five clones of *Populus deltoides*. Large plot sizes (100 trees) enabled valid estimations of volume productivity per hectare. For volume per hectare, average height, diameter at breast height (dbh), and basal area, the mixed-clone plot performance was intermediate compared with the mean of the pure-clone plots. There was slightly higher (though non-significant) volume per hectare (12.8%), mean height, mean dbh, and basal area for the mixed-clone plot compared with the average of the pure-clone plots. Hypothetically, stand development may have enabled the faster-growing, dominant clones eventually to control the stand so that the stand attributes were raised closer to that expected of the superior clones.

In a previously unpublished study with *P. deltoides*, G S Foster (USDA Forest Service, Huntsville, Alabama, USA), R Rousseau (Westvaco Co, Wickliffe, Kentucky, USA), and W Nance (USDA Forest Service, Gulfport, Mississippi, USA) established a mixing study with two locations (James River Co, Vicksburg, Mississippi, and Westvaco Co, Wickliffe, Kentucky, USA), four replications per location, and seven clones. The plot size was 64 trees in a square plot with the inner 36 trees as the measurement plot. A spacing of 3.66 m x 3.66 m was used, yielding measurement plot sizes of 0.048 ha. Monoclonal plots were planted for each of the seven clones, and binary-clone plots were established for seven pairs of clones. Each binary combination was represented by two plot types: (i) 75% Clone A/25% Clone B and (ii) 25% Clone A/75% Clone B. With four plot types (two monoclonal plots and the clone mixture at two ratios), a replacement series graph of volume per plot could be drawn. Total height and dbh were measured at ages two, three, and four, and whole-tree volume was totalled on a plot basis. Two of the seven pair combinations are presented in Figure 1. These two are presented here because of the contrasting results obtained. Different clones were represented in Mixes 1 and 2. In Mix 1, the results were opposite at the two locations, yet the mixed-plot yields are virtually linear across the replacement series. In Mix 2, the ranking of the two clones was the same at both locations; however, the mixed plot 75% C:25% D over-yielded the best pure-clone (C) plot by a large margin. These results show that field results for mixed-clone stands *versus* mosaics of monoclonal stands may vary

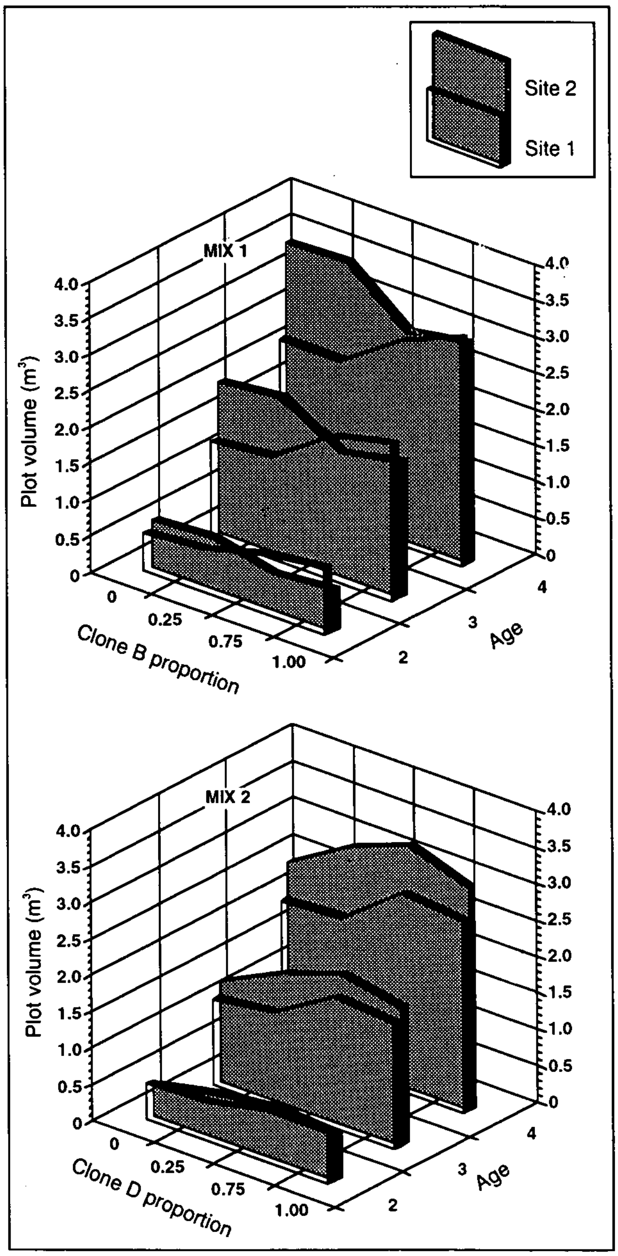

Figure 1. Plot volume production of *Populus deltoides* clones at ages 2, 3, and 4 at two planting sites in a replacement series study with binary-clone pairs. Mix 1 has clones A and B, and Mix 2 has clones C and D. At each of the four sample proportions, the ratios sum to 100% (ie 0% A/100% B)

dramatically by site and may be specific to the particular set of clones.

Theoretical considerations argue against mosaics of monoclonal stands; yet experimental results generally have failed to support the expected superiority of mixtures. The potential advantages of mixtures are: '(i) increased yields through the exploitation of favorable interactions between component genotypes; (ii) greater stability of performance in diverse environments; and (iii) a reduction in disease and insect damage' (Marshall 1977). Mixed genotype stands should afford more resistance or tolerance of pest attack as non-susceptible genotypes will help slow the spread of the pest (Marshall 1977; Heybroek 1982), but mosaics of monoclonal stands may be an acceptable compromise with certain diseases (Heybroek 1982). Actual results with agronomic crop species (Trenbath 1974; Marshall 1977) and tree species (Markovic & Herpka 1986) generally have shown little or no greater yield of mixtures over the average of the monoclonal plots. If such studies are conducted in pest-infested environments, the mixtures might fare much better (Kroll, Moore & Lacy 1984).

Practical arguments can be made to support either deployment strategy. From a management standpoint, the mosaics of monoclonal stands offer the forest manager the chance to observe the performance of single clones. This observation will lead to extremely valuable information on clonal growth and yield, clonal wood properties and log characteristics, clone/site interaction, and resistance to adverse environmental factors (including pest resistance). If a single clone succumbs to an adverse environmental factor prior to harvest, the affected stand can be removed and replanted. However, if the clones are mixed, then a certain percentage of all trees in the stand may succumb, dropping the stand yield below an economic threshold. Forest managers may take more risk with short-rotation intensive management or agroforestry plantings, and may therefore exclusively plant mosaics of monoclonal stands. Managers working with species with medium-length rotations should be more cautious and may want a portion of their reforestation with each of the two alternatives. Managers with long rotations may want to use mixed-clonal stands as an insurance against losing the stands after many years of investment and growth.

Another aspect which can influence the choice of strategy for clonal deployment is the quality of wood produced by the stand. In the case of pulp production, for example, some characteristics should be maintained within a narrow band of variation in the production population (Demuner *et al.* 1991). Uniform wood properties in pulp optimise paper quality produced by a mill. This leverage point influences the adoption of mosaics of monoclonal stands because, within each stand, the characteristics of the wood produced will be homogeneous and completely predictable.

Attributes of clones which influence deployment

Few theoretical or empirical results have been published regarding the relationship between physical attributes and clonal performance in monoclonal or mixed-clone blocks. Markovic and Herpka (1986) noted a slight, yet non-significant, growth advantage for the mixed plot over the average of the monoclonal plots. G S Foster, R Rousseau and W Nance (unpublished) found a linear relation between plot volume and proportion of each clone in a two-clone replacement series, while in a second two-clone replacement series the same relation was curvilinear (Figure 1).

Why do clones interact in a variety of ways, additively, over-yielding, or under-yielding? Crown or root system architecture of the clones may help explain their interaction. Clones that have narrow crowns and root systems and otherwise use their allocated growing space efficiently (termed 'crop ideotypes') may interact in an additive fashion in a replacement series. Clones that have broad crowns and otherwise take more than their allocated growing space (termed 'isolation ideotypes') may perform poorly in either pure plots or mixtures with other clones that are isolation ideotypes. The most efficient mixtures may be between clones which are crop and isolation ideotypes, thereby more completely using all available resources. Attributes which may serve as mechanisms for these interactions include live crown length, crown radius, leaf area index, height, dbh, depth of root system, and horizontal spread of root system.

Another general mechanism for inter- and intraclonal interaction is through diversity of resistance to adverse environmental factors. Performance of monoclonal stands of susceptible clones could be severely reduced, even to zero by complete mortality. Disease resistance provides an interesting case of this class of interaction. Mixtures of clones with varying degrees of resistance could result in lower net loss than mosaics of monoclonal stands, as resistant trees tend to slow the rate and severity of disease infestation among susceptible genotypes (Heybroek 1978, 1982). The negative side of the mixtures is that salvage of the susceptible trees would be much more difficult than with monoclonal stands.

CONCLUSION

A successful clonal tree improvement and reforestation programme depends on the development of appropriate clones and the deployment of those clones, based on knowledge of inter-tree competition and interaction with the environment. Clones must be developed which have substantial developmental homeostasis in order to interact favourably with changing environments. Breeding methods are available to enhance genetic variability within the offspring genotypes for traits which determine adaptation to the environment, while at the same time encouraging development of extreme genotypes for productivity traits. Appropriate genetic tests must be used to assess these somewhat different types of traits: survival and adaptation *versus* productivity. A series of tests combined with selection to test fewer and fewer clones with increasing numbers of ramets is recommended.

Clonal deployment varies with rotation length and types of adverse environmental factors (eg diseases or drought) that the forest stand will encounter. A high degree of genetic homeostasis must be built into forest stands by careful clonal deployment. Mosaics of monoclonal stands may be particularly useful for short-rotation management in the absence of adverse environmental factors. As the rotation length and the probability of adverse environmental factors increase, either a mixture of mosaics of monoclonal stands and clonal mixtures or entirely clonal mixtures should be used. Monoclonal stands are particularly useful for gaining information on specific clones.

These strategies for clonal development and deployment, based on experience with a limited number of tree species, should be applicable to the large number of tropical tree species which are largely undomesticated. In the case of such species, where tree improvement programmes have often not yet been initiated, the first priority may be to identify rapidly superior individuals in wild populations (see Ladipo *et al*., pp239–248; Lawson, pp112–123). Where the users of clonal technologies are small-scale farmers rather than industrial concerns (eg see Mesén, Boshier & Cornelius, pp249–255), novel strategies may have to be developed to mitigate risk. The application of clonal techniques in such situations offers great prospects for increasing gains and stimulating reforestation in the future.

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Regeneration of new forest resources

Indigenous trees in West African forest plantations: the need for domestication by clonal techniques

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ABSTRACT

Forests in West Africa have recently been disappearing at 1.2 million ha (4%) per annum, yet the area planted annually with trees was only 36 000 ha in the mid-1980s, and is now very much less. Many tree planting schemes, particularly in Cameroon, have failed because of inadequate site clearance and subsequent neglect of maintenance. Yet the yield of several species in research plots has been found to be acceptably high, and a number of species, such as *Terminalia ivorensis, T. superba, Triplochiton scleroxylon* and *Aucoumea klaineana*, can achieve an average diameter of 60 cm in 25–30 years. The economic returns from rotations of 30 years or less are highly attractive, even with poor markets for thinnings. Internal rates of return between 9% and 20% have been calculated for such stands in Cameroon. However, private sector and farmer confidence in the wisdom of tree planting is only likely to be encouraged by: (i) financial incentive schemes; and (ii) the development of techniques for selection and improvement of faster-growing and more valuable planting stock than has been available up to now. There is a particular need for an international hardwood improvement programme in West and Central Africa.

INTRODUCTION

Whilst reasonable information is available from West Africa on the yield and profitability of exotic species of *Pinus, Tectona, Eucalyptus* and *Gmelina* (Allison *et al.* 1986; Horne 1967; Lowe 1976; Kio *et al.* 1989; Ball 1992), it is more difficult to obtain reliable data on the native hardwood species which are being 'domesticated' and used in timber plantations. Three indigenous species have been planted widely in West Africa: *Triplochiton scleroxylon* (obeche, samba, wawa, ayous), *Terminalia ivorensis* (black afara, framiré), and *Terminalia superba* (white afara, fraké, limba). However, many of these plantations were established on a small scale, and few analyses exist of their establishment costs, yields and likely profitability. This paper therefore:

- considers the need for tree plantations in West Africa;
- summarises existing information on plantation yields of indigenous species;
- comments on the likely profitability of these plantations;
- describes the efforts being made by the Cameroon Forest Management and Regeneration Project to improve the management and yields of indigenous tree plantations; and
- speculates on the potential for vegetative propagation and clonal selection to increase the growth rates and marketability of native hardwood species.

DEFORESTATION AND REFORESTATION IN WEST AFRICA

The average annual rate of deforestation in West Africa from 1981 to 1985 (the most recent reliable data) was 2.2% overall, and 4.1% in closed forest. These are the highest regional figures in the world, and compare with an average annual loss of closed forest of 0.6% in Africa and a global average of 0.3% (Table 1).

Official statistics also indicate that 36 000 ha of plantations were established annually in West Africa during the mid-1980s. This figure is very small compared with the 1.7 million ha of forest which were being lost annually at the time, and it is even less significant when one considers the poor maintenance and survival of these plantations, and the fact that they were usually established in areas of existing forest. Furthermore, there is little doubt that the rate of plantation establishment has declined considerably since the mid-1980s.

Thus, although West Africa has recently suffered the greatest proportional loss of forests in the world, it has an almost insignificant replanting programme. Considerable recognition exists of the economic, environmental and social costs of unabated removal of forests. In Nigeria, for example, it is calculated that the decrease in soil fertility and water quality caused by deforestation costs more than US$5 billion annually (World Bank 1992b). However, there is no evidence of tree planting programmes being supported on a sufficiently large scale to relieve the pressure on

Table 1. Rates of deforestation and tree planting in West Africa (source: World Resources Institute 1992)

	Extent of natural forest and woodland (kha in 1980)			Annual deforestation (1981–85) (kha)				Plantations (kha)
	Closed forest	Open forest	Other woodland	Closed forest		Total forest		
				(kha)	(%)	(kha)	(%)	
Benin	47	3 820	6 832	1	2.6	67	1.7	0
Côte d'Ivoire	4 458	5 376	15 390	290	6.5	510	5.2	6
Ghana	1 817	6 975	9 480	22	1.3	72	0.8	2
Guinea	2 050	8 600	9 000	36	1.8	86	0.8	0
Liberia	2 000	40	5 640	46	2.3	46	2.3	2
Nigeria	5 950	8 800	49 450	300	5	400	2.7	26
S. Leone	740	1 315	4 278	6	0.8	6	0.3	0
Togo	304	1 380	3 720	2	0.7	12	0.7	0
West Africa	17 267	36 306	104 690	703	4.1	1 199	2.2	36
Cameroon	17 920	7 700	15 600	80	0.4	110	0.4	1
Central Africa	170 395	11 915	71 575	307	0.2	575	0.2	3

undegraded natural forests, neither is there much consensus on how forest regeneration is best encouraged.

There are five approaches to forestry management in the humid forest zone.

Conservation schemes

These schemes often require that logging ceases, and place severe constraints on villagers' activities. Governments may be granted loan remission, and villagers given new facilities, but conservation 'exclusion zones', which do not allow local populations to utilise timber or game, are unlikely to encourage a genuine commitment to conservation among the community (Besong 1992).

Sustainable management of the natural forest

This ideal has many adherents, but few genuine practitioners. Techniques for the effective management of natural forests are poorly understood, and there are many management and economic problems. Some recent results, involving careful inventory and selection of trees to be felled, together with selective poisoning of competing low-value trees, have enhanced the growth of commercial species (by up to 6–7 m^3 ha^{-1} yr^{-1}) without excessive environmental damage (Jonkers 1987; Maitre 1987). However, the cost of felling competing trees is high, natural regeneration is often unreliable, and the yield from even well-managed natural forest in West Africa is unlikely to exceed 5 m^3 ha^{-1} yr^{-1} (Kio & Ekwebam 1987; Nwoboshi 1987), which is less than half the yield of most plantation species in the area.

Enrichment planting

This is the process of under-planting valuable species in partially cleared natural forest. It is appropriate if the forest has insufficient natural regeneration for natural forest management to succeed, but is too valuable (economically or ecologically) to be completely replaced by plantations. It also offers the opportunity to use genetically selected planting stock, or species which were not present in the original forest. Under-planting can take place in lines, as scattered groups, or in a heavily cleared forest where only middle-aged timber species of good form have been retained. Unfortunately, enrichment planting has seldom been carried out well: light-demanding species have often been established in excessive shade and weeding operations have usually been neglected (Anon 1989).

Industrial plantation after complete clearance

This has been the principal technique used in large plantation schemes financed by international lending institutions. Typical examples are the Subri industrial plantations in Ghana (Plumptre & Earl 1986), the World Bank afforestation programmes in Nigeria (Kio *et al.* 1989), and the state forestry plantations in Côte d'Ivoire (SODEFOR) (Dupuy 1985). Unfortunately, all these plantations were established in reasonably productive forest reserves, partly to gain revenue from the forest clearance, and partly because this was the only land freely available to the state. Development banks are now less keen on this type of scheme, especially if the plantations are run by state forestry organisations. There have been too many examples in the past of inefficient management, over-emphasis on planting targets, and gross neglect of maintenance operations (World Bank 1992a). The banks and aid agencies are, therefore, shifting the balance of their funding away from industrial forestry schemes (the 'forest-first approach') and towards environmental conservation, natural forest management and community forestry (World Bank 1991). However, it is in plantation programmes such as that of SODEFOR that there are genetic improvement schemes for indigenous hardwoods (see Ladipo *et al.*, pp239–248).

Community tree plantations

These have not been much practised in the humid forest zone. They are likely to take place in conjunction with farming, either as 'taungya' or in mixture with fruit trees or other perennial crops like coffee or cocoa, and therefore involve reasonably complete forest clearance. Degraded forest and derived savanna zones are most appropriate. However, community plantation schemes have often been limited by an unenthusiastic uptake of tree planting by villagers, particularly where it is difficult to define the ownership of trees on communal land (World Bank 1992a; Flint 1992). These 'people-first' schemes have met many of their targets but have not established large areas of forest because of their intrinsically small-scale approach, problems of land tenure, and a lack of motivation for farmers to plant tree crops which bring little financial benefit for many years. Thus, it is extremely encouraging that the World Bank is about to launch a pilot 'tree planting incentive scheme' in Nigeria which envisages the reimbursement (after *successful* establishment) of 75% of standard planting and maintenance costs to companies, communities and individuals who plant at least 5 ha of land (one ha in cases of environmental degradation). Individuals must possess the land title before funds can be provided, but assistance will be given with the process of land registration (World Bank 1992b).

Large-scale afforestation in future is likely to require a mixture of community and industrial planting. Both approaches have been hindered in the past by human, fiscal and institutional problems. This paper will not consider these difficulties further, but will concentrate on the technical questions which impede the introduction of a significant indigenous hardwood planting programme in West Africa, namely:

- the growth rates of plantations of indigenous species;
- appropriate silvicultural methods;
- the likely economics of plantations; and
- improvements which can be gained from the multiplication and selection of genetically superior planting stock.

YIELD OF PLANTATIONS

Information on the yield of plantations of indigenous species in West and Central Africa is sparse. Several hundred sample plots have been established in research and commercial plantations, but have often been destroyed by fire, logging and/or neglect. Results are extremely variable, with differences in soil type, planting stock, planting methods, disease attack and subsequent thinning making it difficult to draw conclusions. Most plantation research has been devoted to a small number of faster-growing species.

Terminalia ivorensis

Much of the reliable information on *T. ivorensis* (framiré) comes from Côte d'Ivoire, where infrequent measurements exist from 13 plots installed by the colonial forest service, and more regular data from 209 plots established since 1965 by the Centre Technique Forestier Tropical (CTFT) (Beligne 1985). The results are heavily influenced by initial shading, planting density and subsequent thinning, with establishment and growth being more rapid in plots which had received intensive manual or mechanical clearance of the original forest cover. *T. ivorensis* is a species which is light-demanding for maximum growth, and begins to suffer growth checks even before the tree crowns touch (Lowe 1974), indicating the need for a heavy thinning regime.

Before 1972, the CTFT plots received only partial clearance of the original forest, either using the 'line planting' technique (with 8–25 m between lines, *sensu* Aubreville 1953) or 'manual recru' (cutting the undergrowth to knee height, and poisoning the overstorey – but leaving some of the large trees in place – which was not recommended in Catinot's (1965) definition of the recru system). These plots have grown more slowly than the later 'intensive plantations' and average 8.3 m^3 ha^{-1} yr^{-1} by 30 years, with a maximum annual volume increment at 15 years of 9.7 m^3 ha^{-1} yr^{-1}. The minimum rotation length with these 'extensive plantations', to reach an average diameter of 50 cm, is 43 years.

In 1972, CTFT introduced more intensive forest clearance methods. These plots recorded a maximum annual diameter increment of 5.5 cm yr^{-1} at year 3, and the average annual diameter increment is projected to remain more than 2 cm yr^{-1} until the age of 20 (Beligne 1985). The maximum annual wood volume increment of 24.7 m^3 ha^{-1} yr^{-1} was achieved at year 6, and the 70 final crop trees alone were increasing their volume at more than 10 m^3 ha^{-1} yr^{-1} by year 10. Rotation lengths can be predicted from these 'intensive plantations' of 20 years to 50 cm average diameter or 36 years to 60 cm diameter.

The average productivity of *T. ivorensis* (framiré) in SODEFOR is reputed to be 11.5 m^3 ha^{-1} yr^{-1}, although there is some doubt about whether it has been achieved in practice (Aitken *et al.* 1992).

T. ivorensis (idigbo) has also been widely planted in Nigeria. Sanders (1953) and Horne (1962) quote annual diameter increments ranging from 2.2 cm yr^{-1} for an 11-year-old plot to 1.9 for a 30-year-old trial at Sapoba. No recent yield information has been found except for a nine-year-old plantation in Imo State which has an average diameter at breast height (dbh) of 16.1 cm (Mbakwe 1990). The Nigerian *Forestry Sector Review* (World Bank 1992b) gives the expected yield of *T. ivorensis* in plantations as 10–12 m^3 ha^{-1} yr^{-1}, which is the highest of the species quoted.

T. ivorensis (emire) was widely planted in Ghana between 1930 and 1960, but yield information does not appear to have been collated (World Bank 1988). However, it is no longer regarded as a safe plantation species in Ghana because of widespread mortality observed in middle-age plantations (Ofosu-Asiedu & Cannon 1976).

In Cameroon, *T. ivorensis* (framiré) has been used in both research and commercial plantations. The ex-CTFT 1972 research plantations at Bilik (Mbalmayo Forest Reserve) have an average diameter in excess of 60 cm after 20 years for the 70 largest trees per hectare (Lawson, Perem & Foahom 1993), despite damage from a serious fire in 1983. Previous measurements had reported an average diameter increment of 4 cm yr^{-1} during the first six years (Grison 1979) and 3 cm yr^{-1} over the first ten years (Foahom 1982).

The Office National de Développement de Forêts (ONADEF) is responsible for 22 500 ha of moist-forest zone plantations in Cameroon, which date back to 1937 but were mainly planted between 1972 and 1989. Unfortunately, at least 40% of these plantations have completely failed, and much of the remainder has suffered severe growth checks due to inadequate weeding, or to planting in heavy shade. A recent provisional inventory of these plantations (ONADEF 1992; Lawson & Ngeh 1993) has enabled tentative estimates of yield to be derived. The 4120 ha of *T. ivorensis* plantations demonstrate a wide range of survival and growth rates (Figure 1).

Terminalia superba

Terminalia superba has been widely planted in Congo, where a clonal selection programme has been implemented (Koyo 1983, 1985), and Zaïre (limba), usually in association with plantains. It is also an important plantation species in Côte d'Ivoire and Cameroon (fraké), but to a lesser extent in Ghana and Nigeria (afara). Diameter growth is usually 2–3.5 cm yr^{-1} up to year 10, and is maintained above 2 cm yr^{-1} in the final crop trees to at least year 20 (Groulez & Wood 1984). Height growth is around 1.1–1.5 m yr^{-1} during the first ten years. However, rates of volume production may be lower than those of *T. ivorensis*, with 8.4 m^3 ha^{-1} yr^{-1} measured from an 18-year-old plantation in Congo, and around 7.5 m^3 ha^{-1} yr^{-1} predicted at year 40. Yields are particularly influenced by soil fertility. In Côte d'Ivoire, experimental plantations are reported to yield around 10 m^3 ha^{-1} yr^{-1} by year 15, but Aitken *et al.* (1992) quote 12.3 m^3 ha^{-1} yr^{-1} as the expected yield of the SODEFOR commercial plantations, with a final diameter of 45 cm at 25 years.

Triplochiton scleroxylon

T. scleroxylon comprises the majority of all wood exported from Ghana (wawa); it has top place in

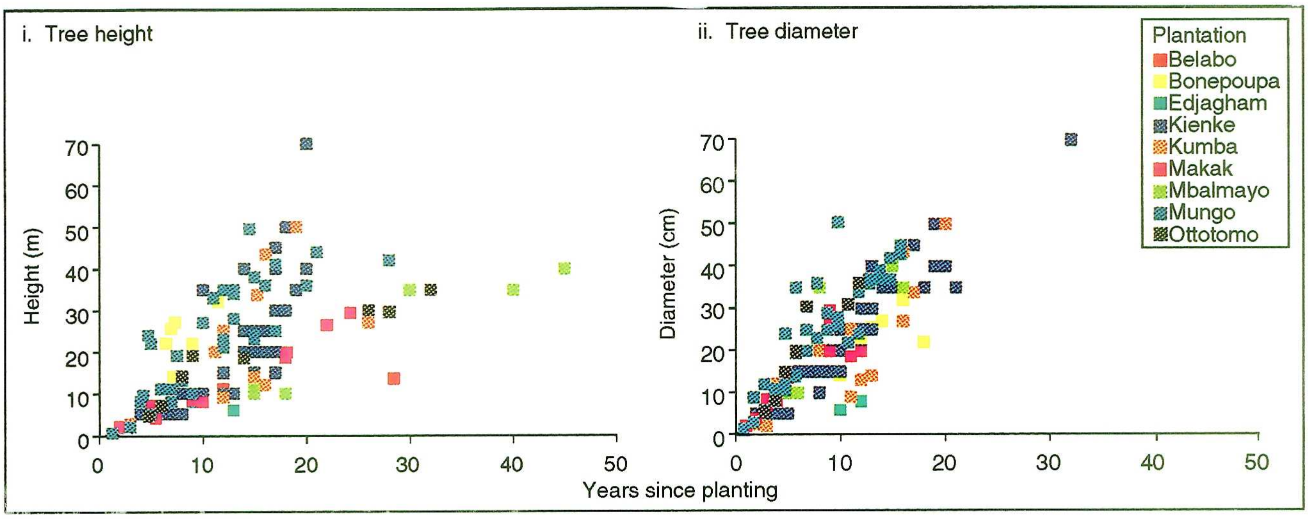

Figure 1. Tree height (i) and diameter (ii) of 118 plantations of *Terminalia ivorensis* (framiré), inventoried by the Office National de Développement des Forêts in 1990 (ONADEF 1992; Lawson & Ngeh 1993). These data were collected by a large number of teams, without adequate standardisation of methods, and should therefore be regarded as provisional

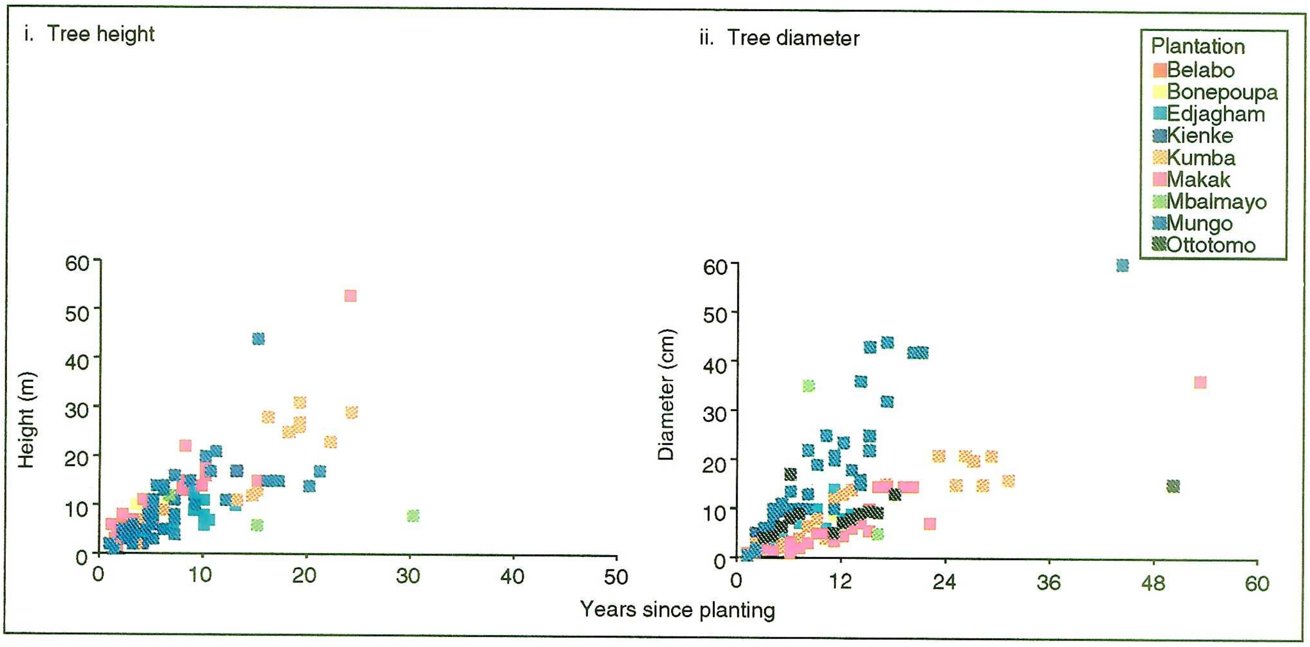

Figure 2. Tree height (i) and diameter (ii) of 112 plantations of *Lovoa trichilioides* (bibolo), inventoried by the Office National de Dévéloppement des Forêts in 1990 (ONADEF 1992; Lawson & Ngeh 1993). These data were collected by a large number of teams, without adequate standardisation of methods, and should therefore be regarded as provisional

Cameroon (ayous) and is a major component in what remains of the Nigerian (obeche) and Ivoirian (samba) forests. It has been used as a plantation species in all these countries, but never on a large scale, probably because of the difficulty in obtaining reasonable quantities of seed (Jones 1974).

In Ghana, research plots of *T. scleroxylon* (Forest Products Research Institute (FPRI) 1972) have produced high diameter increments, ranging from 1.2 cm yr^{-1} in a ten-year-old trial at Pra Annum to 3.0 cm yr^{-1} in a six-year-old trial at Subri. Generally, growth rates are in excess of 2 cm yr^{-1}.

In Nigeria, research plots have achieved 27.1 cm dbh by 29 years at Sapoba and 27.1 cm after 31 years at Gambari (Abayombi & Nwaigbo 1985). This growth rate does not seem rapid but the 100 largest stems ha^{-1} are projected to grow at an average 1 cm yr^{-1} over the first 60 years (Ball 1975).

Many more experimental plantations have been established in Côte d'Ivoire, and annual diameter increments average 1.2–2.1 cm during the first 20 years for trials in partial shade, and 1.9–3.2 cm in completely cleared areas (Dupuy & Bertault 1985). The older plantations had mean annual volume increments ranging from 4–7 m^3 ha^{-1} yr^{-1} for the sparse plantations established under cover (100–150 stems ha^{-1}), to 7–10 m^3 ha^{-1} yr^{-1} in the taungya plantations (250–350 stems ha^{-1}). The younger plantations established after complete clearance averaged 13–18 m^3 ha^{-1} yr^{-1} (175–300 stems ha^{-1}) after 13 years. No extrapolations have been made from these trials to the final expected yield and rotation length of plantations, but a yield of 12.3 m^3 ha^{-1} yr^{-1} is predicted for the SODEFOR commercial plantations, with a final diameter of 45 cm at 25 years (Aitken *et al.* 1992). Initial gains of 14–29% have been reported with genetically selected planting stock used in SODEFOR plantations (Verhaegen *et al.* 1992).

At Makak in central Cameroon, two plots of *T. scleroxylon* were established in 1936–37 at a spacing of 5 m x 20 m. After 46 years, the trees were on average 34 m high and 52.8 cm diameter. At Mbalmayo, also in central Cameroon, five experimental *T. scleroxylon* trials were established between 1966 and 1969. These recorded a mean diameter increment of 1.7 cm yr^{-1} during their first 15 years, and at year 10 the best of these trials achieved 9.5 m^3 ha^{-1} yr^{-1} (Pesme 1986). A further trial of *T. scleroxylon* has been planted at South Bakundu (SW Cameroon), using rooted cuttings without genetic selection, and has achieved an average diameter of 14 cm after only six years (N Songwe, personal communication).

Lovoa trichilioides

Around 6200 ha of *Lovoa trichilioides* have been planted in Cameroon (Lawson & Ngeh 1993), but the average yield achieved is particularly disappointing (1.8 m^3 ha^{-1} yr^{-1}): partly because it was often planted in unfavourable areas, but mainly because of excessive shade and neglect of subsequent maintenance (Figure 2). In the research trials at South Bakundu, a diameter increment of 1.8 cm yr^{-1} was achieved after 18 years (P Shiembo, personal communication), and equally good growth has also been observed for this valuable timber at Sapoba in Nigeria, where it appeared to grow more rapidly after the pole stage, and an average diameter increment of 1.0–1.8 cm yr^{-1} was recorded after 23 years (Nwoboshi 1987).

Other species

Many other native species trials exist in the humid forest zone of West and Central Africa. *Nauclea diderrichii* has been grown in Nigeria since 1918, as a nurse species for more valuable mahoganies, and as a useful species in its own right. Plantations in Sapoba, Ona and Agbodi achieved between 1.2 and 1.6 cm yr^{-1} (Nwoboshi 1987), whilst a plantation at South Bakundu has recently recorded 3.1 cm ha^{-1} yr^{-1} up to year 8 (P Shiembo, personal communication).

Mansonia altissima has also grown reasonably successfully at South Bakundu, with an average mean diameter increment of 1.5 cm yr^{-1} at 18 years (P Shiembo, personal communication), although it is rather susceptible to attacks from defoliating caterpillars (Foahom 1989). *Picnanthus angolensis* (ilomba) is fast-growing in some of the ONADEF plantations in Cameroon (average mean diameter increment frequently more than 2 cm yr^{-1}, even to the age of 40), but has not been the subject of detailed study. *Aucoumea klaineana* (okoumé) has been planted sucessfully in Ghana (FPRI 1974), and in Cameroon (Arnoux 1958; Bibani 1989), with an average diameter increment of 1.7 cm yr^{-1} after 12 years in research plots at Mangombé, and of 1.8–2.5 cm yr^{-1} in commercial plantations near Kribi (Lawson & Ngeh 1993).

Of the non-native hardwood species, *Gmelina arborea, Tectona grandis, Cedrela odorata* and *Melia composita* have been the most successful, and should not be excluded from future planting programmes, even if the preference is for native species.

THE CAMEROON FOREST MANAGEMENT AND REGENERATION PROGRAMME (FMRP)

The FMRP is a bilateral Cameroonian/British programme with a general aim of improving the capacity of Cameroon to carry out wise management and conservation of its moist high-forest areas. It started in July 1991, with an emphasis on the use of improved indigenous hardwood species in artificial plantations, and has the following specific aims.

- To examine and demonstrate the suitability of strongly contrasted silvicultural techniques for forest regeneration after logging.
- To develop a management plan for the Mbalmayo Forest Reserve.
- To provide genetically improved planting stock of selected humid forest species.
- To acquire cost data for establishment and management of plantations using different silvicultural techniques.
- To acquire data on biological changes resulting from different silvicultural treatments.
- To acquire socio-economic data on the effects of different silvicultural treatments on local populations.
- To establish an in-service training capacity in high-forest management techniques and to disseminate results to the forest sector.

The FMRP's planting programme provides an opportunity to demonstrate and study a number of silvicultural options for regenerating degraded forest. Currently these options consist of the establishment of *T. ivorensis, T. scleroxylon* or *L. trichilioides* using the:

- *manual regrowth method*, with complete manual clearance of the original canopy, and cutting of undergrowth at knee height (*sensu* Catinot 1965);
- *enrichment planting method*, with some well-formed individuals of high-value species in the 20–50 cm diameter class retained to form part of the final harvest of the under-planted fast-rotation species;
- *mechanical complete clearance method*, where large trees are felled by chainsaw and pushed by bulldozer, together with smaller trees, into windrows at a spacing of 40–50 m;
- *line planting method*, where V-shaped lines are cut at wide spacing (determined by the ultimate crown diameter of the planted trees) and existing trees are heavily cleared (*sensu* Dawkins 1966);
- *taungya method*, where FMRP undertakes forest clearance and burning, and the villagers hoe, plant and cultivate crops for an initial period of two to four years.

This study to compare silvicultural treatments for the growth of indigenous hardwoods builds on preliminary work at the same site to investigate the effects of some site preparation techniques on the physical and chemical properties of the soil (Ngeh 1989), the spore populations of endomycorrhizal fungi (Musoko 1991; Mason, Musoko & Last 1992) and the physiology of the planted trees (Eamus *et al.* 1990). The preliminary work formed part of a programme linked to the vegetative propagation of indigenous hardwoods and the development of an appropriate silvicultural system for planting clonal material (Wilson & Leakey 1990; Leakey 1991). The current investigation includes a study to determine the effects of silvicultural treatments on the populations of insects, especially the potential pests and their predators and parasites (Watt & Stork 1992). The philosophy behind this project is that, in order to maximise the productivity from genetically selected planting stock, it is important to minimise risk by the retention of biological diversity in the plantation (Leakey *et al.* 1993).

PROFITABILITY OF INDIGENOUS TREE PLANTATIONS IN WEST AFRICA

Ideally, forestry plantations should demonstrate a higher return on capital investment than other commercial alternatives, and/or a more rewarding use of farmers' time and land than alternative crops. There are complications, however. What is a realistic rate to discount future expenditure and revenue? How will the market for timber and thinnings change in the future? Can one account for the risk of fire or disease? Should the balance sheet include environmental conservation and secondary products like bush meat, wild fruits, medicines, rattan, and rafia? An initial attempt has been made at the macro-economic scale in Nigeria to estimate the annual environmental costs of forest clearance (World Bank 1992b). The study concluded that Nigerian sustainable net national productivity has been reduced annually by US$750 million due to lost timber production, $2 billion due to soil degradation, $1 billion due to water contamination, $10 million because of the loss of wildlife, $1 million due to the loss of fisheries, $100 million owing to gully erosion, and $150 million through coastal erosion.

It is not easy to find good records of the cost of plantation establishment and management in West or Central Africa (Skoup & Co 1989; Djomo 1987). Reasonable information is often collected for short periods, but changes of personnel and a lack of standard accounting and coding systems limit the continuity of data collection.

The FMRP aims to collect financial information in parallel to yield and environmental data, and has made an initial estimate of the profitability of four of the silvicultural systems which are being examined experimentally, together with three options under consideration (Table 2). Comparisons of profitability can be made using the internal rate of return (IRR) on capital investment (the aggregate return of all revenues and expenditures over the lifetime of a plantation). This measure emphasises that greatest profitability is achieved when initial costs are minimised and incomes are generated as rapidly as possible (either from early commercial thinnings or by shortening rotation length – perhaps through genetic (clonal) selection).

All the figures derived in Table 2 are speculative: cost keeping has been unreliable; the density and richness of the existing forest are averaged; the effect of silviculture on yields has not been adequately described; and much uncertainty surrounds future timber prices. Nevertheless, estimated IRRs appear to be in the order: manual regrowth < mechanical regrowth < complete clearance < shade trees and cocoa line planting (*sensu* Aubreville 1953) < taungya < short-rotation exotics. The reliability of these assumptions will improve as the FMRP gathers more information. It is not yet possible to eliminate any of the silvicultural options on economic grounds as different options are more appropriate in differing circumstances.

Short rotations of exotic species, like *Gmelina arborea*, have high apparent IRRs, and could possibly be integrated with current fallow rotations. However, they are dependent on markets developing for small roundwood, which will take some time in a country like Cameroon because forest products are still plentiful, there is little market for exotic species, and as yet there is no operational pulp mill.

Taungya offers the advantages of reduced weeding costs and a possible early enhancement to growth as the trees respond to the nutrient pulse provided by wood ash. However, taungya systems require a good relationship between foresters and villagers, and particularly strict control against fires. Taungya is often held to work best when land is in short supply.

Line planting

- 'Francophone', *sensu* Aubreville (1953) (eg Grand Layon), may be carried out where some of the existing high-value trees are preserved to generate thinning revenue and contribute to the final yield. This method is appropriate if the exisiting forest is relatively rich, but management exclusively for natural regeneration is not appropriate.
- 'Anglophone', *sensu* Dawkins (1966), is appropriate where it is carried out in degraded forests. This system aims to produce a virtual monoculture of the plantation species (ie removing all trees which are taller than the arms of a right-angled 'V' centred on each of the planting lines).

The mechanical complete clearance method is unlikely to be applicable where much forest cover remains. It involves the complete destruction of existing forest, and the scraping by bulldozer of felling debris into windrows. Planting operations are cheaper and easier after this type of ground preparation, but large windrows may make 10–20% of the area unplantable. Edens (1992) calculated a favourable IRR (Table 2) based on optimistic yield assumptions from early studies in Côte d'Ivoire (Dupuy 1986). However, more recent work there does not confirm that the SODEFOR plantations created using this method have achieved greater yields that those from older manual regrowth plantations (Aitken *et al.* 1992).

Table 2. Preliminary estimate of the profitability of different silvicultural options for the humid forest zone of Cameroon (source: Edens 1992)

Options		Assumptions (costs in Cameroon CFAs)	Total costs ('000 CFAs)	Total revenue	IRR (%)	Comments
1a	Short rotation and fallow cycle (single rotation)	*Gmelina arborea* planted at 3 m x 3 m density, seedling cost 70, 10 days ha^{-1} for prep & planting, no thinning, survival 75%, 8 yr rotation, 2–3 coppice rotations possible, MAI* 18 m^3 yr^{-1}, 2 MD* weeding ha^{-1} yr^{-1}, sawing efficiency 22%, logging cost 30%, sawing & marketing cost 40% on ex-mill price of 61 000 m^{-3}	153	530	18.6	20% lower yield reduces IRR to 15.1% Market for small sawlogs exists in Nigeria, but not yet in Cameroon. This option could fit into the normal bush/fallow cycle
1b	Two rotations	10 days ha^{-1} pruning & weeding at end of 1st cycle	208	106	20.9	20% lower yield gives IRR of 17.7%
2a	Taungya (no payment to farmers)	*Terminalia superba* planted at 9 m x 9 m spacing, delivered seedling cost 100, supervision costs 10 000 in yr 1, 5000 in yrs 2–5 & 2000 thereafter, average MAI 9 m^3 yr^{-1}, standing value 20 720 m^{-3}, 35-year rotation with thinning at yr 22, farmers' revenue not included, but weeding costs excluded	140	664	15.5	This spacing requires very good planting stock 9 m x 4.5 m spacing would allow earlier thinning
2b	Taungya (medium payment to farmers)	As above but with farmer payments of 25 000 for planting and maintenance of 5000 yr^{-1} for 1st 8 years	221	6640	13.2	This payment may ensure better weeding
3	Shade tree crop	Cocoa understorey which yields from yr 10–50. Plantation on field assumed. 1st thinning at 14, 2nd thinning at 25, 3rd thinning at 35 (to 50 trees ha^{-1})	–	–	Approx 10	Cocoa needs early shade. Many thinning and farmer compensation options can be costed
4a	Manual recru (fully manual)	Planting *Terminalia ivorensis* at 5 m × 5 m spacing. MAI of 9 m^3 yr^{-1}, man days assumed (in yr) are 51(yr1), 3(yr2), 7(yr3), 7(yr4), 6(yr5), 6(yr6), & 1 thereafter, thinning at yr 25	378.5	7589	8.9	Removal of total overstorey but maintenance of controlled shrub layer
4b	Manual recru (semi-mechanical)	Brushcutters reduce labour input by 66%	339.5	7589	9.2	Labour costs are high in Cameroon
5	Mechanical recru ha^{-1}	Caterpillar undertakes initial partial clearance @ 30 000 ha (assuming 100 ha minimum)	–	7589	9.2	
6	Line planting (grand layon)	Lines planted at 10 × 5 m spacing with overstorey largely cleared but 3 valuable species retained in 40–60 cm diam class, 3 in 20–40 cm diam class & 6 in 5–20 cm diam class. Thinning at 20 yrs with 10 m^3 of high-value species & 20 m^3 of whitewood, final cut at 40 yrs gives 360 m^3 & 5 m^3 of mahogany	119.5	7948	13.6	Establishment costs are lower because of wide spacing. Early thinning revenue valuable
7	Complete clearance	Mechanical clearance of site, windrows burnt and re-raked, total machine costs 290 000 ha^{-1} (based on Ivory Coast experience), intensive weed control. Total establishment costs 506 000 ha^{-1}. MAI 12.5 m^3 yr^{-1}. Thinnings at yr 3, 6, 9, final cut at yr 20	597	6453	10.3	IRR highly sensitive to preparation cost and yield changes. More risky option

*MAI, mean annual increment: MD, man days

Shade trees and perennial crops could be an attractive option for community forests, and may also provide a means of establishing trees among illegal cocoa plantations in forest reserves. Shade trees are best above cocoa, but moderate shade can also be tolerated by coffee and a number of important crops like yams, cocoyams and pineapple. The growth increment of widely spaced timber trees will be considerable, though regular pruning is required to maintain good form in species which are not naturally self-pruning.

A modified form of the *manual regrowth* method has been the main method of forest regeneration used recently in Cameroon. Non-commercial species and all trees under 60 cm dbh were normally felled to waste or poisoned. Planting operations were, therefore, extremely labour-intensive, often involving up to 200 man days ha^{-1} or £400 ha^{-1} (Lawson 1993). In practice, resources were often not available for sufficient initial poisoning or subsequent weeding, and the majority of plantations have failed or been severely checked. Nevertheless, the manual regrowth method may remain the favoured option in circumstances where salvage felling is carried out immediately before planting, and where the environmental and economic risks of mechanical clearance are not acceptable.

The estimated internal rates of return are encouraging, particularly for the short-rotation (18.6%), taungya (15.5%) and line planting systems (13.6%). However, the models include only modest assumptions for supervision and overheads. Before the dissolution of the previous state forest regeneration agency in Cameroon (ONAREF), plantation overheads were running at 350%, not including headquarters costs (Lawson 1993). Whilst the new state regeneration organisation (ONADEF) may be more efficient than its predecessor, it is likely that funding agencies will in future favour private sector planting rather than supporting bureaucracy. Unfortunately, there are few spare resources in the private sector of most West and Central African countries, and little industrial or farmer confidence in tree planting. Even the favourable IRRs given below are unlikely to be sufficiently large, or free from risk, to encourage large-scale planting without the impetus of carefully directed incentive schemes.

IMPROVEMENTS IN YIELD AND PROFITABILITY THROUGH CLONAL SELECTION

Ladipo *et al.* (pp239–248) have reviewed the development of forest tree improvement programmes in West and Central Africa over the past 25 years. Considerable advances have clearly been made with the development of vegetative propagation techniques for important plantation species, and some native multipurpose trees. Clonal seed orchards have been established in several countries, and efforts are being made to develop disease-resistant clones and juvenile tests which predict the likely branching pattern of clones in later life.

Populus, Pinus and *Eucalyptus* lead the way in demonstrating yield improvements through the selection of superior clones: a good example being the Aracruz *Eucalyptus* plantations in Brazil (Zobel, Van Wyk & Stahl 1983), where the 100 best clones have more than doubled the production of unimproved stock. However, few clonal trials have yet been established and protected to demonstrate these potential gains with West African species. With *Triplochiton scleroxylon*, Leakey and Ladipo (1987) suggest that selecting clones with above-average volume and stem form would improve yields by 31%. Choosing the top 10% would increase yields by 81%. Research in clonal propagation has been underway in Côte d'Ivoire since the 1960s (Bonnet-Masimbert 1970), but the first controlled comparisons of the yield and form of clonal *versus* unselected material were established in 1987, and now cover some 24 ha (Verhaegen *et al.* 1992). After only two years, the clonal material averaged 14% greater height increment, but the above-average clones averaged a 40% height advantage. These apparent genetic gains are similar to those attained at the same age in Nigeria (Ladipo *et al.*, pp239–248).

In Cameroon, the tree improvement component of the Forest Management and Regeneration Project has restored the Parc de Bouturage facilities established under a previous World Bank programme at a 7 ha site in the Mbalmayo Forest Reserve. An area containing 240 m^2 of mist beds, 40 non-mist propagators (120 m^2), coppice-bed areas, and a drip irrigation system for up to 4 ha of stockplants has now been established. Approximately 0.4 ha has been planted with 357 clones of *Triplochiton scleroxylon*, 129 clones of *Lovoa trichilioides* and 24 clones of *Terminalia ivorensis*; 1700 *T. ivorensis* plants have been established as stockplants.

Following the ideas of Russell and Libby (1986), and the advice of Leakey *et al.* (1993), the FMRP is adopting the following low-technology strategy for clonal collection, selection and testing.

Collection of germplasm

Seed collection has concentrated on *Triplochiton scleroxylon*, and 16 provenances are now represented, including two from Nigeria. Collections will be extended to other species and countries. In Cameroon, a bounty payment to villagers is made for seed (from identified trees) when it is delivered to forest offices. In addition, cuttings have been collected from the stumps of 20 *T. scleroxylon* plus-trees identified in plantations of different ages. Attempts have also been made to locate shoots growing on the cut stumps of superior trees which were selected by exploiters. However, the inventory information currently kept by logging companies does not locate stumps sufficiently accurately to allow them to be relocated.

Nursery screening

The first stage of a clonal selection programme is underway, using a test which measures the response of seedlings to decapitation at 60 cm and the standardisation of leaf number to two leaves. The number of lateral shoots produced in standardised conditions and the time required to reassert apical dominance appear to be well related to the growth and form of the tree after four years (Ladipo, Leakey & Grace 1991a, b), and it is hoped that they will also be so in later life. This predictive test is being used to select 2% of the 14 000 *T. scleroxylon* seedlings currently in the nursery, which will be established as stockplants and used in the field screening phase.

Field screening

The FMRP's 1993 planting programme for *T. scleroxylon* (50 ha) is being used as a second-stage screening for clones identified in the predictive test. A 14 ha 'research zone' will be planted with 20 clones (from ten different provenances), replicated twice in each of five silvicultural treatments. The 46 ha 'demonstration zone' will also be used for clonal planting but not on a replicated planting pattern. Thus, a larger number of clones, with fewer ramets per clone, will be screened for field performance in lines of 20 trees. The lines will be labelled at the time of planting.

Field testing

This phase, which has not yet commenced, will involve replicated clonal plantings with those clones which have performed well in the previous phases. Field testing requires a significant land area and needs large numbers of ramets per clone in a randomised experimental design.

Clone to silviculture matching

Clones may respond differently to planting in partial overhead shade (enrichment planting), in full sun (complete clearance), or where side shade from herbaceous vegetation is encouraged (line planting, manual recru, taungya). The FMRP will gain some information on possible clone/silvicultural interactions from the statistically designed planting in the 'research zone'.

Clonal demonstration lines

Small, and unreplicated, plantings are planned close to the FMRP's headquarters to demonstrate to farmers and other visitors the differences in growth rate and stem form between selected clones and unselected seedlings.

Germplasm bank

Clones and plants of seedling origin which are not incorporated into the project's clonal planting programme will, however, be established and maintained as a gene bank.

Clonal seed orchards

A tree breeding programme is not planned at this stage under FMRP. However, in order to permit genetic recombination between selected clones, it is the intention to establish a clonal seed orchard of main species (*Terminalia ivorensis, Triplochiton scleroxylon* and *L. trichilioides*) using five to ten ramets of each of the most successful clones.

CONCLUSIONS

It is clear that good genetic material is continuously being lost as forests are selectively cleared of the most valuable species and individuals. Natural regeneration is often inadequate to sustain continuous production. Viable seed is difficult to obtain for some species, and of doubtful genetic quality for others. However, considerable scope exists for extraction licences to be linked to regeneration activities. It is hoped that, through the results of FMRP, logging companies will see the commercial potential of establishing plantations of domesticated hardwoods, and distributing selected seed and improved clones to villagers.

Given the threat to the forest gene pool, the promise of a renewed private planting programme, and our ignorance of propagation techniques and growth potential of many potentially important species, it is more than ever necessary to co-ordinate national germplasm collection and breeding efforts on native hardwood trees through a regional hardwoods improvement programme, similar to that proposed by Leakey and Grison (1985). This programme should not be narrowly based on two or three fast-growing species, but should include a range of timber and multipurpose species (eg *Baillonella toxisperma, Garcinia kola* and *Prunus africana*).

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The role of tree domestication in agroforestry

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ABSTRACT

Agroforestry is both an interdisciplinary approach to land use and a set of integrated land use practices. The maintenance and use of a broad genetic base have been a central theme in the development of agroforestry, in terms of utilising undomesticated species for productive purposes and of conserving biodiversity through the use of agroforestry practices in the protection of natural habitat.

The importance of domestication depends upon both the extent to which undomesticated species are utilised and the extent to which their use is controlled. Despite the development of data bases and directories of multipurpose trees, it is not easy to appraise the current status of domestication. While there are ubiquitous reports of localised tree utilisation, it is often unclear whether they refer to the exploitation of wild vegetation or controlled husbandry of the resource.

More than a thousand multipurpose tree species are cited as being utilised, but there are only about 25 species for which there is sufficient knowledge to support promotion at farm level. Despite this vast potential for new domestication, most agroforestry research and development projects concentrate on a few fast-growing exotic tree species, grown in regular arrangements. These technologies do not enjoy high rates of adoption among resource-poor farmers. In contrast, traditional agroforestry practices often involve spatially and floristically complex mixtures of indigenous species.

There is a need to collect and collate basic information on the propagation, ecology, silvicultural management and crop compatibility of more of the thousand or so species that are currently utilised locally, but which are not well documented. Farmers should be encouraged and supported in their efforts to grow and manage the tree species that they value locally, where they consider appropriate within their agricultural systems.

INTRODUCTION

Agroforestry is a relatively new subject for scientific study but a traditional practice with a long history in many parts of the tropics (King 1968; Nair 1989). Existing reviews (Huxley 1983a, b, 1985; Burley, Huxley & Owino 1984; Burley 1987) and practically oriented texts (Wood & Burley 1991) discuss general aspects of multipurpose tree improvement, and other papers in this volume consider the progress being made in this area with specific examples (see Simons, MacQueen & Stewart, pp91–102). This paper concentrates on the use of woody perennial species within agricultural practice and the consequences of their genetic improvement for the interactive role of agroforestry trees. This focus is appropriate because the multipurpose role of agroforestry trees distinguishes them and their improvement from general forestry activity. It is essential for effective progress in agroforestry development that these aspects are brought together and combined with the local experience of farmers.

Examples of two widespread but contrasting agroforestry practices are used to illustrate the general points made in the text. The first of these practices is the use of dispersed trees in crop fields, a system which is particularly important in the drylands of Africa, but has parallels in other continents. The second is the multilayered homegarden, which occurs worldwide. Both these systems have been reviewed and put in context by Von Maydell (1987) and Soemarwoto (1987), respectively. For convenience, the word 'tree' is used in this paper to refer to all woody perennials, rather than being restricted to those of a certain stature.

DEFINITION OF AGROFORESTRY

Agroforestry has been defined as the set of land use practices which involve the deliberate combination of woody perennials and herbaceous crops and/or animals on the same land management unit, in some form of spatial arrangement or temporal sequence, such that there are significant ecological and economic interactions between woody and non-woody components (adapted from Lundgren 1987). Although the prevailing definition now in use, it does not distinguish between agroforestry as an interdisciplinary approach to land use and as a set of integrated land use practices, and, while implying consideration of agronomic aspects at the field scale, it is not explicit about the consideration of the impacts of agroforestry practices on whole-farm systems and their aggregated effects at landscape and regional scales. The agroforestry approach combines the study of woody perennials, herbaceous plants, livestock and people, and their interactions with one another in farming and forest systems. It embraces an ecosystem focus considering the stability, sustainability and equitability of land use systems, in addition to their productivity (see Conway 1987; Marten 1988). Consideration of social as well as ecological and economic aspects is implied.

AGROFORESTRY AND BIODIVERSITY

The maintenance and use of a broad genetic base have been a central theme in the development of agroforestry, in terms of utilising undomesticated species for productive purposes (Pickersgill 1983; Burley 1987; Prance 1990a) and of conserving biodiversity through the use of agroforestry practices in the protection of natural habitat (Oldfield 1988; Prance 1990b). While it has been suggested that for undomesticated trees with potential for exploitation 'the best place for conservation is in cultivation' (Simmonds 1985), agroforestry may involve a reduction in genetic diversity, when compared with the natural vegetation it may replace. In tropical rainforest, up to 300 species of tree and liana have been reported from one hectare (reviewed in Prance 1989, 1990b). Although between 70% and 100% of rainforest tree species may be utilised by local people (Balée 1986, 1987; Broom 1990), 20–30 is the typical number of tree species where they are deliberately cultivated in forest gardens or orchards (Padoch & De Jong 1987; Perera & Rajapakse 1991). The large number of tree species utilised should not be confused with the much smaller number cultivated. While human selection in cultivation may modify genotypes in desirable ways, extraction of wild resources may result in negative selection pressure for desirable traits.

Although multilayered garden systems are clearly much more diverse in terms of number of species of higher plants than either conventional agriculture or plantation forestry, much agroforestry research and development has involved mixtures of only two species, with the introduction of a single tree or shrub species into cereal cropping and the woody component often spatially confined, as exemplified in hedgerow intercropping (Kang & Wilson 1987).

DOMESTICATION OF NEW SPECIES

Analyses of the vegetation structure and dynamics of natural ecosystems (Oldeman 1983), and the indigenous knowledge of local practitioners (Walker, Sinclair & Muetzelfeldt 1991) might be expected to be principal sources of information about tree species and how they might be utilised in agroforestry. The importance of making progress in the domestication of agroforestry trees depends upon the extent to which undomesticated species are currently utilised, the extent to which their use is controlled, and the potential for genetic gains. Despite the development of data bases and directories of multipurpose trees, it is not easy to appraise the current status of domestication. While there are ubiquitous reports of localised tree utilisation, it is often unclear whether these refer to the exploitation of wild vegetation or to controlled husbandry of the resource.

It is logical to distinguish, as far as possible, utilisation, protection and management. The acquisition of materials from trees without regard to their survival is no more than utilisation. Protection advances the process by involving more restrained intervention with the conscious intent that the individual plant should survive and recover sufficiently to allow re-exploitation at a future date, including measures intended to enhance natural regeneration. Management, in contrast, is manipulative rather than opportunistic, by actively promoting regeneration and plant establishment.

Domestication implies that the management process influences the genotypes being utilised, but, for agroforestry tree species mentioned here, only the most preliminary steps towards domestication have been taken, and with a minimal number of species.

THE EXTENT OF LOCAL DOMESTICATION

Attention has recently focused on the indigenous management of forest and woodland resources and individual trees on farms (see reviews by Mathias-Mundy *et al.* 1991; Prance 1991; Shepherd 1992).

Dryland Africa is a convenient case to illustrate the sort of documentation available of indigenous management activity, made possible by Shepherd's (1992) analysis of more than 100 bibliographic summaries. There are ubiquitous examples of utilisation of a wide range of species, and some reports of protection, such as selective pollarding of valuable trees by the Turkana in northern Kenya (Barrow 1988). Raison (1988) reports that in Mandara, Cameroon, a shift from stand to individual tree management occurs as parkland agroforestry practices are intensified.

Protection of naturally regenerated seedlings from grazing, even during the dry season, has been reported from parkland agroforestry practices in Burkina Faso (Marchal 1983), but there are very few documented examples of indigenous tree planting. It has been suggested that deliberate planting of trees has not constituted a significant part of the development of various parkland agroforestry systems in the Sudano-sahelian zone of Africa (Raison 1988), which have developed by selective cutting of natural forest cover and management of natural regeneration (World Bank 1985). Barrow (1988) suggests that the impacts of increasing human and animal populations are not being incorporated into indigenous resource management strategies by the Turkana, indicating that, despite a need for more interventionist management, it has not developed spontaneously.

In a global context, the extent of undocumented indigenous knowledge of the ecology of tree species which are utilised by local people is thought to be significant, as evidenced by the burgeoning interest in ethnoecology (Prance 1991). This information requires novel methods to be adequately appraised; such methods are only now being developed and applied (Walker *et al.* 1991).

AGROFORESTRY TREE SPECIES

Present concern is with the members of a new generation of tropical multipurpose trees. Over 1000 multipurpose tree species are listed by Von Carlowitz, Wolf and Kemperman (1991), but present knowledge of the vast majority is too superficial to enable their routine management as resources. In terms of the tropics, for fewer than 50 of these species is there sufficient knowledge to support promotion at farm level, half of them being familiar because of long usage in conventional forestry or horticulture. The new generation of species represents the remainder of this small group. Only about 25 species are involved (Table 1), all of which either have been neglected by forestry and horticulture or are now more prominent in agroforestry roles than in other, longer-standing roles. It is only during the last 20–25 years that enough information has been amassed to justify including them among options for extensive use as planted resources in agroforestry systems. In many cases, efforts to publicise their value and potential have been reflected in the appearance of monographic or other broad treatments bringing together existing knowledge (Table 1). For the other species listed, the principal geographical region of use is indicated, within which published documentation is accessible and widely known and would allow preparation of unified accounts, although none has yet appeared.

Consideration of the details of collating and interpreting information on additional multipurpose tree species is outside the scope of this account, but it is relevant to consider how such species should be identified. In this process the impressive advances in international liaison co-ordinated by the Food and Agriculture Organisation (FAO) through the Panel of Experts on Forest Gene Resources should be noted. The Panel drew up a priority list of tree species for improvement and conservation in 1968 (FAO 1969), and at subsequent meetings reviewed and updated it. The list, worldwide in scope, has gradually absorbed multipurpose trees since the original version appeared. For example, the initial list omitted all West African savanna trees except *Khaya senegalensis.* Subsequently, multipurpose trees were added to the lists, including *Acacia*

Table 1. Tropical multipurpose trees with a comprehensive knowledge base generated by agroforestry interests

Species	Noteworthy references/Geographical region where native
Acacia mearnsii	Sherry (1971)
A. nilotica	Fagg & Greaves (1990b)
A. senegal	Cheema & Qadir (1973); Philip (1975)
A. tortilis	Fagg & Greaves (1990a)
Albizia lebbeck	India
Alnus acuminata	Central America
Balanites aegyptiaca	Hall & Walker (1991)
Bombacopsis quinata	Central America
Calliandra calothyrsus	National Research Council (1983)
Casuarina equisetifolia	Midgeley *et al.* (1983); National Research Council (1984a)
Erythrina poeppigiana	Nitrogen Fixing Tree Association (1993)
Faidherbia albida	Felker (1978); Centre Technique Forestier Tropical (1988)
Gliricidia sepium	Withington, Glover & Brewbaker (1987)
Grevillea robusta	Harwood (1989)
Guazuma ulmifolia	Central America
Leucaena leucocephala	National Research Council (1984b); Lulandala & Hall (1991)
Mimosa scabrella	Brazil
Parkia biglobosa	Bonkoungou (1986)
Prosopis cineraria	Mann & Saxena (1980)
P. chilensis	Simpson (1977)
P. tamarugo	FAO (1981); Habit (1985)
Sesbania grandiflora	Nitrogen Fixing Tree Association (1990a, b)
S. sesban	Nitrogen Fixing Tree Association (1990a, b)
Treculia africana	Bijtterbier (1981)
Vitellaria paradoxa	Bonkoungou (1987)
Ziziphus mauritiana	India

nilotica, *A. senegal*, *A. tortilis*, *Dalbergia melanoxylon*, *Faidherbia albida* and *Vitellaria paradoxa* (FAO 1977), *Parkia biglobosa* (FAO 1984) and *Acacia seyal* (FAO 1988). Additional species may be expected to be included in the future, such as *Balanites aegyptiaca* and *Ziziphus mauritiana* and members of the Capparidaceae.

THE ROLE OF AGROFORESTRY SPECIES IN RELATION TO TREE IMPROVEMENT

Agroforestry trees have often been considered synonymous with multipurpose trees (MPT) and the concept of simultaneous production of different above-ground parts, such as fruit, leaves for fodder, stems and branches for wood (Huxley 1985; Burley 1987; Wood & Burley 1991). However, for the few agroforestry species for which there have been selection and breeding programmes, there has been a tendency to select divergent genotypes for different purposes. A notable example is *Leucaena leucocephala*, where a shrubby, heavily branching form has been bred for fodder as opposed to arboreal types for wood production (Brewbaker 1987). Similar strategies are being actively applied for *Prosopis* species (Felker, pp183–188) and *Acacia auriculiformis* (Booth & Turnbull, pp189–194). This evidence suggests that, as domestication progresses, the multipurpose nature of agroforestry trees will be replaced by single-purpose genotypes selected for yield of priority parts of the plant along conventional forestry lines, although alternative approaches have been proposed (Simons *et al.*, pp91–102). The logical outcome of selecting for single-purpose genotypes is to negate the multipurpose nature of the species.

This scenario ignores the fact that agroforestry trees are part of an agricultural system; they may have important roles that contribute to sustainability, particularly in relation to soil protection and improvement, and will compete with agricultural crops for light, water and nutrients. In this context, agroforestry trees are always multipurpose, regardless of what is harvested and extracted from the system. Consequently, the farmer is presented with a series of trade-offs determined by the allocation of plant biomass to different parts of the tree, which is the primary aspect manipulated during selection and breeding. These trade-offs are discussed below. What is clear is that the interactive behaviour of the tree within the agricultural system represents an obligatory multipurpose character of agroforestry genotypes, even if they are selected with only a single harvestable output in mind. The significant interactive roles of such trees need to be explicit in the development of selection criteria, and the specification of the associative ideotypes proposed by Huxley (1985). At present, it is difficult to be explicit about many of the selection criteria required because of a lack of knowledge about functional relationships below-ground.

HARVESTED BIOMASS *VERSUS* RECYCLING

The economic reasons for incorporating trees in farming systems are many, often representing a need to produce material on-farm that was previously available from a now-dwindling forest resource. A major reason for the international prominence of agroforestry is the perceived ability of trees to contribute to the sustainability of staple food production in low-input farming systems.

Yield improvements through the breeding of agricultural crops have been achieved largely by increasing the harvest index, and secondarily by increased adaptation to agronomic environments (Cannell 1985). The fundamental efficiency of the use of absorbed radiation is conservative across species and environments, and there is no evidence that it has been altered through domestication (Russell, Jarvis & Monteith 1989). Increasing the harvest index of agroforestry trees may lead to higher returns in the short term from the harvested product, but may cause problems of system sustainability in the longer term, if less plant biomass is recycled in the soil (Young 1989). Because fine root and mycorrhizal turnovers have been calculated to contribute two to four times more N and six to ten times more P and K than above-ground litterfall in tree plantations (Bowen 1984), a reduction in root biomass in favour of the harvested shoot could have significant effects on the soil nutrient status in agroforestry systems.

SOIL AMELIORATION *VERSUS* COMPETITIVE EFFECTS

Farmers may often face a trade-off between longer-term benefits of trees, such as soil structural amelioration (Van Noordwijk, Widianto & Kurniatun-Hairiah 1991), and immediate competition with the crop for resources. Threshold levels of staple crop production may be a high priority and it may be desirable to select trees as much in relation to their effect on companion crops as to their productivity. This selection can be achieved by evaluating genotypes on-farm rather than on-station (see Clement & Villachica, pp230–238), which represents a shift from conventional forestry approaches and has obvious cost implications for selection and breeding programmes.

SHOOT *VERSUS* ROOT AND THE IMPORTANCE OF NICHE DIFFERENTIATION

An important ecological basis for yield advantages through the intimate integration of trees with agricultural crops in agroforestry practices, as opposed to growing trees and crops separately, is that the combined system will utilise environmental resources more efficiently than monocultures through niche differentiation in space and time. It has been demonstrated by controlled experimentation that, if two non-interbreeding populations are grown together at high density, then natural selection may favour a divergence in behaviour, such that each population ceases to make such heavy demands on resources needed by the other (Harper 1977). Marked differentiation within a single *Trifolium* (Leguminosae) species has been found over small distances, with a variety of forms each adapted to live with different associated grass species (Turkington 1975). The striking temporal niche differentiation of the *Faidherbia albida* canopy, which is leafless during the rainy season when intercropped cereals are developing their canopy, is readily observed and well known (Felker 1978). However, much agroforestry is predicated on an assumption of niche differentiation below-ground.

The extent to which this differentiation actually occurs in agroforestry is not clear. Tree root systems typically have lower root length densities in upper soil layers than herbaceous crops, as well as greater distances between roots and deeper root penetration (Bowen 1985). Examination of vertical distributions of fine roots of several tree species used in agroforestry in Morogorro, Tanzania (including *Cassia siamea, Leucaena leucocephala* and *Prosopis chilensis*), however, showed them to be similar to that of maize (Jonsson *et al.* 1988). Ong *et al.* (1991) have shown strong competition for water and nutrients between *Leucaena leucocephala* and millet in hedgerow intercropping on alfisols in semi-arid tropical conditions.

Bowen (1985) has suggested that the production and turnover of fine roots and mycorrhizas are general adaptations of tree root systems that confer flexibility, permitting phenotypic adaptation to a wide range of site conditions. Soil conditions may consequently be more significant in determining root distribution at a particular site than the actual species planted. For example, Hall and Walker (1991), in reviewing literature on *Balanites aegyptiaca*, found a wide range of architectural patterns of the gross root system from studies at different sites. Agricultural intercrops are likely to alter soil conditions through resource consumption and, therefore, to affect tree root distribution. There are few comparative data on tree root distributions in relation to different intercrops. In silvopastoral experiments, the allocation of biomass to roots in *Prunus avium* increased, and the vertical distribution of roots in *Fraxinus excelsior* was downwardly displaced, as a result of competition with aggressive swards (Campbell & Mackie- Dawson 1991; Tomlinson 1992). Similarly, the density of pigeon pea roots was reduced in the top 15 cm of soil when grown with sorghum in India (unpublished data of Y S Chauhan, cited in Ong *et al.* 1991). These observations indicate a response to reduced water and nutrient availability in upper soil layers as a result of resource consumption by companion crops, and suggest that mixtures of trees and crops may exhibit more extensive niche differentiation than expected from their root distributions in monoculture.

There is a danger that selection based on altering the partitioning of carbon towards particular above-ground organs could result in lower partitioning to roots, and that this may influence the root competition between the tree and the crop. Conversely, there is an opportunity for selecting trees specifically to reduce root length density in upper soil layers and to increase rooting below 30 cm, thereby selecting genotypes likely to exhibit enhanced ecological combining ability with staple crops.

ABOVE- AND BELOW-GROUND CONNECTIVITY

Selection of genotypes in an agroforestry context is further complicated by interactions between canopy and root systems which may be influenced by silvicultural manipulations such as pruning, and by effects of past development of tree root systems on subsequent rooting patterns. The possibilities for manipulating canopy architecture through pruning have been discussed by Cannell (1983), and the importance of phenology and entrainment in the management of multipurpose trees have been stressed by Huxley (1983c, 1985).

By way of example, *Peltophorum pterocarpum* was identified, through screening various indigenous species, as suitable for alley cropping on acid soils in the humid tropics in Sumatra, Indonesia (Van Noordwijk *et al.* 1991). The tap root and horizontal 'sinkers' developed from branch roots some distance from the stem, and penetrated to below 1 m into a zone of iron concretion, but lower pruning height resulted in more, smaller-diameter branch roots in the top 10 cm of soil.

P. pterocarpum also provides a convenient example of the importance of successional phases in agroforestry when planted into *Imperata cylindrica* grassland (Webb *et al.* 1984). The tree develops a deep root system in response to competition from the grass which it then shades out, leaving what may be a complementary rooting pattern for subsequent intercropping with cereals. Selection criteria for a suitable tree in this case might involve:

- deep rooting combined with a strong downward displacement response in vertical root distribution to competition in surface soil – suitable in the first phase; and
- a reduced surface root proliferation response to shoot pruning – suitable in the second intercropping phase.

Clearly, the selection requirements for woody species that will be optimal through several intercropping phases are complex, and trade-offs in the functionality of the genotype in different stages are likely.

BASIC DATA FOR MODELLING APPROACHES

The way in which trees interact with crops and animals in given environmental contexts is central to their suitability as agroforestry species. Key processes that determine yield in combinations of trees and crops (eg light and rainfall interception, nutrient and water uptake) and measurable tree variables (eg leaf area and root length density) can be combined in physiologically based models to investigate the effect of incorporating a range of tree frequencies in various arrangements on farmland (reviewed in Muetzelfeldt & Sinclair 1993). Recent developments in sensing equipment permit easier and less destructive measurement of leaf area in individual trees (Lang & McMurtrie 1992) and of root structure and dynamics (Atkinson & Mackie-Dawson 1990). There is, therefore, an opportunity to collect basic information on many new agroforestry species, by making non-destructive measurements through seasonal cycles. This collection could be done for species currently retained at low frequencies on farmland, and the data then used to investigate the effects of higher tree frequencies and the impact of possible changes in tree form and phenology that might help in specifying appropriate associative ideotypes.

COMPARATIVE EVALUATION OF AGROFORESTRY TREES IN DRYLAND AFRICA: A CASE STUDY

This section presents growth data of agroforestry tree species grown in cultivated field situations on vertisolic soil in dryland Africa, and will illustrate and develop some of the general points made earlier. The experimentation is reported more fully elsewhere (Verinumbe *et al.* 1992).

Context

As population pressure increases throughout the sudano-sahelian zone of Africa, forcing a decrease in the length of the bush/fallow cycle and the progressive removal of trees from the landscape, farmers in the region perceive a decrease in soil fertility and a reduction in water available for crop growth. These conditions result in lower crop yields and people having to walk further to collect firewood, fodder and fruit. Agroforestry practices involving the planting and retention of trees on crop land have been proposed as simple solutions to these problems, building on a long tradition of farmers retaining low densities of trees (10–30 ha^{-1}) on farm land (Nye & Greenland 1960). Current research explores the hypothesis that the turnover of biomass from trees, planted at stocking densities in the order of ten-fold higher than those traditionally retained on crop land, can improve soil structure, leading to increased infiltration and penetration of water and subsequent improvement in the productivity and sustainability of food crop and tree production. This rests on the premise, investigated here, that locally used tree species can be established in cultivated fields and can realise substantive growth when intercropped.

Location

The New Marte experimental site (12°15′N, 13°52′E) is situated in north-eastern Nigeria between the town of Maiduguri and Lake Chad at the northern limit of the Sahel transition zone (White 1983). The soils are fine-textured chromic vertisols derived from alluvial and lacustrine deposits. Mean annual rainfall is just under 650 mm; mean monthly precipitation exceeds 50 mm only for the period June–September.

Objectives

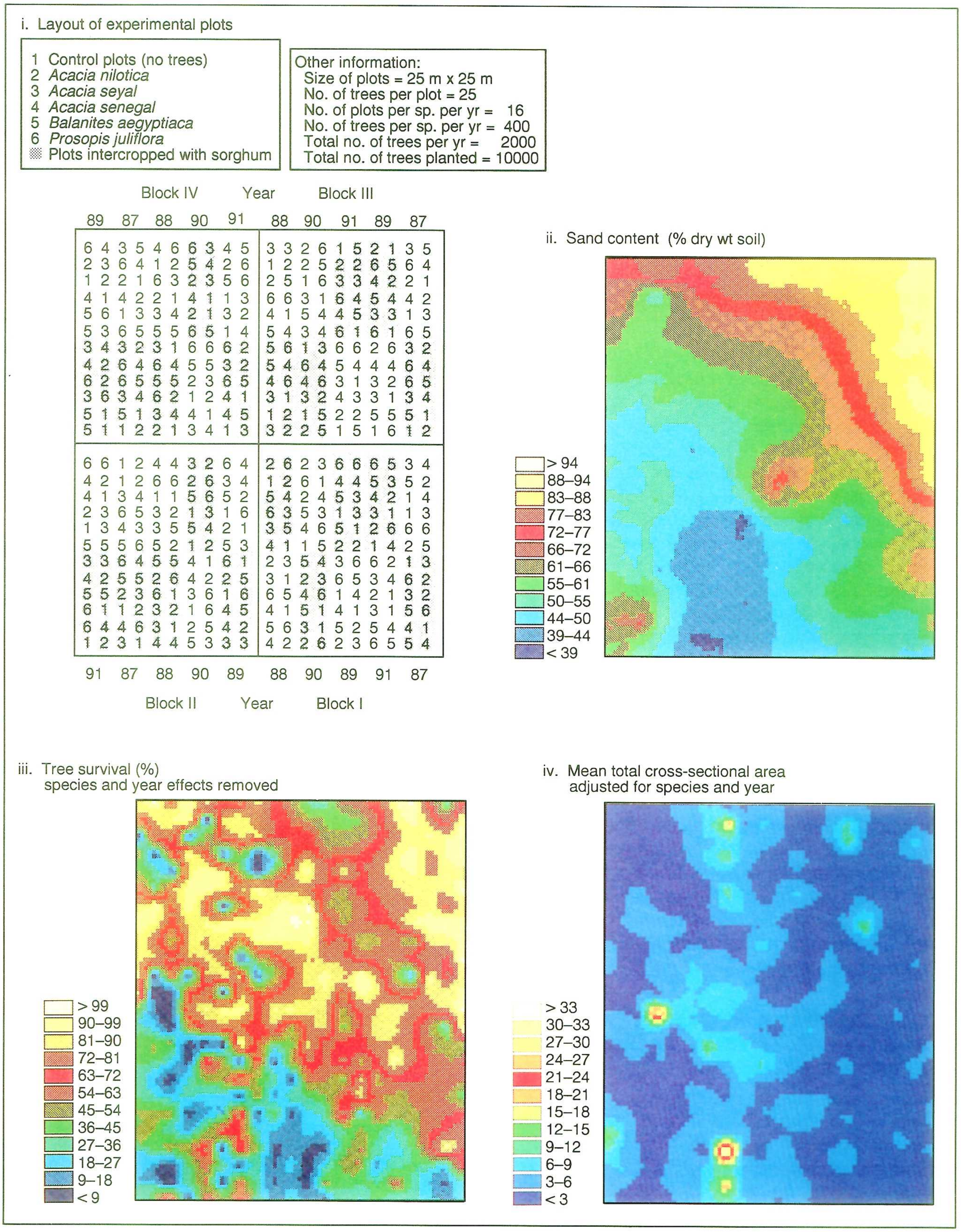
The experimental objectives involved the quantitative appraisal of the establishment and growth of five locally used tree species identified in a survey of traditional agroforestry practices and markets in the region (Verinumbe 1991). These five species, *Acacia nilotica, A. seyal, A. senegal, Balanites aegyptiaca* and *Prosopis juliflora,* were evaluated over five successive years of planting, in relation to varying annual rainfall pattern and soil conditions, and an assessment was made of the impact of intercropping on tree establishment and performance.

Experimental design

The experimental design incorporated treatments of:

- five tree species, including a control with no trees;
- five successive years of planting; and
- plus or minus intercropping.

The trees were planted in a randomised split-split plot design, with double replication at the lowest level that allowed sufficient residual degrees of freedom to make comparisons between species (Figure 1i). The trees were dispersed throughout cultivated plots at a stocking rate of 400 trees ha^{-1}.



i. Layout of experimental plots

1 Control plots (no trees)
2 *Acacia nilotica*
3 *Acacia seyal*
4 *Acacia senegal*
5 *Balanites aegyptiaca*
6 *Prosopis juliflora*
▨ Plots intercropped with sorghum

Other information:
Size of plots = 25 m x 25 m
No. of trees per plot = 25
No. of plots per sp. per yr = 16
No. of trees per sp. per yr = 400
Total no. of trees per yr = 2000
Total no. of trees planted = 10000

Block IV Year Block III

89		87		88		90		91		88		90		91		89		87	
6	4	3	5	4	6	6	3	4	5	3	3	2	6	1	5	2	1	3	5
2	3	6	4	1	2	5	4	2	6	1	2	2	5	2	2	6	5	6	4
1	2	2	1	6	3	2	3	5	6	2	5	1	6	3	3	4	2	2	1
4	1	4	2	2	1	4	1	1	3	6	6	3	1	6	4	5	4	4	2
5	6	1	3	3	4	2	1	3	2	4	1	5	4	4	5	3	3	1	3
5	3	6	5	5	5	6	5	1	4	5	4	3	4	6	1	6	1	6	5
3	4	3	2	3	1	6	6	6	2	5	6	1	3	6	6	2	6	3	2
4	2	6	4	6	4	5	5	3	2	5	4	6	4	5	4	4	4	6	4
6	2	6	5	5	5	2	3	6	5	4	6	4	6	3	1	3	2	6	5
3	6	3	4	6	2	1	2	4	1	3	1	3	2	4	3	3	1	3	4
5	1	5	1	3	4	4	1	4	5	1	2	1	5	2	2	5	5	5	1
5	1	1	2	2	1	3	4	1	3	3	2	2	5	1	5	1	6	1	2

91		87		88		90		89		88		90		89		91		87	
6	6	1	2	4	4	3	2	6	4	2	6	2	3	6	6	6	5	3	4
4	2	1	2	6	6	2	6	3	4	1	2	6	1	4	4	5	3	5	2
4	1	3	4	1	1	5	6	5	2	5	4	2	4	5	3	4	2	1	4
2	3	6	5	3	2	1	3	1	6	6	3	5	3	1	3	3	1	1	3
1	3	4	3	3	5	5	4	2	1	3	5	4	6	5	1	2	6	6	6
5	5	5	6	5	2	1	2	5	3	4	1	1	5	2	2	1	4	2	5
3	3	6	4	5	5	4	1	6	1	2	3	5	4	3	6	6	2	1	3
4	2	5	5	2	6	4	2	2	5	3	1	2	3	6	5	3	4	6	2
5	5	2	3	6	1	3	6	1	6	6	5	4	6	1	4	2	1	3	2
6	1	1	2	3	2	1	6	4	5	4	1	5	1	4	1	3	1	5	6
6	4	4	6	3	1	2	5	4	2	5	6	3	1	5	2	5	4	4	1
1	2	3	1	4	4	5	3	3	3	4	2	2	6	2	3	6	5	5	4

Block II Year Block I

ii. Sand content (% dry wt soil)

iii. Tree survival (%)
species and year effects removed

iv. Mean total cross-sectional area
adjusted for species and year

Figure 1. Plans of the experimental site at New Marte

i. Layout of experimental plots

ii. Spatial variation of sand content across the site

iii. Spatial variation of tree survival across the site measured in 1991 after effects of species and year of planting have been removed

iv. Spatial variation of total cross-sectional area of stem measured in 1991 after effects of species and ear of planting have been removed

Data were analysed using an angular (for survival data) or logarithmic transformation to equalise the variance. Results are presented as back-transformed means, with effective standard errors, where appropriate. The variability of surface soil properties was obtained from analysis of surface (0–10 cm) soil samples (200 g), collected by auger over the experimental area. Two samples were taken in each plot, one directly under the tree canopy and one mid-way between adjacent trees. While a full set of analyses have been completed on these samples, only data on particle size (measured using a Micrometrics X-ray sedigraph machine) are presented here. Quadratic interpolation was used to map tree and soil data spatially (Figure 1), to identify systematic trends and localised variation at the site.

Results and discussion

A distinct change is apparent from clay-rich soils in the south-west (SW) to sand-rich in the north-east (NE) (Figure 1ii), reflecting the varying content of lake-deposited material to superimposed and intercalated wind-blown sand. Blocks 1 and 2, with a higher clay content at the surface, were subject to more severe seasonal ponding and cracking and, therefore, longer periods of waterlogging in the wet season. Other soil parameters show similar trends; for example, pH, measured in water, varies from <5 in the SW to >7.5 in the NE (median=6.3), indicating the introduction of calcareous material associated with the wind-blown sand. Tree survival (Figure 1iii), plotted across the site, after species and year effects were removed, follows the trend in soil texture, with high survival in Blocks 3 and 4, where soil was lighter-textured at the surface, and poor establishment in the clay-rich part of the site. Observations at the site suggest that survival was most affected by a few particularly severe flooding events, which occurred in the wetter years and were aggravated by the soil conditions in the southern blocks. The total cross-sectional area of tree stems (TCSA), when effects of year and species were removed, did not vary appreciably across the site (Figure 1iv), suggesting that, while the degree of waterlogging was critical for the survival of newly planted seedlings, it did not affect subsequent tree growth.

The species fall into three groups in terms of their TCSA after four years' growth (Figure 2i). *Prosopis juliflora* and *Acacia nilotica* had a significantly greater TCSA than the other species, and both *A. seyal* and *A. senegal* showed significantly faster above-ground growth than *Balanites aegyptiaca*. *P. juliflora* grew faster initially, being larger than all other species at both two and three years after planting. *A. nilotica* was larger than all other species except *P. juliflora* three years after planting, and not significantly different from *P. julifora* after four years. Tree height (Figure 2ii) followed a similar pattern, but the mean crown diameter of *A. nilotica* remained significantly less than *P. juliflora*, even at four years after planting, causing less interference with the sorghum intercrop (Figure 2iii). There was no significant effect of intercropping on tree survival or growth.

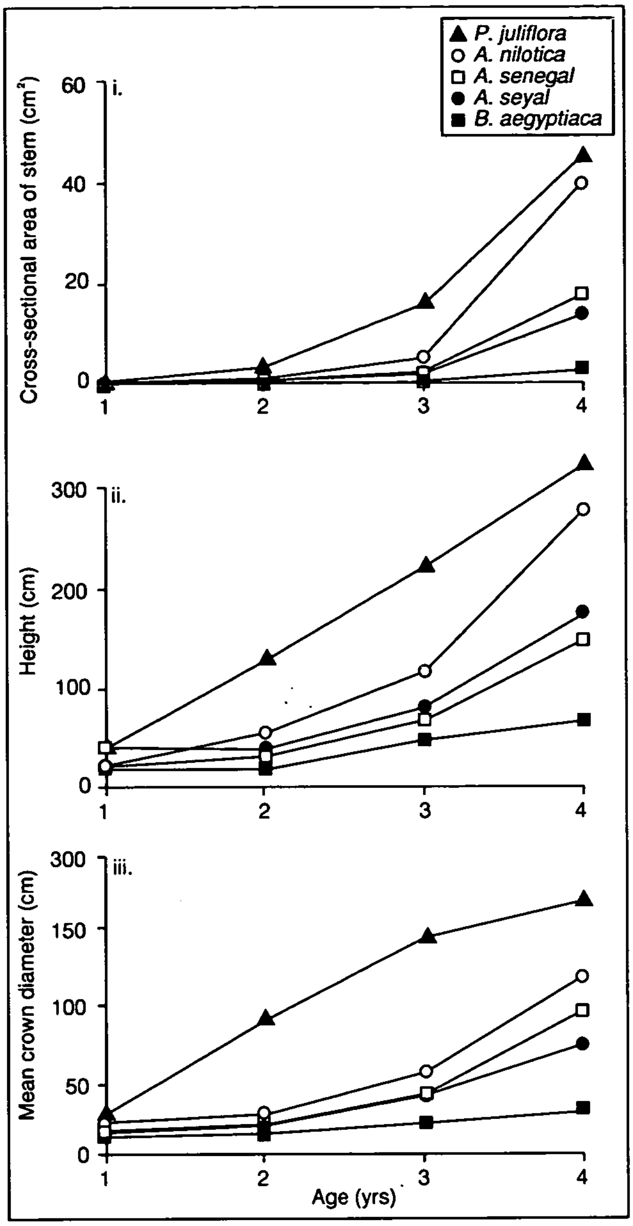


Figure 2. Comparative growth of five tree species planted over four years at New Marte. The graphs show back-transformed mean values and effective standard errors of measurements made on the nine central trees in each plot of (i) total cross-sectional area of stem (measured as the sum of the three largest stems per tree); (ii) height; and (iii) mean crown diameter

While the means and effective standard errors calculated on a transformed scale are appropriate for making species comparisons, the raw means and standard deviations (Table 2) reflect high intraspecific variability of tree growth

Table 2. Within-plot raw mean and standard deviation (SD) of total cross-sectional area of stems (TCSA), height and mean crown diameter (MCD) by species for five agroforestry tree species grown in cultivated plots at New Marte, NE Nigeria, planted in 1987 and measured in 1991 (data from Verinumbe *et al.* 1992). For full species names, see text

Growth	*A. nilotica*		*A. seyal*		*A. senegal*		*B. aegyptiaca*		*P. juliflora*	
variable	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
TCSA (cm^2)	53.5	32.3	28.5	18.9	24.3	15.6	6.29	8.10	61.5	46.5
Height (cm)	298.8	77.4	201.2	58.9	162.3	56.3	82.3	38.6	346.3	99.0
MCD (cm)	128.9	45.0	94.2	37.5	100.7	31.9	38.7	22.8	184.3	49.8

within plots, which is relevant to tree planting in cultivated fields by farmers. The coefficient of variation (CV) of stem cross-sectional area at four years ranged from 60% to 75% for most species, but was roughly twice as high for *B. aegyptiaca* than the other species. Height and crown diameter were less variable (CVs typically 25–40%, although approaching double this range for *B. aegyptiaca*).

Despite faster initial growth, *P. juliflora* was less suitable for use in fields than *A. nilotica* because it had a more spreading crown, which interfered with the intercrop. *B. aegyptiaca* was by far the slowest-growing species in the experiment, but is commonly protected and managed by farmers in cultivated fields. While the reason may be largely that the tree produces highly valued fruit, even in low-rainfall years, a high root/shoot partitioning ratio in early years of growth may be associated with ecological combining ability in intercropped cereals. Research now in progress at New Marte (Sinclair *et al.* 1992) involves detailed measurement of water uptake and the growth of trees and intercropped sorghum, and will allow comparison of the tree species in relation to staple crop yield and water use efficiency of individual components and the system as a whole.

There is a marked contrast between the slower-growing fruit and gum-producing species used in fields by farmers and the faster-growing, often exotic, species that have been the main focus of agroforestry research and development efforts. Much of the basis for expectations of sustainability benefits from trees on crop land has been associated with tree foliage biomass, of considerable nutrient content, being recycled in the system. High above-ground biomass production was suggested by Young (1989) as a fundamental characteristic of soil-improving trees. There is clearly little scope with the slow-growing fruit trees favoured by farmers in semi-arid conditions: foliage was never more than 5% of total tree biomass in *B. aegyptiaca* trees ranging from 10 kg to 600 kg total biomass, measured in Senegal and Burkina Faso (Bille 1978, 1980).

Agroforestry practices involving the slow-growing, deep-rooting, drought-resistant species that are valued locally for their fruit and the faster-growing legumes may be appropriate for the region, and would combine the accepted economic value of the fruit with the service roles of carbon and nitrogen addition to the soil. Mixtures of species would also reduce the risk of loss of production from trees, in relation to both pest and disease attack and drought.

The high intraspecific variability recorded suggests that there may be considerable scope for improvement through selection and breeding in terms of above-ground growth, although spatial variability in soil conditions and other environmental factors could be expected to account for more than half of the phenotypic variation measured. Farmers typically retain or plant small numbers of trees in their fields to minimise competition with intercrops, leaving little scope for selection after tree establishment; therefore, the reliable performance of individuals is particularly important.

One means of increasing the reliability of performance is to maximise the suitability of the planting site. This has often been achieved by improving the soil by cultivation and the addition of inorganic fertilizers to produce more uniform field conditions; it requires substantial inputs of capital and support energy. More recently, it has been suggested that traditional farming methods may be effective in the utilisation of heterogeneous resource bases, such as that in Figure 1, because mixtures of species and genotypes are used in such a way that different genotypes are matched to microsite conditions (Anderson & Sinclair 1993). Differences in soil conditions, and higher crop productivity, have frequently been reported under crowns of *Faidherbia albida* trees growing in crop fields across its natural range, and in northern Nigeria in particular (Verinumbe 1991). As with much soils research in agroforestry, however, soil has usually been sampled at one point in time from nearby sites with different tree cover, so that it is unclear to what extent trees have improved soil conditions by their presence or have grown in patches of better soil in the first place (Sanchez 1987). If farmers are, in fact, able to optimise use of a spatially variable soil system, then they must be able to:

- recognise and characterise different microsites;
- know the micro-environmental requirements of different species; and
- match species to microsites.

While there are many examples from various parts of the world of detailed local classifications of soil, vegetation and site type, and of their correspondence with scientific categories (Brokensha, Warren & Werner 1980; Richards 1985), there is less documented evidence relating to indigenous knowledge of species' requirements. One of the most frequently repeated claims in the agroforestry literature is that the seemingly random arrangement and composition of multilayered homegardens in Africa, Asia and Central America are, in fact, the end result of a complex process of matching species to microsites by farmers (Michon 1983; Fernandes, O'kting'ati & Maghembe 1984; Jacob & Alles 1987). No evidence supporting these assertions has been presented, but research in progress (Walker *et al.* 1991) addresses this type of question directly. Farmers are asked about the ecological interactions occurring in the agroforestry practices that they operate, and their answers are then formally represented in computerised knowledge bases that are transparent and can be interrogated. Recent fieldwork involving interviews with farmers in Kandy District, Sri Lanka, yielded over 3000 factual statements about species' interactions in forest gardens (Walker & Southern 1992). The resulting knowledge base contains information of ecological relevance to 180 species, with a significant amount of information for about 15 of them (about 200 statements on each).

CONCLUSIONS

There is a need to collect and collate basic information on the propagation, ecology, silvicultural management and crop compatibility of more of the 1000 or so agroforestry species that are currently utilised locally but are not well documented. Priorities have been identified informally by farmers in what they have selected to grow and on a formal international basis by the FAO. Interdisciplinary co-operation is required to capture and combine knowledge from local people, the existing ecological literature, and experimentation complementing the collection, evaluation and conservation of germplasm with the development of agroforestry systems that extend rather than supplant local practice. Farmers should be encouraged to grow and manage the tree species they value locally, where they consider appropriate, within their agricultural systems. Recent developments in sensing equipment for analyses of canopy and root structures of individual trees should enable interactive processes in agroforestry to be explained in terms of measurable tree variables. Modelling efforts based on this approach could enable the investigation of the likely effect of different tree frequencies on system performance from basic data that could be readily collected for a wide range of new species.

The extension of technology packages has proved less effective in agroforestry development than incremental improvements building on local practice (Buck 1990; Bunderson *et al.* 1990). Fundamental research that establishes yield responses to parameter changes has been recognised as complementary to adaptive research trials comparing alternative technology designs on-farm (Scherr 1990). However, the design phase in the well-known agroforestry diagnosis and design procedures developed at the International Centre for Research in Agroforestry (ICRAF) (Raintree 1990) has not been justified by field experience. This casts doubt on the common assertion that there is a primary requirement in agroforestry development for adaptive research, leading to rapid extension of technology packages that can be extended to farmers (Beer, Borel & Bonnemann 1990; Van den Hoek & Bekkering 1990), rather than a need to support farmers in making decisions about incorporating trees within their farming systems, based on the results of more fundamental research. In the context of the domestication of new species, the priority may turn out to be the collection of basic information on the canopy and root systems of the many trees currently used by farmers, to provide better advice on the likely impact of introducing or increasing their density on farmland, rather than concentrating on the development, on-station, of a necessarily small number of improved genotypes.

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Use and potential of domesticated trees for soil improvement

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ABSTRACT

The ancient and widespread use of tree and bush fallows to restore soil productivity following several years of cropping has resulted in research aimed at identifying, planting and managing trees for soil improvement. The goal is either to reduce the traditional fallow periods (normally between four and 25 years), or to eliminate the fallow period by introducing systems in which 'soil-improving' trees are managed together with crops or pasture species (agroforestry). Trees commonly used by farmers for soil improvement include *Acioa barteri, Calliandra calothyrsus, Cassia reticulata, Erythrina poeppigiana, Faidherbia albida, Gliricidia sepium, Inga edulis, Leucaena leucocephala, Prosopis cineraria,* and *Sesbania sesban.* Although many of these species are largely undomesticated, several are currently the focus of genetic improvement programmes (Owino, Oduol & Esegu, pp205–209; Simons, MacQueen & Stewart, pp91–102; Milimo, Dick & Munro, pp210–219). The possibility exists that in such programmes, selections could be made for tree characteristics to significantly improve soils. A synthesis of the research data from work on acid and high base status soils in the humid, subhumid, and semi-arid regions of Central and Latin America, Africa and Asia is used to evaluate critically 'tree/soil improvement' hypotheses related to nutrient cycling, organic matter additions, and nitrogen fixation. These hypotheses are discussed in the context of developing domestication strategies for multipurpose species, taking account of the influence of the species on the soil environment.

INTRODUCTION

The claim that trees have the potential to improve soils probably originates from the fact that forest fallows have been used to restore soil productivity, as shown in the traditional and widespread practice of shifting cultivation (Greenland & Nye 1959). In addition, there exist several traditional land use systems in which farmers retain trees on farmland. Recognition of the importance of the existing, but little studied, integration of trees in tropical land use systems led to the term 'agroforestry' (Bene, Beall & Cote 1977).

Increased yields have been reported for crops and forage grasses in close proximity to trees, and this increase has been partly attributed to improved chemical and physical properties of soil as a result of tree growth (Nair 1984). Several hundred semi-domesticated tree species are currently being used by farmers in the tropics. If these species can be utilised to counteract the soil-degrading effects of cropping and animal husbandry, farmers in the tropics who are currently practising shifting cultivation may not need to slash-and-burn additional forests every two to four years. The objective of this paper is to examine critically 'tree/soil improvement' hypotheses in relation to some of the semi-domesticated tree species that have not yet been used to any significant extent in plantation forestry. Because multipurpose tree species with potential for soil improvement are currently the focus of considerable scientific research in the context of agroforestry (Young 1989), we will examine primarily agroforestry data sets to test the key tree/soil improvement hypotheses related to organic matter additions, nutrient cycling, and nitrogen fixation, and will consider the ways in which the domestication of tropical forest trees can enhance soil improvement.

TREE-BASED CROPPING SYSTEMS IN THE TROPICS

Trees in rotation with crops (forest fallows)

Shifting or 'slash-and-burn' cultivation is a major form of land use in the tropics (Greenland 1974). Farmers typically clear about one hectare of primary or secondary forest, burn it, and then plant crops for one or more years, taking advantage of the nutrients released in the ash. Once yields decline or the weeds are no longer easily controlled, the site is abandoned. The nutrient accumulation by the forest fallow, the shading out of weeds, and the action of tree roots and associated micro-organisms and fauna are the processes by which the potential soil productivity is gradually improved to a state approaching that of a primary forest.

In areas of high population pressure, such as Nigeria, farmers are no longer able to leave the land fallow for a long period and resort to 'accelerated or biologically enriched fallows', involving tree species such as *Acioa barteri, Alchornea cordifolia, Anthonotha macrophylla, Gliricidia sepium* and *Harungana madagascariensis* (Okafor 1982; Okigbo 1983). In SE Asia, farmers use *Calliandra calothyrsus* (National Research Council (NRC) 1983) and *Leucaena leucocephala* (NRC 1984) as fallow species.

Trees in association with crops

In the sahelian and sudanian zones of West Africa, farmers maintain and manage around 20 different tree species on crop lands. Of these species, *Faidherbia albida* (Charreau & Vidal 1965) and *Parkia biglobosa* (Kessler 1992) have been reported to improve soils. Farmers in the semi-arid zones of India commonly retain and manage tree species such as *Prosopis cineraria* (Aggarwal *et al.* 1976), *P. juliflora* and *Delonix elata* (Jambulingam & Fernandes 1986) for fuelwood, fodder and soil improvement. In north-eastern Thailand, where multipurpose trees are maintained or planted on paddy fields, significantly higher contents of organic matter and soil macronutrients were found in fields with the nitrogen-fixing *Samanea saman* than in fields with non-leguminous trees (Sae-Lee, Vityakon & Prachaiyo 1992). Other tree species used to improve soils include *Sesbania sesban* (Evans & Rotar 1987), *Erythrina berteroana* and *E. poeppigiana* (Ramiréz *et al.* 1990).

TREE CHARACTERISTICS FOR SOIL IMPROVEMENT IN THE TROPICS

Fast-growing tree species are major components of agroforestry technologies (Nair, Fernandes & Wambugu 1984). With the exception of *Leucaena leucocephala* (Brewbaker 1990), the great majority of tree species have only just begun to be scientifically tested for their biological potential, adaptability to site conditions, and responses to management factors such as pruning, fertilization, and competition with agronomic crops.

On the more fertile soils, the presence of apparently sustainable agroforestry systems indicates that the tree component contributes to reduced erosion and efficient nutrient cycling (Alpizar *et al.* 1988). On acid, infertile soils, the potential of trees to increase nutrient inputs or reduce losses is limited by chemical constraints to root expansion. High aluminum (Al) saturation in the subsoil, low concentrations of calcium (Ca) and phosphorus (P), and a lack of weatherable minerals can severely limit plant productivity, and thereby reduce nutrient capture and recycling, compared with more fertile sites (Szott, Fernandes & Sanchez 1991). Adaptability to soil chemical and physical conditions is an obvious but vital requirement for any tree species to contribute to soil improvement. Desirable characteristics for soil-improving trees include the following.

Above-ground biomass production: around 2 Mg (megagram) ha^{-1} yr^{-1} for semi-arid regions, 4 Mg ha^{-1} yr^{-1} for subhumid regions and 8–10 Mg ha^{-1} yr^{-1} for the humid tropics (Table 1). These values are based on estimates by Young (1989) of organic residues required to maintain soil organic carbon at 7.5, 15 and 30 Mg ha^{-1} for each region, respectively.

Nitrogen fixation potential: 10–200 kg N ha^{-1} yr^{-1}, based on estimates from various species in the tropics (Peoples & Herridge 1990). The lower values are likely to be encountered for trees in the semi-arid tropics and also on acid soils with low P availability in the humid tropics.

Low fine root (<2 mm diameter) density in the topsoil: for example, no more than 30% of fine roots in the top 15 cm of the soil, and these preferably concentrated close to the stem (eg *Acioa barteri*, as described by Ruhigwa *et al.* 1992).

Capacity to form effective mycorrhizal associations with native populations of vesicular–arbuscular (VA) mycorrhizal fungi or ectomycorrhizal fungi (see Lapeyrie & Högberg, pp158–164; Mason & Wilson, pp165–175)

Moderate to high nutrient concentrations in leafy biomass (eg 2.0–3.5% N, 0.2–0.3% P, 1–3% potassium (K), and 0.5–1.5% Ca). Interpreting data for micronutrient concentrations in tree and shrub biomass is still difficult.

Appreciable nutrient concentrations in the root systems. For comparison, fine and coarse roots from two primary rainforest sites in Asia (Andriesse 1987) had the following mean concentrations: 0.66% N, 0.04% P, 0.55% K, 0.85% Ca, and 0.18% magnesium (Mg). Obviously, these values are likely to change with soil type, vegetation and root sizes.

Different rates of leaf litter decay: rapid litter decay (1–3 weeks) where tree biomass is used to provide nutrients to associated crops, or slow (2–6 months) decay when tree biomass is used as mulch for weed suppression and soil protection.

Table 1. Biomass production by tree species in alley cropping on fertile and infertile soils in the humid, subhumid, and semi-arid zones of the tropics (source: 1. Singh *et al.* 1989; 2. Hocking & Rao 1990; 3. Kang, Wilson & Sipkens 1981; 4. Fernandes 1990; 5. Ruhigwa *et al.* 1992; 6. Evensen 1989; 7. Kass *et al.* 1989; 8. Rosecrance, Brewbaker & Fownes 1992)

Species	Trees (nos ha^{-1})	Tree age (month)	Prunings (nos yr^{-1})	Dry matter (Mg ha^{-1} yr^{-1})	Ref
Hyderabad, India; rainfall 750 mm yr^{-1}; alfisol, pH 7.0, P=8 ppm (Olsen)					
Leucaena leucocephala	2 000	48	ND[1]	1.4 l	1
	833	48	ND	7.4 l+w[2]	2
Ibadan, SW Nigeria; rainfall 1280 mm yr^{-1}; alfisol, pH 6.2, P=25 ppm					
Leucaena leucocephala	10 000	36	6	6.51	3
Yurimaguas, Peru; rainfall 2200 mm yr^{-1}; ultisol, pH 4.2–4.6, P=8 ppm (Olsen)					
Inga edulis	8 888	11	3	9.6 l+w	4
Gliricidia sepium 14/84	5 000	11	3	8.1 l+w	
Gliricidia sepium 34/85	5 000	11	3	1.8 l+w	
Onne, SE Nigeria; rainfall 2400 mm yr^{-1}; ultisol, pH 4.0, P=50 ppm (Bray–1)					
Acioa barteri	2 500	48	ND	13.8 l+w	5
Alchornea cordifolia	2 500	48	ND	14.9 l+w	
Cassia siamea	2 500	48	ND	12.2 l+w	
Gmelina arborea	2 500	48	ND	12.3 l+w	
Sumatra; rainfall 2575 mm yr^{-1}; oxisol, pH 4.1, P=4.8–6.8 mg kg^{-1} (Melich I)					
Paraserianthes falcataria	19 900	09	4	4.9 l+w	6
		21	4	9.7 l+w	
Calliandra calothyrsus	19 900	09	4	6.8 l+w	
		21	4	10.7 l+w	
Gliricidia sepium	10 000	09	4	0.6 l+w	
		21	4	1.4 l+w	
Costa Rica; rainfall 2640 mm yr^{-1}; inceptisol, pH 4.3–4.8, P=8–15 ppm (Olsen)					
Gliricidia sepium	6 666	24	2	9.6 l+w	7
		60	2	15.2 l+w	
Erythrina poeppigiana	555	24	2	7.4 l+w	
		60	2	11.1 l+w	
Western Samoa; rainfall 3000 mm yr^{-1}; mod. fertile inceptisol, no soil data					
Calliandra calothyrsus	5 000	48	3	12.1 l+w	8
	3 333	48	3	7.6 l+w	
Gliricidia sepium	5 000	48	3	10.7 l+w	
	3 333	48	3	6.5 l+w	

[1] ND, not determined

[2] l, leaves and green shoots; w, woody material

Absence of toxic substances in the foliage or root exudates. For example, in the acid savannas (cerrado) of Brazil, some species have been shown to accumulate 4000–14 000 mg kg^{-1} of Al in the foliage (Haridasan 1982). Non-accumulator species typically have Al concentrations <200 mg kg^{-1}.

Other desirable characteristics of soil-improving trees remain to be identified, and there is considerable potential for exploiting the intraspecific genetic variation in the characteristics listed. Several tree species with soil-improving characteristics can be identified:

- acid soils, humid tropics: *I. edulis, Cassia reticulata, Cassia spectabilis, Erythrina berteroana, G. sepium* (OFI 14/84) and *Paraserianthes falcataria*;
- non-acid soils, humid and subhumid tropics: *Calliandra calothyrsus, Erythrina fusca, E. poeppigiana, G. sepium* and *Leucaena leucocephala*;
- non-acid soils, semi-arid tropics: *F. albida, Cassia siamea, Prosopis cineraria, P. juliflora* and *Sesbania sesban.*

TREE/SOIL IMPROVEMENT HYPOTHESES

Sanchez (1987) formulated the agroforestry hypothesis that 'appropriate agroforestry systems have the potential to control erosion, maintain soil organic matter and soil physical properties, augment nitrogen fixation, and promote efficient nutrient cycling'. What distinguishes agroforestry from other cropping systems is the presence of trees, either in association or in rotation with annual crops and/or animals. The hypothesised advantages of agroforestry are thus directly related to the presence, function, and management of the tree component and the interactions with the crop and/or animal components (Lundgren & Raintree 1983).

The rationale for the hypothesis that soil improvement in agroforestry is superior to that in other cropping systems is that the nutrient exports via the harvest of crop and animal products, erosion, leaching and volatilisation, and the deterioration in soil physical properties due to cropping or grazing, can be counteracted by the tree component. This process may occur *via:*

- nutrient uptake by deep-rooted trees allowing for capture and surface deposition of nutrients beyond the reach of crop roots (more efficient nutrient cycling);
- increased amounts of organic inputs to the soil maintaining soil organic matter and thus improving soil structure and nutrient status; and
- increased nutrient additions to the soil from N fixation and dust or aerosol interception by tree canopies.

These hypotheses are examined below.

Nutrient cycling and nutrient pumping

According to the 'nutrient pumping' hypothesis, nutrients absorbed from the subsoil are used in tree growth and eventually deposited in or on the surface soil via root and leaf litter production, nutrient leaching from foliage, and pruning of leaves or branches (Nair 1984; Young 1989). Nutrient pumping is one of the most frequently cited potential advantages of incorporating trees into cropping systems (agroforestry), and is based on the general belief that trees have deep spreading root systems capable of exploiting a greater soil volume than those of annual crop plants. The careful combination of trees and crops with different rooting characteristics offers the possibility of increasing the productivity of admixtures by optimising the complementarity of soil nutrient exploitation. Factors such as the spatial distribution and temporal patterns of root growth are clearly important, and should influence the choice of species or genotypes to be used.

Research on a variety of soil types and in different climates has involved the injection of ^{32}P at different soil depths and varying distances from the stems of banana (*Musa* spp.), cocoa (*Theobroma cacao*), coffee (*Coffea arabica*), coconut (*Cocos nucifera*) and oil palm (*Elaeis guineensis*). Results showed that 30–85% of P uptake occurred within a depth of 30 cm and a distance of up to 1 m from the stems of banana, cocoa and coffee. In coconut and oil palm, however, P uptake from similar zones accounted for less than 20% of the total applied. The uptake of P from a depth of 45 cm or greater and 1.5 m or further from the stem was less than 4% for the majority of tree crops, but up to 15% for coconut (International Atomic Energy Agency 1975). Indirect evidence of nutrient uptake by trees from the subsoil is provided by studies on *Eucalyptus* and *Prosopis* that showed water uptake from soil depths of 5 m or greater (Stone & Kalisz 1991). *Leucaena leucocephala* in an alley cropping system depleted soil moisture to a depth of 60 cm (Singh, Ong & Saharan 1989).

In spite of the potential for deep rooting possessed by many tree species, most roots do not reach great depths, because of the presence of physical or chemical barriers in the soil. Barriers to root expansion restrict the absorption of nutrients, such as P and K, that diffuse slowly in the soil and are depleted rapidly from localised pockets around roots, or those such as Ca, which is absorbed mainly through unsuberised root apices. However, root penetration of these barriers does occur. Adaptations to high soil Al concentrations exist in many plants (Marschner 1986). Furthermore, localised discontinuities in these barriers, caused by changes in soil texture, mineralogy, or biotic factors such as soil macrofauna, may permit roots of non-tolerant plants to grow through. The importance of these factors to nutrient uptake and cycling on infertile soils deserves further attention.

In summary, the greatest opportunity for nutrient pumping by deep-rooted trees exists on relatively fertile soils where physical barriers to root penetration are absent.

Organic inputs and soil organic matter

It has been hypothesised that the presence of trees in agroforestry systems results in concentrations of soil organic matter (SOM) that are adequate for maintaining soil fertility and productivity (Young 1989). Organic inputs to the soil consist of the above- and below-ground litter, crop residues, mulches, green manures and animal manures. Soil organic matter is the result of the partial or complete transformation in the soil of these inputs. Trees may be managed to provide large quantities of biomass for use as organic inputs. Furthermore, considerable scope exists for selecting between and within tree species for different chemical compositions and decomposition rates of the biomass produced. This option offers a means of manipulating nutrient release from biomass inputs, soil microbial activity, and the rate of conversion of these organic inputs to SOM.

The quality of organic inputs is one of the factors that influences the rate of decomposition and release of nutrients from organic residues. Research on tropical plant species has shown that indices of quality (eg C/N or lignin/N ratios) which are adequate for temperate zones (Melillo, Aber & Muratore 1982) may not be the best predictors of N mineralisation from leguminous materials in the tropics. N release patterns may be more closely related to tissue polyphenolic contents than to lignin or N contents or lignin/N ratios (Palm 1988). In general, on fertile soils, leaf litter quality is higher and decomposition faster than on acid, infertile soils. Very little is known about the quality of root litter. Root litter from trees may differ from that of annual crops in proportions of fine to coarse roots, the amount of lignins and polyphenols present, quantities of secondary or allelopathic compounds, and nutrient concentrations. Conventional indices of quality may not, therefore, be good predictors of tree root decomposition.

Organic phosphorus is the most important source of P in highly weathered tropical soils (Tiessen, Stewart & Cole 1984). Incorporation of fast-growing trees into tropical farming systems offers the potential to increase this organic P pool. Tiessen, Salcedo and Sampaio (1992) found a 28% increase in organic P in the soil but only a 9% increase in total P during a ten-year bush fallow. There is even some evidence that some species are able to utilise insoluble forms of soil P not used by crop species (Ae *et al.* 1990).

The role of soil organic matter in contributing to soil fertility and productivity was summarised by Alison (1973) as:

- a source of inorganic nutrients to plants;
- a substrate for micro-organisms;
- an ion exchange material;
- a factor in soil aggregation and root development; and, consequently,
- a factor in soil and water conservation.

Despite these potential effects of SOM, there exist several cases where no consistent correlation has been found between total SOM and existing or potential soil productivity (Sanchez & Miller 1986). As a result, research has focused on several conceptual fractions of SOM based on different turnover times in the soil, as a function of chemical structure and association with soil particles (Parton *et al.* 1987).

A key issue involves the possibility of influencing soil improvement via the selection and management of tree species or genotypes with differing litter qualities. Litter that decomposes at a slow rate (low quality) is likely to lead to the formation of slow and passive fractions of SOM which are less important in short-term nutrient availability but which play an important role in maintaining soil structure. In managed fallow or plantation systems where trees are used to regenerate soil productivity, the use of domesticates with low-quality, slowly decomposing materials would build up the organic pools of nutrients and buffer long-term nutrient availability and release. In systems where trees and crops are grown simultaneously (eg alley cropping), the use of a mixture of species or genotypes with different litter qualities may be advisable.

N fixation by trees

There are around 650 species of nitrogen-fixing trees and shrubs (see Sprent, pp176–182). Some tree species appear to have a higher capacity for nitrogen fixation than others. Published estimates of the amount of N fixed by N-fixing trees are in the range 10–500 kg N ha^{-1} yr^{-1} (Young 1989). The proportion of tissue nitrogen in trees derived from fixation can vary between 4% and 80% (Peoples & Herridge 1990; Danso, Bowen & Sanginga 1992). In addition to differences in N fixation among tree species, large differences exist among genotypes within a species. Sanginga, Bowen and Danso (1990) reported two- or three-fold differences in N fixation among genotypes of *F. albida* and *L. leucocephala* after 12 weeks and 70% differences after 36 weeks.

The potential N contributions of leguminous tree species to the soil are often not realised, however, because of high soil acidity, low soil nutrient contents (Szott *et al.* 1991), and low soil moisture contents (Venkateswarlu, Korwar & Singh 1990). Studies of leguminous annuals have shown that low concentrations of P in acid soils can severely limit nitrogen fixation (Barea & Azcon-Aguilar 1983). There is, however, a lack of experimental data for leguminous tree species. In P-deficient soils, the planting of N-fixing tree species with crops may actually result in competition for P between the trees and the associated crops. The addition of moderate amounts of P fertilizer to the trees could alleviate the competition for phosphorus. Effective symbiosis with compatible vesicular–arbuscular (VA) mycorrhizal fungi (see Mason & Wilson, pp165–175) will also be important.

N-fixing trees probably contribute little N directly to the soil environment in excess of their own N requirements for growth, but this situation can be overcome by shoot pruning and the application of this biomass to associated crops (eg in alley cropping). In addition to the release of N and other nutrients from the decomposing biomass, shoot pruning brings about an additional contribution of N to the soil via the death of fine roots and nodules. In a pot experiment with *I. edulis*, shoot pruning resulted in significant reductions in fine root biomass, total root length infected with VA mycorrhizal fungi, and numbers of active nodules, relative to non-pruned control plants (Fernandes 1990). The renewal of nodulation and nodule function may be further suppressed by the release of N from the decomposing prunings, fine roots and nodules (Danso *et al.* 1992).

In summary, a number of factors can affect N fixation in trees. They include soil acidity, low soil P, VA mycorrhizal fungi, high soil N, rhizobial strains, soil moisture and temperature, tree age, shoot pruning, and tree genotype. Optimisation of N fixation by tree species will require not only selections among and within tree species for adaptability to soil factors adversely affecting N fixation, but also selections for enhanced efficiency of tree/rhizobial/VA mycorrhizal associations.

SIGNIFICANCE OF TREES AS NUTRIENT EXPORTERS

While trees may contribute significantly to soil improvement, they can also have adverse effects on soils and associated crops or pasture species. These potential negative effects include biomass and nutrient export from the site through tree harvests, as well as competition for nutrients and moisture between the trees and associated crop species. We review these issues through discussion of three types of agroforestry systems: domesticated timber tree-based systems, tree/perennial crop systems, and pruned hedgerow intercropping systems.

Timber-based systems

Tabora (1991) compared three perennial agroforestry species in terms of their impact on annual nutrient removal: an abaca-based (manila hemp, *Musa* sp.) system, a coconut-based system (*Cocos nucifera*), and a *Paraserianthes falcataria* pulpwood production system. The abaca system was found to sustain the least nutrient exportation, with only 4 kg of macronutrients (sum of elemental N, P, and K) removed ha^{-1} yr^{-1} in the fibre harvest. Abaca fibre is a highly cellulosic material composed of only 1.0% ash. The coconut-based system removed double this quantity of nutrients, while macronutrient exportation of the *Paraserianthes* wood production system was an order of magnitude higher (Table 2). In a 6.8-year-old plantation, Halenda (1989) estimated that harvesting *A. mangium* stems alone would have resulted in the export from the site of 284 kg N, 15 kg P, 225 kg Ca and 24 kg Mg ha^{-1} respectively. Clearly, although the trees accumulated considerable biomass and nutrients, tree harvesting for two or three rotations would result in a nutrient-depleted site.

Table 2. Estimated nutrient export per hectare per year of three agroforestry systems (source: Tabora 1991)

Component	Biomass (t ha^{-1})	N content (kg)	P content (kg)	K content (kg)
Coconut kernel removed	1.4–1.9	00.87	04.46	03.34
Abaca fibre removed	1.1	01.38	00.05	02.76
Albizia wood removed	12.0	NA*	42.00	18.00
Albizia litter recycled	4.8–6.2	99.36	03.12	31.08

*NA, not available

Tree/perennial intercropping

Alpizar *et al.* (1986) and Fassbender *et al.* (1988) inventoried the nutrient uptake and flows in two agroforestry systems composed of cocoa planted at 1111 trees ha^{-1}, in association with either *Erythrina poeppigiana* or *Cordia alliodora* serving as shade and timber trees spaced at 278 trees ha^{-1}. Biomass accumulation in stems of *C. alliodora* was 2.5 times higher than in *E. poeppigiana*. The latter accumulated the majority of its biomass in branches and leaves, which recycled in the system through pruning and litterfall. The total annual net primary productivity of the two systems, however, was fairly similar (21.6 *versus* 21.3 t ha^{-1}).

Nutrient accumulation in the standing biomass was much higher for the timber trees than for the cocoa. This fact might have induced serious competition for nutrients, were it not for the relatively limited nutrient removal demands of the system, in comparison with the abundant nutrient cycling occurring within it. Annual nutrient extraction from the system through the harvest of cocoa pods and husks was relatively low (compared with annual crop systems) at 19–25 kg N, 4.0–4.3 kg P and 28–27 kg K. There was also a low proportion of nutrient exportation compared with the total nutrient concentration of the standing biomass (5% N, 8% P and 8% K). The recycling of nutrients by residues returning back to the soil system exceeded removal by 5.9–6.8 times in the case of N, and by 3.8–4.8 times for P, and about 2 times for K. Only one of the overstorey trees was a nitrogen-fixing species (*E. poeppigiana*). The cocoa/*E. poeppigiana* combination registered a total increase of 80 kg N ha^{-1} in the soil/plant system over a five-year period, indicating an annual contribution from fixation equivalent to 18 kg N ha^{-1}.

Pruned tree hedgerows

Direct nutrient exportation in alley cropping or hedgerow intercropping systems may occur by the use of leaves and green stem prunings as animal fodder, or by the harvest of poles, fuelwood, or fruits. Indirect export occurs through the harvest of annual crops obtaining nutrients from hedgerow litterfall and prunings. The harvest of economic products results in direct nutrient exports but contributes to the productivity and profitability of the system. Farmers practising alley cropping often find that the economic value of hedgerow prunings when used as animal fodder may often exceed their value as green manure (Kang, Reynolds & Atta-Krah 1990). This practice may, however, result in an accelerated decline in soil fertility. The increased quantity of animal manure that results from greater fodder production can be returned to the field, along with additional inorganic fertilizer, to at least partly offset the losses. Otherwise, the increased rate of soil nutrient removal may jeopardise the long-term sustainability of the system.

SIGNIFICANCE OF TREES AS COMPETITORS FOR RESOURCES IN AGROFORESTRY SYSTEMS

The very nature of agroforestry dictates that resource competition largely controls system viability and productivity. The development of systems involves the search for tree domesticates to fill complementary or synergistic niches that minimise resource competition. Limited research during the past decade has begun to explore the nature of tree/crop interactions (Ong *et al.* 1991). The concepts of resource sharing in agroforestry systems were reviewed by Buck (1986).

The tree component of agroforestry tends to have a competitive advantage over an annual crop, owing to its dominant stature, both above- and below-ground. As in any intercropping system, competition may increase the production of the system as a whole, or help stabilise outputs when resource supply is erratic (Monteith, Ong & Corlett 1991).

Below-ground competition

In water-limited environments, the potential of agroforestry is strongly influenced by the major tree/crop differential in ability to capture soil moisture. Severe reductions in crop yields in alley cropping are often observed in the semi-arid tropics, drawing the viability of these systems into question, eg in India. Studies with root barriers have indicated that these reductions are mainly due to competition for water (Singh *et al.* 1989). The presence of a shallow root barrier (to 0.5 m depth) was sufficient to eliminate a yield reduction in cowpea and sorghum yield. Ong *et al.* (1991) found that root barriers eliminated crop yield reductions in tree/annual crop associations, and concluded that competition for water was the driving factor. Roots of *Leucaena leucocephala* were abundant in the top 30 cm of soil in adjacent alleys, contrary to the assumption that tree roots do not compete with crops.

Malik and Sharma (1990) observed that *Eucalyptus tereticornis* extracted five times more water than mustard from a 150 cm soil profile at the tree/crop interface, when grown in a hedgerow cropping system in a semi-arid environment. Mustard and wheat yields were reduced by 47% and 34%, respectively, in adjoining 10 m wide strips. Likewise, boundary plantings of *L. leucocephala, Eucalyptus camaldulensis, Albizia procera,* and *Morus alba* reduced yields of wheat by 15–70% up to 4 m away in adjoining fields (Akbar *et al.* 1990). These results emphasise the importance of taking water use characteristics into account during any domestication programme.

Because uptake of N, P and K is most strongly regulated by plant demand and plant demand is strongly related to growth, it follows that competition between soil-improving trees and associated crop or pasture species may be minimised if the trees and associated species differ in phenology. In many tropical tree species, rapid growth and high nutrient demand occur during the rainy season. An exception to this pattern is provided by *Faidherbia albida*, which loses its leaves at the beginning of the wet season. Presumably, this timing would result in less nutrient demand and less nutrient competition with annual crops during the wet season.

Demand for nutrients is generally highest during the period of growth in foliage and fine roots, which usually occurs within the first ten to 20 years of tree growth, although root accumulation may continue to occur for longer periods of time. Because internal re-translocation is limited in young trees, high demand is placed on soil stocks (Miller 1984). The implication is that competition for nutrients and water is likely to be most severe during the early stages of tree growth and will decrease as the trees get older, because of the increasing importance of internal re-translocation and the expansion of the tree roots into previously unexplored soil. If tree products are being harvested, however, the nutrient exports in the harvested fraction will reduce internal re-translocation and increase competition between trees and associated vegetation, as the trees seek to compensate for the exported nutrients (Atkinson 1986).

Although the soil volume explored by tree roots might be expected to increase as the trees age,

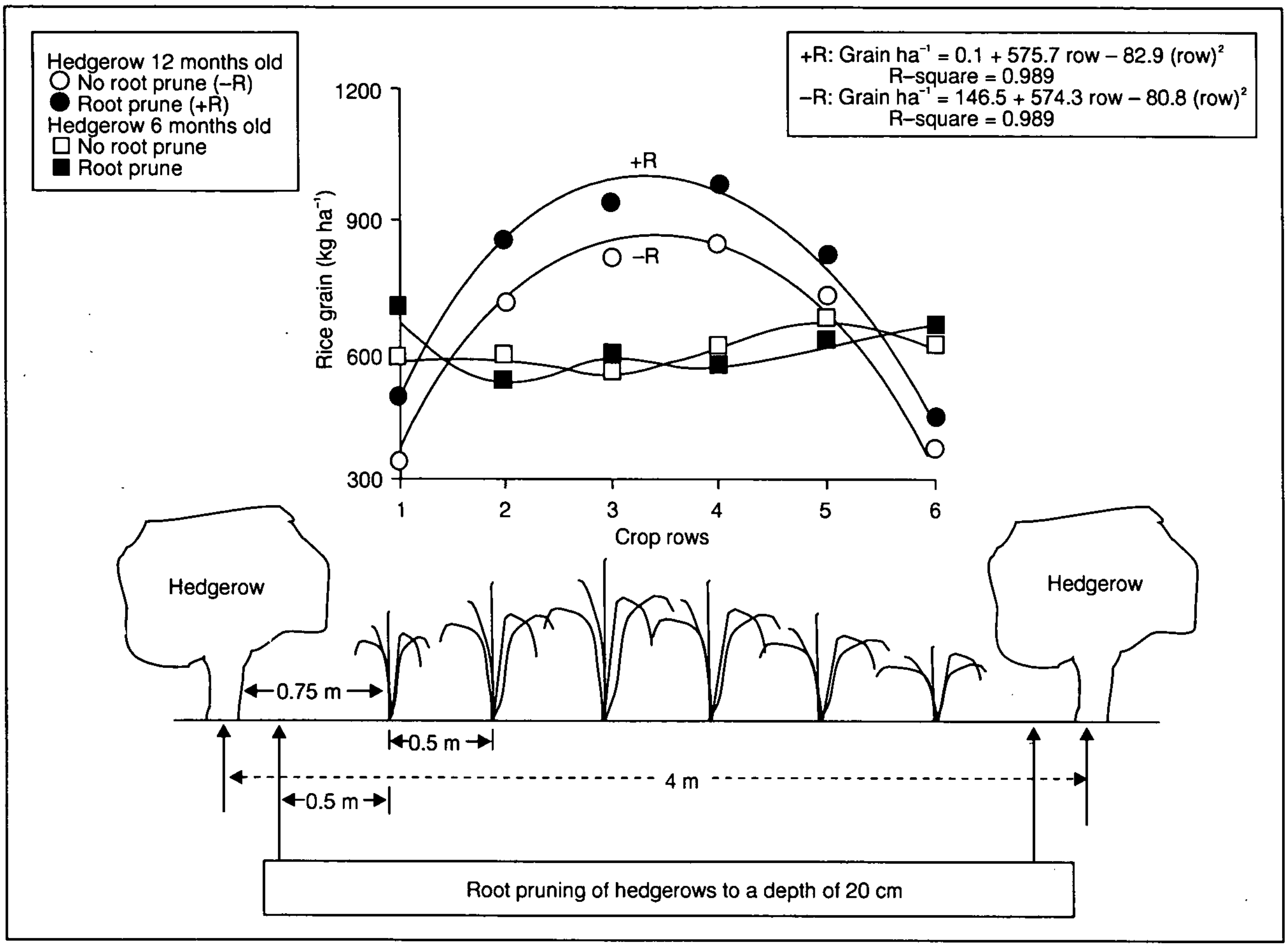

Figure 1. Rice grain yield with distance from hedgerows of *Inga edulis*, as affected by age of hedgerow and pruning of hedgerow roots (source: Fernandes 1990)

differences in rooting volume vary among species, provenances and individuals of a species (Jeník 1978), and may therefore be the subject of selection during tree improvement. More equitable sharing of below-ground resources between trees and associated vegetation could be accomplished by:

- selection of appropriate genotypes or ideotypes;
- varying plant spacing and time of planting;
- and the use of above- or below-ground pruning, shade, and liming.

In an alley cropping experiment on acid soils (Fernandes 1990), root pruning of hedgerow roots significantly increased crop yields in the second year of tree/crop interaction (Figure 1).

Perhaps the most cost-effective technique would be to use species and provenances that have complementary patterns of nutrient uptake. This possibility presupposes knowledge regarding the spatial and temporal patterns of nutrient uptake and/or rooting patterns. While data on rooting patterns of the more recently domesticated trees are very scarce, genetically based differences in rooting patterns exist even among provenances (Vandenbeldt 1991). In a study of 15 provenances of *G. sepium*, there were significantly different patterns of vertical root distribution among provenances 20 months after growth in the field (Fernandes 1990). Such differences offer the potential of selecting adapted germplasm for optimising the desired effects of trees on soils.

Tree species used in agroforestry systems are commonly selected for their ease of establishment, fast growth, ability to coppice vigorously, high foliage production, N-fixing ability and high rates of production of useful products such as wood or fruits (Kang *et al.* 1990). These trees are typical of the 'competitive' ideotype as described by Donald and Hamblin (1976). Invariably, high tree productivity is associated with high nutrient demand and high nutrient uptake efficiency. On infertile soils, however, these tree characteristics will increase competition for nutrients and water between trees and associated crops, thereby negating any beneficial effects that the trees have on soil chemical or physical properties. Trees of the 'crop' ideotype, however, are not strong competitors, and make efficient use of those site resources to which they have access (Cannell 1978). Trees with a crop ideotype are likely to be more suitable than trees with a competitive ideotype for agroforestry systems in which trees and crops are present simultaneously.

Above-ground competition

Theoretical aspects of above-ground interactions in agroforestry systems were reviewed by Monteith *et al.* (1991). The taller-tree component tends to exert changes in four types of microclimatic influence on an associated annual crop: light interception, rainfall interception, saturation vapour pressure in the canopy, and crop temperature. The effect on the crop may be negative or positive, depending on the environment, and particularly on the degree of water deficit.

Shading effects tend to be particularly pronounced on short-statured crops grown in association with tree hedgerows, such as upland rice. Solera (1992) inserted root barriers next to hedgerows of *Gliricidia sepium* and *C. spectabilis* in the southern Philippines, and observed that the dry matter yield reduction that occurred in the rows of rice nearest to the trees was not caused by below-ground competition. The 50 cm tall hedges apparently caused a deleterious shading effect on the rice, even though the trees were pruned frequently during the growing season. These results contrast with observations from semi-arid areas, where above-ground interactions were found to be of minor importance compared with below-ground competition for soil moisture (Ong *et al.* 1991). The importance of tree architecture and of matching trees to their light environments are discussed elsewhere in this volume (see Oldeman & Sieben-Binnekamp, pp25–33; Fasehun & Grace, pp148–157).

Allelopathy

There is evidence that at least some tree species observed in agroforestry systems produce phytotoxins that can directly affect germination and growth of common agricultural crops (Bhatt & Todaria 1990). The species include *Adnia cordifolia, Alnus nepalensis, Celtis australis* and *Prunus cerasoides*. The significance of this allelopathy at the field level, however, is not yet known, and there is little information concerning intraspecific variation in this characteristic.

CONCLUSIONS

The mechanisms by which trees may improve soils are now reasonably well understood. That certain tree species can improve soils is shown by the regeneration of soil productivity in fallows. Pioneer species that possess adaptive characteristics to overcome soil constraints can play a key role in modifying the site for late successional species. The timeframe for this modification is usually long (10–20 years). It is hypothesised that it is possible to combine trees and crops in certain proportions so that crop yield is increased by soil-improving trees. Evidence so far has shown that, on fertile soils where nutrients are not limiting, this result can be achieved. On nutrient-poor soils, however, tree/crop competition is usually so severe that the intensive management of both components is required before any soil improvement is obtained from the associated trees. The use of well-adapted tree domesticates in managed fallows, together with minimum levels of inorganic inputs, could significantly shorten the time for regenerating soil productivity on acid soils.

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Matching trees to their light environments

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ABSTRACT

Radiant energy striking the earth's surface is in the waveband 310–2300 nm, of which the visible part ('light') and also the photosynthetically active radiation (PAR) fall between 400 and 700 nm. There are differences in the incident solar radiation and patterns of PAR in the open, in dense forest, and in gaps. The spectral shifts and light absorbance at different wavelengths, especially the red/far-red ratio, play significant roles in seed germination and plant photomorphogenesis. Plants are classified as light-demanders and shade-tolerators based on their response to irradiance. Pioneers are light-demanders, having photosynthetic attributes similar to weeds. Compared to late successional species, they display higher stomatal conductances, light compensation points and dark respiration rates. Most tropical tree species used in plantations and agroforestry systems are pioneers. Research needs to focus on the ecophysiology of tropical trees, the influence of red/far-red ratio and sunflecks on plants growing on the forest floor, so as to match trees effectively to their light environments.

INTRODUCTION

An essential part of the domestication process in plants as well as animals is the accumulation of knowledge on the characteristics of species, so that strengths and weaknesses peculiar to each genotype may be revealed. In the case of trees, this implies an understanding of growth in relation to the environment, and in relation to silvicultural practices. The growth of trees in the forest is determined by the expression of physiological processes within specific environmental regimes. Of all the above-ground environmental factors affecting the growth and development of the tropical rainforest plants, light is the most variable, complex and least readily quantified. Only part of the solar radiation incident on earth (waveband 400–700 nm) is active in photosynthesis. This waveband is referred to as photosynthetically active radiation (PAR).

Light climates vary widely between forests, between habitats within a forest, and within a single habitat. Nevertheless, some generalisations can be made that are relevant to the dynamics of tropical forests. The solar radiation incident on the forest canopy is composed of two different forms: direct beam, and radiation diffused by the earth's atmosphere, usually referred to simply as 'direct' and 'diffuse' respectively (Chazdon 1988). These two forms penetrate the forest canopy in different ways, as a result of their different angular properties (Anderson 1964a, b; Hutchinson & Matt 1977). When the sun is shining, predominantly direct-beam sunlight passes through holes in the canopy, arriving at the forest floor as sunflecks. If the holes are small, the sunfleck is less intense than full sunlight, but nevertheless the light is ten or 20 times as bright as in the adjacent shaded region. As the solar angle changes, each sunfleck traverses across the forest floor, exposing seeds and seedlings to a large stepwise change in photon flux density (PFD), which may in some cases be beneficial and in others deleterious (Chazdon 1988).

Diffuse light incident on the forest canopy penetrates all canopy openings, although not always equally. As both direct beam and diffuse skylight pass through vegetation, the spectral quality is altered by selective absorption, transmission and reflection of the wavelengths by foliage, and to a lesser extent by branches and tree trunks. Thus, the light climate at a particular location in the forest is determined by three major factors, as enumerated by Chazdon and Fetcher (1984a), namely:

- position of the sun (solar elevation and azimuth);
- atmospheric condition (cloudiness and aerosol content); and
- vegetation structure (pattern in vertical and horizontal plants; leaf angle distribution).

Both the photon flux density and spectral distribution are significantly affected by the forest vegetation. Blue and red wavelengths are selectively absorbed by chlorophyll, and shadelight is consequently enriched in green and far-red. Sunflecks contribute significantly to the total PAR available in the forest understorey (Chazdon 1988), typical values for Australian rainforest being 50% of the total available photons. Similar figures have been reported as 70% for Nigerian forest (Evans, Whitmore & Wong 1960), 50% for Singapore forest (Whitmore & Wong 1959) and 60% for forest in Ecuador (Grubb & Whitmore 1967). Direct measurements of photosynthesis under sunflecks have shown that sunflecks make an important contribution to the daily photosynthesis (Pearcy & Calkin 1983).

The light climate in canopy gaps is highly variable. Much of the variability in light between gaps can be attributed to gap size (Chazdon & Fetcher 1984b; Denslow 1987). Gap orientation, the height of the surrounding forest, topography and solar angle are other important factors affecting gap light climates. The increased light availability in gaps is extremely important for the distribution and the regeneration of many tropical plant species.

The difference in red/far-red (R:FR) ratios between gaps, forest canopy and shaded understorey may affect seed germination and seedling growth. Spatial patterns in light and shade may be explored by traversing sensors through the forest, passing through gaps of varying size (Figure 1). Photon flux densities in the largest gaps in a forest in Nigeria were around 2000 μmol mm^{-2} s^{-1}, whilst in the densest shade they were as low as 50 μmol m^{-2} s^{-1}. The R:FR ratios were strongly correlated with photon flux densities in this example (Figure 1). Values of R:FR ratio exceeding 1 occurred in direct sunlight, and much lower values, around 0.2, occurred in the densest shade as a result of the low absorptivity of leaves to far-red radiation. Similar data from other types of tropical forest have been reported by Chazdon and Fetcher (1984a).

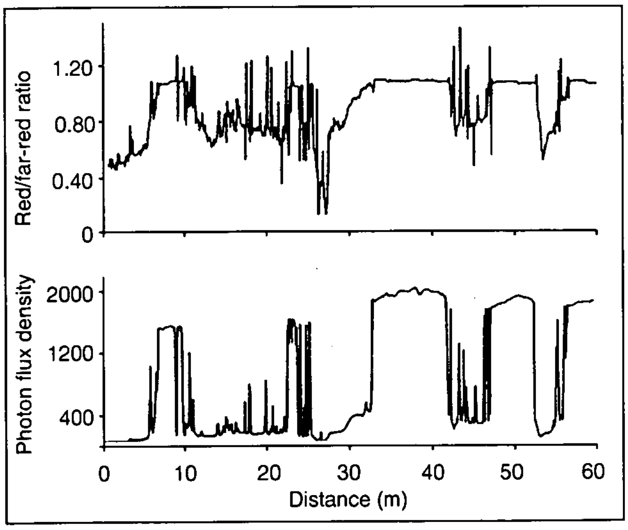

Figure 1. Signatures of a disturbed forest made by traversing light sensors along a 60 m transect of a secondary tropical forest at Ibadan, Nigeria. The transect passes through a small gap at 7–10 m, and larger ones at 30–42 m and 46–53 m. The upper graph shows the red/far-red ratio, and the lower is the photon flux density (μmol photons m^{-2} s^{-1}) (data of J Grace, I Riddoch, F E Fasehun & D Ladipo, unpublished)

PHOTOSYNTHETIC PERFORMANCE IN CONTROLLED CONDITIONS

Photosynthetic adaptability to shade has been widely studied in herbaceous species and in temperate trees (Björkman & Holmgren 1963; Björkman 1981; Bazzaz & Carlson 1982). Recently, with the advent of field-portable gas exchange equipment, there has been an upsurge of interest in tropical trees (Fasehun 1980; Langenheim *et al.* 1984; Mooney, Field & Vazquez-Yanes 1984; Kwesiga, Grace & Sanford 1986; Oberbauer & Strain 1984; Pearcy, Osteryoung & Calkin 1985; Pearcy 1987; Thompson, Stocker & Kriedemann 1988; Hogan 1988; Ramos & Grace 1990; Riddoch *et al.* 1991). Gas exchange parameters have been shown to depend on the light climate during growth and leaf development, with strong evidence for a morphogenetic effect in response to a reduced red/far-red ratio (Kwesiga *et al.* 1986). In most of the studies, increases in the amount of light led to increases in rates of stomatal conductance, photosynthesis and dark respiration, and ultimately to higher growth rates.

There is considerable variation in the *extent* to which the light regime during growth influences photosynthetic characteristics. For example, Ramos and Grace (1990) found rather small differences between light response curves of leaves grown in high and low light in four South American species, the largest difference being in the fast-growing *Cordia alliodora* (Figure 2). A similar variation in responsiveness between fast- and slow-growing species was noted by Riddoch *et al.* (1991) for West African species. The fast-growing *Nauclea diderrichii* displayed an extra layer of palisade cells when grown in bright light, and its leaves were increased in thickness, but the relatively slow-growing *Entandrophragma angolense* did not develop extra palisade, and the rate of photosynthesis at high light was less responsive than in *Nauclea*. Much of the observed acclimation is the result of an increase in the amount of photosynthetic machinery per unit area of leaf, which must depend on the capacity of the leaf to undergo a photomorphogenetic response to a changing light regime, as well as on the availability of nitrogen, required particularly for synthesis of the carboxylating enzyme, RUBISCO. These relationships are best investigated by reference to the relationship between photosynthetic rate, A, and internal CO_2 concentration, C_i, as the rates of photosynthesis can then be observed in the absence of stomatal limitations to the diffusion of CO_2 into the leaf. From such relationships (Figure 3), the activity of RUBISCO under non-limiting

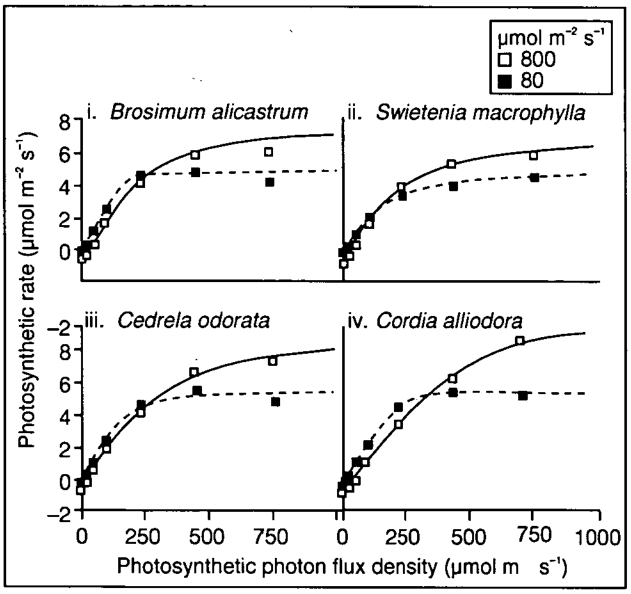

Figure 2. Light response curves of photosynthesis of four tropical tree species grown under 'sun' (open squares, 800 μmol m^{-2} s^{-1}) and 'shade' (filled squares, 80 μmol m^{-2} s^{-1}). Each line is the non-rectangular hyperbola obtained from the model using the parameters in Table 1 and setting g_s to that found at the highest photon irradiance. Data points are the means of five replicates (source: Ramos & Grace 1990). Note that the initial slope (quantum efficiency) is not much changed; shade-grown plants show saturation at lower photon flux density; and the late successional species (i) and (ii) are very little affected by growth conditions

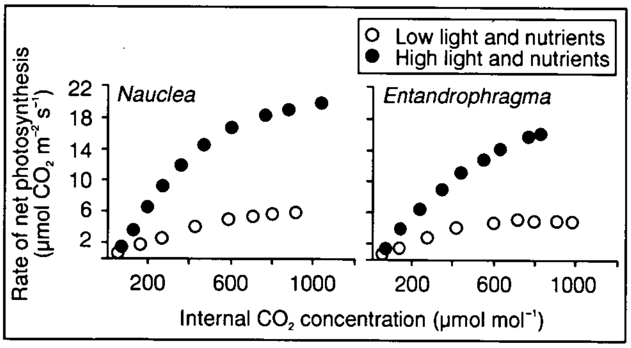

Figure 3. A/Ci curves obtained for *Nauclea diderrichii* and *Entandrophragma angolense* at four treatments. The data are from the median case of three runs. Note the similarity between *A*/*C*i curves of the two species when the plants are grown in low light. In high light, the *Nauclea* curve shows a steeper initial slope than the *Entandrophragma* curve, showing an enhanced capacity to fix CO_2 (source: Riddoch, Lehto & Grace 1991)

CO_2 can be found (as d*A*/d*C*i), as well as the photosynthetic rates at CO_2 saturation. The relatively fast-growing *Nauclea diderrichii* takes up no more N per leaf area than the slower-growing *Entandrophragma* when grown under high light, but apparently uses it more efficiently as judged by d*A*/d*C*i and A_{max} (Table 1). *Entandrophragma* has more mass per unit area of leaf, presumably associated with the tough and long-lived characteristics of its leaves.

Leaves raised under one light regime may acclimate when moved to a new light regime, even when they are fully expanded in the first instance. For example, in the Asian species *Bischofia javanica*, leaves developed under high light showed a large negative net photosynthetic rate when transferred to low light, but within seven days the rate increased and became equal to that of leaves which had been grown under low light (Kamaluddin & Grace 1992a). These changes involved considerable re-organisation of photosynthetic machinery, including a reduction in mass per unit leaf area, an increase in chlorophyll content and a decline in the chlorophyll a:b ratio.

The transition from low to high light is perhaps the more interesting one, as it occurs in many silvicultural manipulations, and also when the canopy is opened by the falling of a tree. In this case, leaves which have developed at extremely low photon fluxes are exposed suddenly to full daylight. It is well known that exposure of shade-adapted leaves to high light results in photoinhibition of photosynthesis (Kok 1956; Critchley & Smillie 1981; Langenheim *et al.* 1984; Oberbauer & Strain 1984). This photoinhibition is usually manifested by a reduced quantum yield and light-saturated capacity of photosynthesis, a reduced electron transport activity, and altered chlorophyll fluorescence characteristics. It is likely that shade understorey seedlings suddenly exposed to high light during gap formation in the forest canopy always suffer photoinhibition and chlorophyll destruction. Such processes have been studied in controlled environments.

Kamaluddin and Grace (1992b) examined the potential for light acclimation in shade-grown seedlings of *Bischofia javanica*: they grew the seedlings under simulated forest shade light

Table 1. Enhancement of RUBISCO activity, A_{max}, mass and nitrogen content in leaves developed under high (700 μmol m^{-2} s^{-1}) as opposed to low (30 μmol m^{-2} s^{-1}) light. All data are on a leaf area basis (source: Table 1 of Riddoch *et al.* (1991)

	RUBISCO activity per area of leaf (μmol m^{-2} s^{-1})	A_{max} (μmol m^{-2} s^{-1})	Mass per area (g m^{-2})	N per area (g m^{-2})
Nauclea diderrichii				
Low light	0.0118	7.3	23.2	0.64
High light	0.050	20.8	62.5	1.31
Enhancement factor	x4.2	x2.8	x2.4	x2.0
Entandrophragma angolense				
Low light	0.0125	5.6	41.6	0.69
High light	0.036	16.9	71.4	1.40
Enhancement factor	x2.8	x3.0	x1.7	x2.0

(40 μmol m^{-2} s^{-1}) and, after the transfer of the seedlings to a higher irradiance (1200 μmol mm^{-2} s^{-1}), they observed changes in chlorophyll induction kinetics, net photosynthesis, leaf chlorophyll and leaf anatomy. They reported that the leaves grown under low light displayed photoinhibition immediately after transfer to high light. The photoinhibition lasted for some days before the leaves acclimated to the higher light (Figure 4). Although the light-saturated photosynthetic rate declined from 3 to 2 μmol m^{-2} s^{-1} over seven days, and chlorophyll content declined by 50% over 15 days, the leaves survived and acclimated. Over 20 days, leaf mass per unit area increased to almost the value of leaves grown in high light, and palisade thickness doubled. Photosynthetic rate increased to 6, μmol m^{-2} s^{-1}

It is clear from this discussion that leaves have considerable potential to acclimate to the changes in photon flux that occur naturally, although there may well be important differences between species in the ease with which this acclimation can occur.

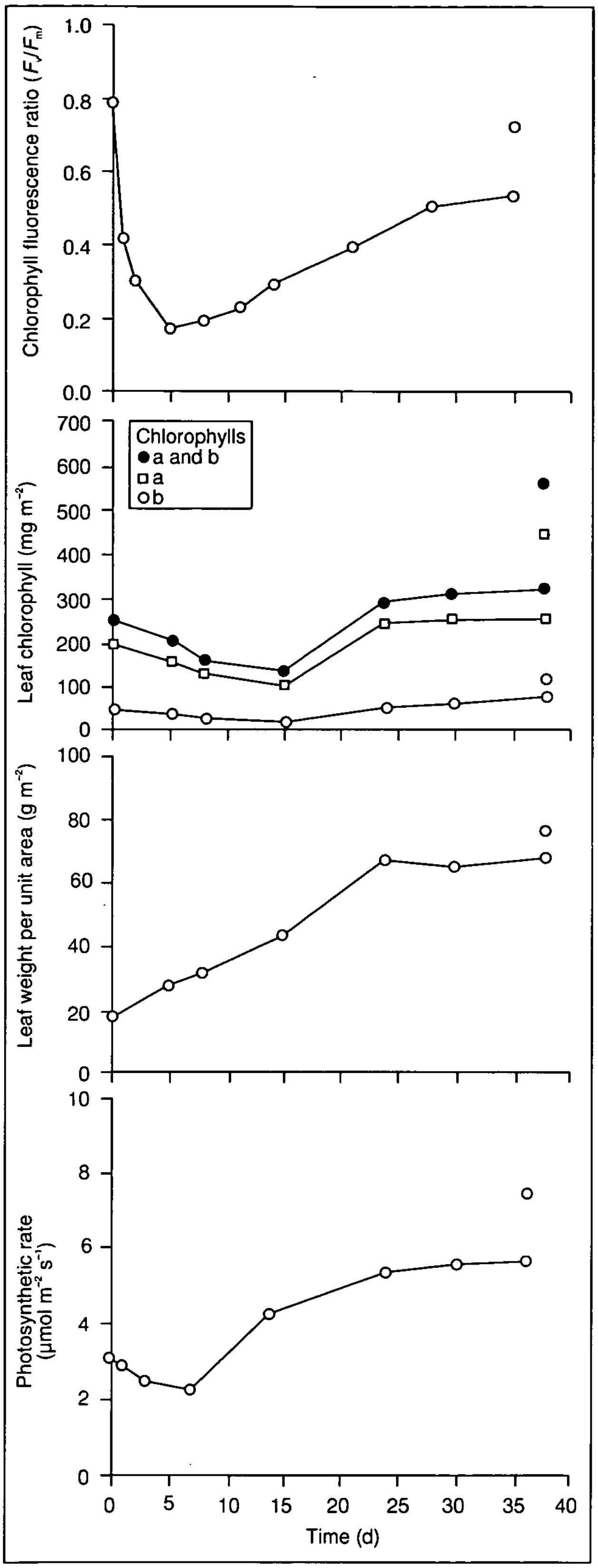

Figure 4. Acclimation of shade-grown leaves of *Bischofia javanica* on transfer from simulated shade (PAR = 40 μmol m^{-2} s^{-1}, R:FR = 0.15) to simulated open conditions (PAR = 1200 μmol mm^{-2} s^{-1}, R:FR = 1.95). The chlorophyll fluorescence ratio (top graph) is a measure of photoinhibition. The isolated point at the right-hand side of each graph is the value for leaves which formed in bright light, whereas the connected values are leaves formed at low light which are acclimating to bright light (source: Kamaluddin & Grace 1992b)

PHOTOSYNTHETIC RATES OBSERVED UNDER FIELD CONDITIONS

Photosynthetic rates of nine species were studied at the Gambari Forest Reserve, Ibadan, Nigeria (Riddoch, Lehto & Grace 1991). This study was designed to test the hypothesis of Bazzaz and Pickett (1980) and Bazzaz and Carlson (1982) that pioneer species have an enhanced capacity to utilise the high photon flux density associated with gap formation. Species chosen included two herbaceous weeds (*Chromolaena odoratum* and *Piper umbellatum*), as well as pioneer and late successional trees. Light response curves were obtained by aggregating measurements of photosynthesis obtained over the course of the day, and statistical comparison was made after fitting the non-rectangular hyperbola model of Jarvis, Miranda and Muetzelfeldt (1985) to the data (Figure 5; Table 2). This model provides

Table 2. Mean photosynthetic parameters of a range of tropical tree species: dark respiration R_d (μmol CO$_2$ m^{-2} s^{-1}), quantum efficiency a (mol CO$_2$ per mol photon), mesophyll conductance g_m (mol m^{-2} s^{-1}) and light compensation point Q_0 (μmol photons m^{-2} s^{-1}) (source: Table 2 from Riddoch, Lehto & Grace 1991)

	R_d	a	g_m	Q_0
Weeds of forest gaps (2 species, 2 sites)	1.75	0.03	0.028	47
Pioneer trees (5 species, 2 sites)	0.82	0.03	0.021	29
Late successional trees (2 species, 1 site)	0.50	0.03	0.008	18

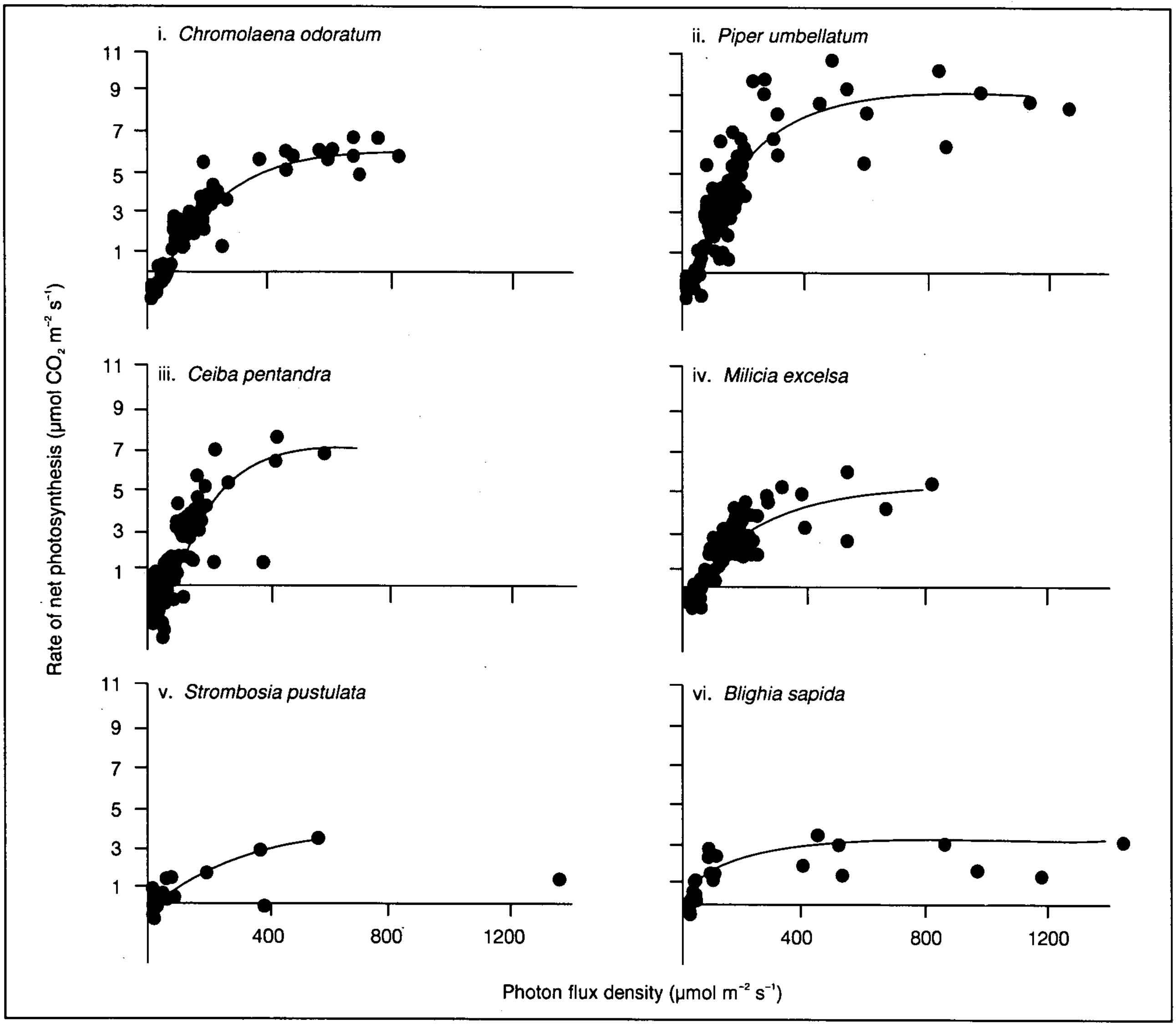

Figure 5. Light response curves of seedlings at plot 2 of the study area in a tropical rainforest in Nigeria (source: Riddoch *et al.* 1991)

estimates of the apparent quantum efficiency *a*, the mesophyll conductance, g_m (synonymous with RUBISCO activity in this analysis), dark respiration, R_d, and the light compensation point as R_d/a. No species displayed particularly high rates of photosynthetic gas exchange, the highest being *Piper* at 11 µmol m^{-2} s^{-1}. *Chromolaena* (*Eupatorium*) *odoratum* displayed rates of only 6 µmol m^{-2} s^{-1}, despite being a fast-growing and very troublesome weed. Pioneer trees (*Ceiba pentandra*) performed in a similar way to *Chromolaena*. When the parameters of the model are compared, it is clear that, despite some variation between the two sites, there are distinct differences between species: late successional trees have low rates of dark respiration and low mesophyll conductances, as well as a low light compensation point (R_d/a).

In most studies of sun and shade acclimation, it has been found that the apparent quantum efficiency (the initial slope of the light response curve) is insensitive to growing conditions (Boardman 1977; Björkman 1981; Kwesiga *et al.* 1986; Ramos & Grace 1990; Riddoch *et al.* 1991). Shade-tolerant species have low light compensation points, not as a result of a high quantum efficiency, but because they have low rates of dark respiration.

Several studies have been designed to investigate the response of leaves to sunflecks. Woodward (1981) pointed out that shade leaves may find it difficult to tolerate the sudden energy loading associated with a sunfleck. First, there may be a rapid rise in leaf temperature and a consequent high transpiration rate and the onset of water deficits. Second, the chlorophyll antennae will receive an increased photon flux of a factor of x50 over normal operating conditions, perhaps causing photoinhibition as suggested from the laboratory experiments mentioned above. Indeed, some species may display subtle leaf movements to reduce the energy loading of sunflecks, as demonstrated in a South American *Piper* by Chiariello, Field and Mooney (1987).

Some species may respond in a positive way to sunflecks, opening stomata to photosynthesise and transpire rapidly, and hence to maximise carbon gain whilst keeping the leaf cool (Chazdon & Pearcy 1986). However, such a positive response was not found in the Nigerian study (Riddoch, Lehto & Grace 1991). Instead, seedlings of late successional species on the forest floor were unresponsive, displaying little or no tendency to open their stomata in response to strong illumination.

RESPONSE TO RED/FAR-RED RATIO

It is now widely appreciated that many of the well-known growth responses to vegetational shadelight are elicited not by shade *per se* but by the reduced red/far-red (R:FR) ratio that vegetational shadelight contains. Shade is detected in the plant by phytochrome, a molecule that changes state according to the magnitude of the ratio. Smith (1981) pointed out that this arrangement is more reliable for detecting shadelight than simply detecting a reduction in photon flux density, as the latter changes with weather conditions and time of year, whereas reduced R:FR unambiguously signals the presence of other vegetation. According to Kwesiga and Grace (1986), tropical seedlings use this detection method to sense the presence of gaps in the canopy. Consider how important it is for a seedling to sense when a gap occurs: a late successional species may have survived for years as a member of the seedling bank, with a very low respiration rate and a near-zero growth rate. When a gap forms, the seedling needs to effect a metabolic change to begin active growth. This hypothesis was supported by the study by Kwesiga and Grace (1986) on the pioneer species *Terminalia ivorensis* and the relatively shade-tolerant species *Khaya senegalensis*. The former responded to a reduced R:FR ratio by accelerating growth, and particularly by leaf area expansion. This response may be interpreted as the correct strategy for a fast-growing species of open sites in the face of competitors. *Khaya*, on the other hand, showed the opposite behaviour, growing in response to a high R:FR ratio, such as might occur at the forest floor when a gap forms. For any seedling on the forest floor, growth in response to a low R:FR ratio would be suicidal, as fast growth with its associated high rate of respiration would simply consume valuable resources with no hope of attaining an emergent position in the canopy.

Recent experiments suggest that the detection system is in the young stem, which is especially responsive to lateral illumination (Ballaré, Scopel & Sánchez 1990). As growth in height can be detected with great precision, it is possible to design a simple screening test for sensitivity to R:FR (Kamaluddin 1991). The phytochrome system may also be used by seeds to detect depth of soil and gaps in the canopy (Vazquez-Yanes *et al.* 1990). Many pioneer species produce large numbers of small seeds which remain dormant in the surface layers of soil, where the R:FR ratio is very low. Species such as *Musanga cecropioides* germinate in large numbers when the canopy is cleared and soil is disturbed; presumably, many species rely on the abrupt change in R:FR ratio as a cue for germination.

SURVIVAL IN SHADELIGHT

Light compensation points of leaves are in the range 10–50 μmol photons m^{-2} s^{-1} (Table 2); the shade under dense canopies may be below 10 μmol photons m^{-2} s^{-1} for much of the day. For the seedling as a whole, light compensation points are low because much of the plant consists of tissues which respire but have a negligible rate of photosynthesis. Most seedlings have chloroplasts in the cells of the stem cortex, and so there may be significant recycling of some respired carbon. Even so, it is surprising that seedlings survive in such conditions. It is presumed that such dense shade strongly discriminates between species, allowing survival of only the most shade-tolerant, and that failure occurs as a result of a negative carbon balance.

However, there are few actual studies of survival in relation to carbon balance. Augspurger (1984) assessed the survival over one year of 18 species of tree seedling at Barro Colorado Island, Panama (Figure 6). The seedlings were grown in plant pots, in open and shaded locations within a glasshouse to simulate sun and shade locations within the forest. No species survived better under shade than under sun, and survival under sun and shade was positively correlated. Generally, those species known to be tolerant of shade survived, with almost no losses under both sun and shade. Light-demanding species grew rapidly in sun, and successively younger leaves matured at larger sizes, but there were always mortalities. In our own study at Ibadan, we have recorded a similar result using a smaller number of species growing in the forest as wildlings. It is perhaps a general and important result that very shade-tolerant species are able to survive best in almost any conditions, whereas 'light-demanders' with high respiration rates and high light compensation points may easily succumb to adverse environmental factors, including attack by insects and fungi as well as abiotic factors.

One intriguing possibility, as yet not examined critically in the field, is that mycorrhizal connections between parent trees and their offspring may provide a significant carbon source for seedlings (Read 1992). If this hypothesis is true, growth of seedlings under shade may to

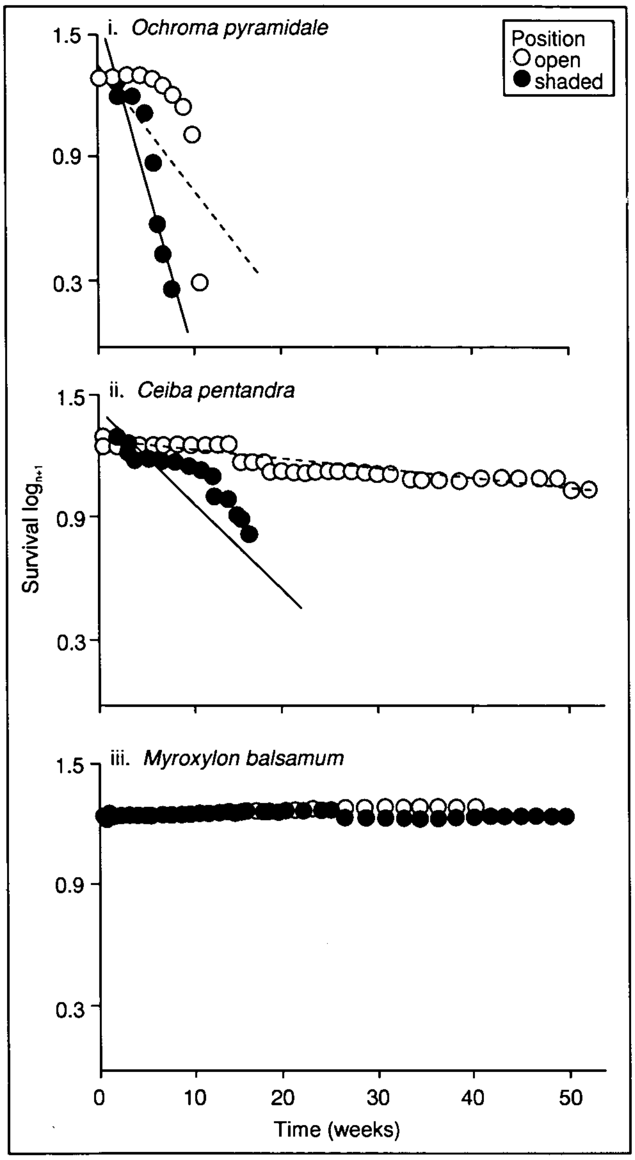

Figure 6. Survival of three contrasting species placed in open and shaded positions. *Ochroma pyramidale* is a very shade-intolerant species which requires large gaps; *Ceiba pentandra* is a pioneer that tolerates semi-shade in small gaps; and *Myroxylon balsamum* is very shade-tolerant. This is a sample of three from the 18 species, redrawn from Augspurger (1984)

some extent be decoupled from the light climate measured at the seedling.

RECOMMENDED SCREENING TRIALS AS AN AID TO DOMESTICATION

At present, there is a worldwide effort to maximise the benefit of forest resources through selection, domestication and breeding, as well as through silvicultural practices aimed at sustainable land use. For tree species which have been exploited in the past, there may be some 'reputation' among foresters and ecologists regarding their behaviour in relation to light, and designations such as 'shade-loving' or 'light-demanding' can be found in the literature (Taylor 1960). However, these designations may not be sufficient, and certainly do not cover all species, not to mention new selections or clones produced in domestication programmes by genetic selection or engineering.

It would clearly be beneficial to screen samples of seedlings for their reaction to shade. Shade-tolerant genotypes, for example, may be required in enrichment planting. Rather few authors have discussed the experimental problems of screening (Lee 1988). The literature is not always helpful, as most authors have examined a small group of species, and each study has had its own characteristic way of simulating shade. This problem is especially acute in the case of the dipterocarp species from the forests of south-east Asia. They are regarded as delicate species, but knowledge of their response to canopy opening in the seedling and sapling phase is scant (Seibert 1990).

In this section we make some recommendations concerning the implementation of a screening project in the nursery.

Measurement of microclimate

Quantum sensors and R:FR sensors are required to measure photon flux density and R:FR ratio. Two sensors of each type would enable comparison of the experimental shade conditions with an open situation. To measure temperature and humidity, a supply of thermometers, thermocouples, psychrometer units or relative humidity sensors are required. To record the data, a sensitive microvoltmeter with data logger should ideally be available.

Manipulation of shadelight

It is not sufficient simply to reduce photon flux by slats or nets, as much of the response exhibited by seedlings is to R:FR ratio. In laboratory conditions, we use combinations of celluloid filters, designed for use with theatre lights. This material is much cheaper than optical glass filters, and seems to be able to withstand continuous exposure to high-intensity lighting. However, it has not been tested under tropical conditions, and it may respond adversely to high ultraviolet radiation and rain. Screening trials might, therefore, be better undertaken in a protected environment, possibly a well-ventilated polythene tunnel or frame.

Experimental units

In the glasshouse, we use plastic tubes to grow small seedlings and to maintain individual control over light climate and microclimate. Normal plant pots are avoided as they provide insufficient rooting volume and thus cause drought. This arrangement is only suitable for very small seedlings. For plants beyond the three-leaf stage, the seedlings outgrow the tubes and must then be grown under large filters supported in frames.

This arrangement is less satisfactory as problems of edge effects arise, and statistical independence is sacrificed. If plants are to be grown beyond the six-leaf stage, it is better to allow them to root in the natural soil. Otherwise, they will outgrow their root containers, and the largest plants will suffer first, thus obscuring treatment effects.

Nutrient supply

In most of our experiments, we have used perlite/vermiculite as a suitable inert mixture to which we add nutrient solutions in a controlled manner. For screening trials, this may not be practical, as the medium may not be locally available, or be too expensive to use on a large scale. Forest soil is very variable, and its properties change rapidly with depth. It does, however, contain spores of mycorrhizal fungi, and this may be preferred (cf Lapeyrie & Högberg, pp158–164; Mason & Wilson, pp165–175). To overcome problems of variability, large supplies of soil should be collected from one place, and mixed well. The supply should not be stored where it will be subject to the leaching effect of rain.

Variables to be measured

Growth may be assessed non-destructively by measuring stem height and counting leaves at successive intervals. Experience suggests that 20 replicates per treatment are required for 95% confidence limits to be ±10% (assuming all replicates survive). Where there is sufficient material to permit destructive sampling, and where there are adequate drying and weighing facilities, growth analysis may be used as it is much more informative (see Hunt 1978). Even very limited destructive harvesting of leaves, to obtain the specific leaf area (area of leaf per mass of leaf), can be very valuable, as this variable is particularly sensitive to changes in the light climate. Photosynthetic response curves require expensive instrumentation and a much higher level of staff training to operate the equipment successfully.

Analysis of data

Large data sets are generated in this kind of work, and it is unwise to rely on manual methods of data processing. Data should be collected in a notebook and transferred to a spreadsheet program on a computer. The data analysis can then be accomplished with an appropriate statistical package. It may be advantageous to collect such data in a standard manner, and to manage data bases through an international network. As well as data on plant growth as a function of the light regime, specimen data on diurnal and seasonal light climates would also be valuable, as they would permit the matching of species to light regime, and enable models of plant growth to be implemented using real data.

CONCLUSIONS

Forest trees display a considerable capacity to adapt to the changes in light climate that are brought about by treefalls and canopy manipulations in silviculture. They do, however, vary substantially in their growth responses to a change in light regime, and in their absolute and relative growth rates. Only part of this variation has anything to do with photosynthesis, although it is photosynthesis that has mostly been studied, usually without much regard to its relationship to assimilate allocation, respiration and the whole plant carbon balance.

Several research priorities emerge from this review.

- There are relatively few studies on the Dipterocarpaceae, despite the economic value of this group and the need to understand their light requirements in relation to current logging practices in Malaysia and Indonesia.
- Seedlings have received much more attention than saplings, and it is important to know the qualitative and quantitative differences in plant response to light as individuals pass through the different stages of their life cycle.
- The relationship between photosynthetic performance, growth and the supply of mineral nutrients is not clear. Seedlings may have a critical dependency on mycorrhizas, and disturbance of the forest floor during logging may affect the nutrient supply.

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Harnessing symbiotic associations: ectomycorrhizas

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ABSTRACT

Ectomycorrhizas are widespread in native tropical forests, and compatible ectomycorrhizal fungi will usually quickly colonise any nursery, as long as no adverse treatments are applied such as soil fumigation or very high applications of fertilizers. It is now possible for the forester to control the nursery microflora and to introduce selected efficient fungi which will then be carried on to the plantation site. The control of mycorrhizal microflora may be viewed as another tool (like breeding or fertilization) to improve tree survival and wood production, and in this way may comprise part of the domestication process.

Most experimental results published so far concern *Pinus, Eucalyptus* and *Pseudotsuga* species. Two years after planting, depending on site, tree species or fungal species used, wood volume production can be increased by a factor of 1.3–1.9. Survival after plantation may be multiplied by a factor of 1.3, and up to 80% of the fertilizer normally applied can be saved. These field results have mainly been published during the 1980s, and none were published before 1976, so that we are still in the research phase of ectomycorrhizal application to forestry. Even when using well-domesticated tree species, we are still experiencing both successes and failures, so the outcome of inoculating relatively undomesticated species is even less predictable, although the potential for improvements in growth and survival is clearly high.

INTRODUCTION

Mycorrhizas are in fashion. Referring to the enthusiasm for mycorrhizas among young foresters in the tropics, J Harley wrote that their 'popularity reflects almost a belief in magic, no less; a belief that some expedient, incompletely understood by most foresters, will right many faults in tree growth and increase production' (Le Tacon & Harley 1990). The aim of this paper is to replace concepts of magic with the facts about the technologies available and the potential of controlled ectomycorrhizal inoculation to promote the domestication of tropical tree species.

DISTRIBUTION OF MYCORRHIZAS

Virtually any tree growing in native forest bears either ectomycorrhizas or endomycorrhizas. Some trees, eg *Eucalyptus* species, some members of the Dipterocarpaceae belonging to the genus *Hopea*, and *Afzelia africana*, simultaneously bear both types of mycorrhiza on the same root system. In *Eucalyptus* roots, both types have even been described on the same root apex, one over the other (Lapeyrie & Chilvers 1985). The interactions between both symbionts on the same tree are still to be understood; they may be complementary or even antagonistic, depending on environmental conditions. Indeed, according to Amorim and Muchovej (1993), endomycorrhizas inhibit the growth of *Eucalyptus* in the nursery.

Vesicular–arbuscular (VA) endomycorrhizas are more common among species of tropical tree than ectomycorrhizas (Janos 1983; Newman & Reddell 1987). However, ectomycorrhizal species sometimes dominate quite extensive forest ecosystems, such as rainforests with Dipterocarpaceae in SE Asia or rainforest and savanna woodland, with Caesalpinioideae in Africa (Alexander 1989; Högberg 1989). It is frequently stated (eg Malloch, Pirozynski & Raven 1980) that such forests are typically monospecific. Closer examinations have revealed that VA endomycorrhizal species may sometimes also form low-diversity stands (Högberg 1989, 1992), and that systems dominated by ectomycorrhizal species may be quite diverse, as for example some African miombo woodlands, which contain both Caesalpinioideae and Dipterocarpaceae, as well as additional genera forming ectomycorrhizas (Högberg & Piearce 1986). In Tanzanian miombo woodland, approximately 40% of species were found to be endomycorrhizal and 20% were ectomycorrhizal, with 50% of the trees bearing endomycorrhizas and 20% bearing ectomycorrhizas. In this instance, 60% of tree volume was associated with ectomycorrhizal fungi, while only 20% was associated with endomycorrhizal fungi (Högberg 1992).

It has been speculated that a lower diversity of forest stands dominated by ectomycorrhizal species could be a result of the lower number of hosts being compatible with the ectomycorrhizal mycelial network (eg Högberg 1992). Many species, not only woody, are capable of sharing the benefits of a VA endomycorrhizal network, and this should promote a higher diversity of VA endomycorrhizal stands. Specificity is crucial; to support the hypothesis, there have been few reports of the extent of specificity among tropical tree species and ectomycorrhizal strains. Smits (1983, 1985) claimed that some dipterocarps only developed ectomycorrhizas with inoculum isolated from the same host species. Inoculation tests on Caesalpinioideae, by Ba and Thoen (1990) using fungi from *Uapaca* spp., have not indicated any compatibility. Based on results from the temperate zone (Duddridge 1986), there has been some controversy about this issue. Cases of strict specificity concerning the whole ectomycorrhizal network could be rather exceptional, and 'specific aggressivity' and/or 'metabolic specificity' may be much more prevalent. Cases of specific aggressiveness have been reported where, among compatible trees and fungi, only some pairings are able to develop quickly the proper infection structure (Lei *et al.* 1989, 1990; Malajczuk, Lapeyrie & Garbaye 1990). Evidence of 'metabolic specificity' has been given by Dell *et al.* (1989), showing that a given fungus could operate different metabolic pathways, depending on the host plant it is infecting.

It is now possible for foresters to manipulate the symbiotic fungal microflora in nurseries, and consequently in plantations. Prime candidates for inoculation tests among indigenous tropical ectomycorrhizal species are members of the Dipterocarpaceae from the rainforests of SE Asia and of the Caesalpinioideae from the rainforest and savanna woodlands of Africa.

REVIEW OF EXPERIMENTAL PLANTATIONS WORLDWIDE

Twenty-seven published accounts of results from forest plantations have been reviewed to judge the potential of ectomycorrhizal inoculations (update of the review by Garbaye 1991). From this review (see Appendix), it is obvious that we are still in an early phase of mycorrhizal research applied to forestry, as these studies have been published only in the past 10–15 years. In addition, 66% of them concerned only three tree genera (*Pinus, Eucalyptus* and *Pseudotsuga*), and only seven of the studies contained comparative plantations established in tropical dry or humid climates. Furthermore, the fungal strains tested belonged to only 18 fungal species, with 60% of the results obtained with only three species (*Pisolithus tinctorius, Laccaria laccata* and *L. bicolor*) and often the same isolate. Therefore, whether using well-domesticated tree species or new undomesticated tropical trees, we still have much to learn from both success and failure.

Of great interest from this survey is the growth stimulation following inoculation of seedlings in the nursery, recorded one to eight years after planting. Depending on the site, the tree species, and the fungus used, wood volume production has been multiplied in many cases by 1.5–2.5. This fact is of particular interest considering that the extra cost due to nursery inoculation is only a few per cent of total plantation cost. The effects are even more dramatic on very poor and/or toxic sites, on which wood volume production was multiplied six- or even 40-fold. Survival after plantation was increased by 30% in most cases and much more (up to 39-fold) on toxic sites.

Interesting conclusions can be drawn from a closer look at two field experiments.

Philippines

In 3-year-old experimental *Eucalyptus deglupta* plantations on industrial plantation sites, the extra wood production attributable to inoculation was 154% (De la Cruz & Lorilla 1990). Comparison of wood production from non-inoculated and inoculated plots, with increasing application rates of a complete fertilizer, showed that, to reach maximum production, mycorrhizal inoculation could replace about 86% of the fertilizers required by uninoculated trees. If fertilizers are readily available at a reasonable cost, then the same experiment shows that, even at high fertility, the trees on the inoculated plots made better use of the fertilizers.

Congo

Pisolithus tinctorius stimulated the growth of *Eucalyptus urophylla* x *E. kirtoniana* (Garbaye, Delwaulle & Diangana 1988). The most important growth stimulation was recorded at 27 months, with 61% extra wood production per hectare. After 50 months, the increase in wood production had dropped to only 29%, apparently because the introduced strain had disappeared from the root system. This result may indicate that the inoculated strain had poor 'specific aggressiveness' (Malajczuk *et al.* 1990) on *Eucalyptus* roots, making it a poor competitor against indigenous unselected strains. Therefore, a selected strain must be efficient, and aggressive, to be competitive.

STRATEGIES FOR STRAIN SELECTION

Very different techniques are available for fungal inoculum production. Some can be produced only by industry and applied in large commercial nurseries, others require the equipment of a basic microbiology laboratory, while some can be applied directly at the nursery level for no real cost. The strategy for strain selection and multiplication depends on the situation and rationale for inoculating the species.

On mining sites, for example, there may be no inoculum available locally, and any fungus can be introduced, with a great chance of success in terms of growth stimulation, so long as it is adapted to the new ecosystem and able to infect the tree being planted. In some situations, there may be no indigenous inoculum compatible with the exotic tree being introduced, as was the case with *Pinus* introductions into Australia and Africa. In this situation, any inoculum collected in the area of origin of the exotic tree should be a satisfactory solution: it could be soil, spores or pure culture.

On very poor toxic soils, dry land or calcareous areas, a fungal strain adapted to this environment and able to correct the physiological disorder suffered by the tree should be selected. This situation is more complex, as the physiological processes involved are in general still poorly understood (eg Lapeyrie 1990). Basic research, as well as time-consuming strain screening, is required to achieve success.

Looking for a fungal strain which is more efficient than locally abundant strains that are well adapted to their environment and to their host plant is a difficult task. Further, there is often a lack of correlation or even a negative correlation between the efficiencies of strains in the nursery and in the field (eg Grove *et al.* 1991). Newly introduced fungal strains should be efficient and competitive. They can be wild isolates or even genetically improved strains, such as the efficient strain of *Laccaria laccata* recently obtained through a breeding programme (W Yan *et al.*, unpublished data).

The case of dipterocarps is interesting, as plantations are being established (see Smits, de Fraiture & Yasman, pp267–272), and it has been suggested that the poor growth and survival of these species in logged forest are due to the absence or death of the mycorrhizal fungi, resulting from logging operations and soil temperature elevation (Lee 1990). Investigation of the mycorrhizal status of wildlings and seedlings in nurseries and after plantation establishment makes it difficult to accept this hypothesis, as all of them are infected by numerous ectomycorrhizal fungi (Lee 1990). Mycorrhizas adapted to the nursery environment are abundant, but their ability to adapt to conditions in the field after planting could affect their ability to survive, to colonise the soil, and to extract nutrients from mineral and organic matter (Nguyen *et al.* 1992; Dighton 1991). Furthermore, their metabolic interaction with the host plant is not known and could be critical.

Few research programmes aimed at understanding the mycorrhizal status of seedlings or cuttings in the nursery have been initiated. The inoculum usually used is either soil from native forest, pieces of carpophores (eg Hadi & Santoso 1988), or pure cultures (eg Lapeyrie, Lee & Sanip 1993). As stated previously, only pure-culture mycelia will allow the selection and use of permanently efficient strains. Recent research testing the specificity of the mycorrhizal associations in dipterocarps has found that young seedlings of *Hopea odorata* and *H. helferi* become well infected after inoculation with a South American strain of *Pisolithus tinctorius* collected under *Eucalyptus* (Y Sanip, S S Lee & F Lapeyrie, unpublished). In this instance, height growth was enhanced by a factor of 1.5 after four months. In addition, *Hopea odorata* cuttings were extensively infected (80% of root apices) by a strain of *Hebeloma crustuliniforme* collected in France under *Picea* (Lapeyrie *et al.* 1993). These promising preliminary results suggest that, in terms of inoculum specificity, dipterocarps probably behave like temperate tree species. However, germplasm banks of mycorrhizal fungi in pure culture, isolated from native dipterocarp forest, are now urgently needed.

CONCLUSION

Inoculation of seedlings with selected fungi can promote symbiotic ectomycorrhizal associations, and improve the establishment and growth of tree seedlings. In this way, ectomycorrhizal inoculation may contribute to the domestication process, so long as it is integrated in a sound programme of nursery and reforestation technologies.

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Appendix. Main results of controlled ectomycorrhizal inoculation applied to forestry (update of the review by Garbaye 1991)

Reference	Tree species	Country	Climate	Soil	Growth parameter	Fungal species introduced	Growth increase compared with non-inoculated plant
Krugner & Pinto (1986)	*Pinus caribaea*	Brazil	Dry tropical	Poor acidic - non-fertilized - fertilized NPK	Height after two years	*Pisolithus tinctorius*	x 1.6 x 2.4
Momoh & Gbadegesin (1981)	*Pinus caribaea*	Nigeria	Semi-humid tropical	? (six different plantation sites)	Height after 30 months	*Pisolithus tinctorius*	x 1.2–1.8 (depending on site)
Ofusu-Asiedu (1980)	*Pinus caribaea*	Ghana	Semi-humid tropical	? (two different plantation sites)	Height after 18 months	*Pisolithus tinctorius* *Rhizopogon luteolus* *Thelephora terrestris*	x 0.6–1 x 1 x 0.8–1.2 (depending on site)
Delwaulle, Garbaye & Okombi (1982)	*Pinus caribaea*	Congo	Humid tropical	Poor sandy	Height after 20 months	*Pisolithus tinctorius*	x 1.2–1.5 (depending on strain)
Delwaulle, Diangana & Garbaye (1987)	*Pinus caribaea*	Congo	Humid tropical	Poor sandy	Height after 12 months	*Pisolithus tinctorius* (spores)	x 1.2
Marx, Hedin & Toe (1985)	*Pinus caribaea*	Liberia	Humid tropical	Cleared native forest	Volume ha^{-1} after three years	*Pisolithus tinctorius* *Thelephora terrestris* unknown (from humus)	x 1.5 x 1 x 1.7
Krugner (1976)	*Pinus taeda*	USA (N Carolina)	Hot temperate	Sandy acidic	Height after one year	*Pisolithus tinctorius*	x 1.6
Berry & Marx (1978)	*Pinus taeda* *Pinus virginiana*	USA (Tennessee)	Hot temperate	Very poor acidic forest soil (2 sites)	Stem volume after two years	*Pisolithus tinctorius*	x 1.5–1.9 x 1.3–1.9 (depending on site)
Marx, Bryan & Cordell (1977)	*Pinus taeda* *Pinus elliottii* *Pinus virginiana*	USA (Florida & North Carolina)	Hot temperate to subtropical	Forest soil of average fertility (two sites)	Stem volume after two years	*Pisolithus tinctorius*	x 1.2–1.5 x 1.2–1.5 x 1.2–1.5 (depending on site)
Ruehle *et al.* (1981)	*Pinus echinata*	USA (Arkansas & Oklahoma)	Hot temperate	Forest soil (two sites)	Stem volume after two years	*Pisolithus tinctorius*	x 1.9–2.4 (depending on site)
Marx, Cordell & Clark (1988)	*Pinus taeda*	USA (Georgia)	Hot temperate	Fertile forest soil	Volume ha^{-1} after eight years	*Pisolithus tinctorius*	x 1.5
Marx & Artman (1979)	*Pinus taeda* *Pinus echinata*	USA (Kentucky)	Hot temperate	Coal mining spoil (very acidic and toxic)	Stem volume after two years	*Pisolithus tinctorius*	x 6.5 x 5.1
Marx (1977)	*Pinus virginiana*	USA (Kentucky)	Hot temperate	Coal mining spoil (very acidic and toxic)	Stem volume % survival (after two years)	*Pisolithus tinctorius*	x 4.3 x 3.9
Marx (1977)	*Pinus taeda*	USA (Georgia)	Hot temperate	Kaolin quarry spoil	% survival after one year	*Pisolithus tinctorius* *Cenococcum graniforme*	x 1.3 x 1.2
Theodorou & Bowen (1970)	*Pinus radiata*	Western Australia	Mediterranean	Acidic soil	Height after one year	*Rhizopogon luteolus*	x 1.5
Stenström, Ek & Unestam (1986)	*Pinus sylvestris*	Sweden	Cold temperate	Forest soil	Stem volume after two years	*Lactarius rufus* *Tricholoma albobrunneum* *Amanita muscaria*	x 1.4 x 1.3 x 1.2
Le Tacon *et al.* (1988)	*Pseudotsuga menziesii*	France	Temperate	Poor acidic (heathland)	Height after five years	*Hebeloma cylindrosporum*	x 0.8
Le Tacon *et al.* (1988)	*Pseudotsuga menziesii*	France	Temperate	Acidic (grassland)	Height after four years	*Laccaria laccata*	x 1.2
Le Tacon *et al.* (1988)	*Pseudotsuga menziesii*	France	Temperate	Acidic (bracken)	Height after three years	*Laccaria laccata* *Laccaria bicolor*	x 1.3 x 1.1
Le Tacon *et al.* (1988)	*Pseudotsuga menziesii*	France	Temperate	Acidic forest soil	Height after one year	*Laccaria laccata* *Laccaria bicolor*	x 1.4 x 1.4
Villeneuve, Le Tacon & Bouchard (1991)	*Pseudotsuga menziesii*	France	Temperate	Acidic sandy forest soil	Height after two years Stem mass after two years	*Laccaria laccata*	x 1.5 x 4.0
Garbaye, Delwaulle & Diangana (1988)	*Eucalyptus urophylla* x *kirtoniana*	Congo	Wet tropical	Poor sandy soil	Volume ha^{-1} after four years	*Pisolithus tinctorius* *Scleroderma aurantium*	x 1.6 x 1.5

Appendix. continued

Reference	Tree species	Country	Climate	Soil	Growth parameter	Fungal species introduced	Growth increase compared with non-inoculated plant
Dixon *et al.* (1981)	*Quercus velutina*	USA (Missouri)	Hot temperate	Acidic forest soil	Dry matter mass after one year	*Pisolithus tinctorius*	x 1.1
Garbaye (1990)	*Quercus robur*	France	Temperate	Acidic forest loam (three sites)	Height increase during first and second year	*Paxillus involutus* *Hebeloma crustuliniforme* *Laccaria laccata*	x 1.2–1.4 (depending on site) x 1.1 x 1
De la Cruz & Lorilla (1990)	*Pinus caribaea*	Philippines	Wet tropical	- degraded & infertile grassland - relatively good site	Stem volume: - after three years - after two years	*Pisolithus tinctorius* (spores)	x 1.4 x 3.2
De la Cruz & Lorilla (1990)	*Eucalyptus deglupta*	Philippines	Wet tropical	Relatively good site	Stem volume after three years	*Pisolithus tinctorius* (spores)	x 2.5
Grove *et al.* (1991)	*Eucalyptus diversicolor* *Eucalyptus globulus*	Western Australia	Mediterranean	Two fertilized sites (cleared forest): - red loam - gravelly red podzolic soil	Above-ground biomass (dry mass) after one year	*Laccaria* sp. *Setchelliogaster* sp. *Amanita* sp. *Protubera* sp. *Hydnangium* sp. *Scleroderma* sp. *Hymenogaster* sp. *Hysterangium* sp. *Descolea* sp.	x 1.0–1.8 (depending on *Eucalyptus* species, fungal strain and site)

Harnessing symbiotic associations: vesicular–arbuscular mycorrhizas

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ABSTRACT

Although the majority of tropical trees form mycorrhizas with vesicular–arbuscular mycorrhizal (VAM) fungi, most mycorrhizal research on tropical trees has been on ectomycorrhizal fungi associated with a few tree species which have been widely planted as exotics in plantations. Despite this, the presence of appropriate and adequate VAM populations is likely to have a significant impact on tree performance, as many tree species are highly dependent upon their mycorrhizal associations for nutrient uptake, particularly in infertile soils.

Although naturally occurring inoculum is widespread in soils, site disturbance (as occurs when land is cleared for planting) can reduce the number of infective propagules, and change the proportions of different fungal species. Hence, the potential for mycorrhizal formation may be lowered at the critical time of tree establishment. The extent to which mycorrhizal populations are depleted and changed is related to the method of site clearance used. Short-term studies indicate that mycorrhizal inoculation improves tree growth in nurseries. Only a few studies have followed the progress of inoculated trees after outplanting. In these studies, improvements in both tree survival and growth rate have been found, but more extensive studies are needed.

A number of options exist for the management of mycorrhizal associations: minimising the change in indigenous populations by use of appropriate site preparation techniques; manipulating damaged populations to increase their inoculum potential; and inoculating trees in nurseries either with single isolates or mixtures. Where the performance of particular tree/symbiont combinations is being assessed, the criteria for selection need to be carefully defined.

INTRODUCTION

Mycorrhizal fungi are an integral part of practically all plant communities, natural or managed, and form the link by which mineral nutrients are transferred from the soil to the plant, while carbon compounds are transported in the opposite direction. Thus, they have a fundamental role in determining plant productivity and in the functioning of ecosystems. Despite their importance, they tend to be ignored by foresters and agriculturalists, although an understanding of their role is essential to the development of sustainable land use systems (Bethlenfalvay & Linderman 1992).

Vesicular–arbuscular mycorrhizal (VAM) fungi possess a worldwide distribution. Published records indicate that 71% of tropical plant species are VAM (Sieverding 1991), and about 95% of the tree species in natural tropical forest ecosystems are mycorrhizal exclusively with VAM fungi (Le Tacon, Garbaye & Carr 1987). Although VAM trees predominate in the tropics, they have until recently received comparatively little attention from mycorrhizal researchers, who have focused instead on a few ectomycorrhizal trees, such as members of the Pinaceae, *Casuarina* and various *Eucalyptus* species which are widely used in plantations (Le Tacon *et al.* 1987; see also Lapeyrie & Högberg, pp158–164). The VA mycorrhizas of the great majority of tropical forest trees, which include many valuable species, are virtually unstudied. The failures of ectomycorrhizal trees as a result of mycorrhizal deficiencies when planted as exotics are well documented (eg Mikola 1970). By comparison, failures or poor performance of VAM trees after planting have rarely been attributed to mycorrhizal problems. The more widespread distribution of VAM fungi might suggest that mycorrhizal deficiencies would be unlikely to occur; however, as this paper will indicate, there are many circumstances in which VAM propagules may be restricted in number or form ineffective associations, resulting in trees performing suboptimally.

Consideration of VAM fungal populations is important not only because of their role in ecosystem function, but also because they have direct and immediate effects upon tree performance. Evidence from short-term studies suggests that many tropical trees are highly dependent upon their VAM associations for survival and growth. Although VAM fungi are widely distributed, site disturbance, such as occurs during land clearance, can adversely affect mycorrhizal populations, reducing the amount of inoculum available to infect root systems during the period when trees are becoming established. Hence, the conservation of indigenous VAM populations, or the inoculation of trees with VAM fungi, may be needed to ensure that adequate inoculum is present to support tree growth.

Unfortunately, while understanding of the ecological role of these fungi has increased in recent years, it has not been matched by developments in their practical application or management. A number of short-term studies have demonstrated that inoculation can improve the growth of trees in nurseries, but (with the exception of the *Citrus* industry) VAM inoculation of trees has not become part of nursery practice. A serious limitation to progress is the lack of evaluations of the performance of inoculated plants over periods longer than a few months, which hampers any appraisal of long-term effects in the field.

IMPORTANCE OF VAM FUNGI FOR PLANT GROWTH IN THE TROPICS

Function and distribution of VA mycorrhizas

The functions of VAM associations have been reviewed extensively elsewhere (eg Harley & Smith 1983; Powell & Bagyaraj 1984; Barea 1991), and will only be summarised briefly here. However, it should be pointed out that the majority of experiments have been conducted in pots, with isolated plants. Observations of the activities of mycorrhizas under field conditions are far more limited, and much work remains to be done to understand their functioning in ecosystems (Fitter 1985).

The mycorrhizal fungus takes up mineral nutrients from the soil, via the extramatrical fungal mycelium which can reach for a considerable distance away from roots. The presence of a widely ramifying extramatrical mycelium is particularly important for the uptake of minerals (P and others) that have a slow rate of diffusion (Cooper 1984). It has been demonstrated that this mycelium can extend phosphate depletion zones up to at least 7 cm from roots, compared with the 1–2 mm depletion zones associated with non-mycorrhizal roots, and therefore it can absorb nutrients from a much greater soil volume than a non-mycorrhizal root (Rhodes & Gerdemann 1975). The ability of mycorrhizal fungi to access P is likely to be particularly important to plants in dry conditions, as the diffusion coefficient for phosphate in soil decreases linearly with increasing soil dryness (Fitter 1985). In addition to the enhancement of nutrient uptake through exploitation of increased soil volume, there is some evidence that VAM hyphae have the capacity to alter the weathering rates of soil P and increase the pool of available P (Bolan 1991). Mycorrhizal infection has also been found to improve plant water relations, as a result of either indirect effects upon plant nutrient status or more direct effects on water uptake (Cooper 1984); improved resistance to pathogens has also been noted (Sharma, Johri & Gianinazzi 1992).

The distribution of VAM and ectomycorrhizal fungi in the tropics is reviewed briefly by Lapeyrie and Högberg (pp158–164). In broader terms, when the major plant communities of the world are surveyed, it becomes apparent that each has its distinctive population of mycorrhizal types: VA, ecto-, ericoid or arbutoid mycorrhizas (Read 1991a). The changes in dominance of different mycorrhizal types in contrasting ecosystems have been attributed to variations in their ability to access or mobilise the plant nutrients that are limiting growth in that particular ecosystem (Read 1991b). Evidence suggests that domination by VAM plant species increases with decreasing soil organic matter and increasing base status of soil, where phosphorus replaces nitrogen as the major limiting nutrient (Read 1991b), although there are exceptions to this rule (Allen 1991). Lowland tropical soils are characteristically lacking in organic matter. In the oxisols and ultisols which account for two-thirds of the world's tropical soils by area, organic matter decomposition is fairly rapid, and there is often little accumulation of litter. These soils are acid clays which possess high potential aluminium toxicity, low cation exchange capacity and, as a consequence, low availability of many minerals (Janos 1987). In this situation, phosphorus is present in soil solution at very low concentrations mainly because of its incorporation into less soluble forms (Alexander 1989). In such circumstances, the formation of effective mycorrhizal associations confers a strong competitive advantage, and mycorrhizal associations with VAM fungi, which (with their extensive extramatrical mycelium) are effective scavengers for phosphate, predominate (Read 1991a, b).

Under these conditions, the uptake of phosphorus by plants, especially tropical trees possessing the coarse root morphology characteristic of obligate mycorrhizal plants (see below), will be limited by the slow diffusion of phosphate ions in the soil and by the development of depletion zones around roots. The presence of effective VAM associations will reduce the constraints of soil nutrition. As it has been estimated (Sieverding 1991) that plant production is limited by low mineral nutrient availability on 30% and by drought on 33% of tropical soils, the development of effective mycorrhizal associations is likely to be beneficial to tree growth over a wide range of tropical sites.

Mycorrhizal dependency

Most plants in natural ecosystems have mycorrhizas (Brundrett 1991). However, the benefit which individuals are likely to receive from the presence of VA mycorrhizas varies according to the plant species under consideration, because plant species differ in the extent to which they depend on VAM fungi for survival and growth at a given soil fertility (Janos 1980a, 1987). They have been characterised as either non-mycorrhizal, obligately mycotrophic or facultatively mycotrophic: obligately mycotrophic plant species cannot grow without mycorrhizas even in the most fertile soil where they normally grow, whereas facultative mycotrophs can survive and grow without mycorrhizas, but perform better when they are mycorrhizal, particularly in less fertile soils (Janos 1987). For tropical plants, dependence upon VA mycorrhizas is related to their root morphological characteristics and phosphate requirements. Superficial, small root systems that have low orders and frequencies of branching, and coarse ultimate rootlets with few or no root hairs, are characteristic of trees having a high mycorrhizal dependency (Baylis 1975; St John 1980; Janos 1987; Manjunath & Habte 1991). Recent studies by Manjunath and Habte (1992) indicate that mycorrhizal dependency is also related to phosphate usage: when non-mycorrhizal plants of species possessing a range of degrees of mycorrhizal dependency were grown in soils containing different concentrations of P, the mycorrhizal-dependent species required higher concentrations of P in the soil solution for maximum dry matter production, while the concentrations of P in their shoots at maximum dry matter production were lower than for non-dependent species.

Occurrence of mycorrhizal-dependent species

In determining the importance of conserving and managing VA mycorrhizal populations in association with tropical trees, an appreciation of the frequency of occurrence of non-, facultatively or obligately mycotrophic tree species is needed.

Certain families of plants, including tropical trees, appear to be characteristically non-mycorrhizal, or to have some non-mycorrhizal genera (Brundrett 1991). They include members of the Lecythidaceae, Sapotaceae and Proteaceae. While extensive studies of mycorrhizal dependency have not been conducted, and more work needs to be done, the results of a study by Janos (1980b) and other studies reported in this review indicate that a high proportion of other trees are likely to be dependent upon their mycorrhizas. In a study of Central American lowland tropical moist forest plant species (Janos 1980b), VAM inoculation improved growth and/or survival of 24 out of the 28 species tested, when they were grown in a sterilised soil in containers. Sixteen of these species ceased growth in the absence of mycorrhizas and were found to be completely dependent on VAM for sustained growth.

The mycorrhizal dependency of plant species appears to be related to their position in the successional development of plant communities (eg Allen 1991; Brundrett 1991). On the basis of his data from the tropical moist forest, Janos (1980a, b) has suggested that early successional species are likely to be facultatively mycotrophic or non-mycorrhizal, with a well-branched root system and small easily dispersed seeds. Seral species tend to be facultative mycotrophs, while mature forest canopy and subcanopy species are obligate mycotrophs, and large-seeded to provide nutrient reserves until the root system has developed mycorrhizal infection to enhance nutrient uptake. Consequently, plants that are less dependent on their VA mycorrhizas or are non-mycorrhizal are likely to become progressively more dominant in disturbed ecosystems where mycorrhizal inoculum is limited (Janos 1987; Miller 1987), although it will depend upon nutrient availability (Allen & Allen 1990). This evidence suggests that there is a direct mycorrhizal role in the determination of the structure and composition of plant communities. These patterns of change in mycorrhizal dependency with ecological succession have important practical implications for the growth of VAM trees in plantations and for the regeneration of degraded land.

Recently, the level of VAM dependency of some fast-growing leguminous trees for sustainable land use systems in the subhumid and semi-arid tropics has been examined (Habte & Turk 1991). Among the plant species that have been suggested as important for reforestation and agroforestry systems are *Leucaena leucocephala*, *Cassia spectabilis* and *Gliricidia sepium* (see Brewbaker & Sorensson, pp195–204; Simons, MacQueen & Stewart, pp91–102). Short-term studies with potted seedlings have shown that *L. leucocephala* is very highly dependent upon VAM fungi (Habte & Manjunath 1987), while *C. spectabilis* and *G. sepium* also exhibit VAM dependency, although to a lesser extent (Habte & Turk 1991).

Throughout the tropics, a clear assessment of the mycorrhizal dependency of tree species would enable much more precise recommendations to be made about the conditions under which different tree species are likely to succeed, and indicate a particular need for inoculation or care in conservation of indigenous mycorrhizal populations when planning for plantations of mycorrhizal-dependent tree species. This information would aid the successful development of domestication strategies and promote predictable harnessing of VAM symbioses in practical forestry across the tropics.

EFFECTS OF DISTURBANCE ON VAM FUNGI

Access to adequate VAM inoculum is, as already indicated, a prerequisite for the growth of many tropical trees because of their dependence upon mycorrhizas. Sources of potential infection are resting spores, fungal hyphae in the soil, and colonised root fragments. These sources of inoculum can be adversely affected by many factors, including fires, soil erosion, loss of vegetation, cultivation, long fallow periods, soil compaction, changes in soil temperature, moisture and chemistry, colonisation by non-mycorrhizal plants, and biocide application (Abbott & Robson 1991; Sieverding 1991). Hence, many of the processes involved in deforestation of tropical forest areas have serious implications for mycorrhizal inoculum and, consequently, the performance of trees other than species which are unresponsive to inoculation. However, there is little quantitative information to indicate the degree of inoculum availability which is required for the growth of obligately or facultatively mycorrhizal tree species. Based on his extensive studies of *Manihot esculenta* (cassava), which is obligately mycorrhizal, Sieverding (1991) has suggested that field responses to inoculation of this crop may be obtained when there are less than 900 indigenous infective propagules per 100 g of dry soil. If tree crops respond in a similar manner, very extensive areas of the tropics are likely to be deficient in mycorrhizal inoculum for acceptable levels of productivity in managed systems.

The different forms of VAM propagules vary in their longevity. While spores can survive for up to several years in the soil, fungal mycelium only retains its ability to infect after separation from the host plant for two to four weeks in field conditions. Colonised root fragments can retain their viability for several months under dry conditions, but rapidly lose viability under moist conditions (Hetrick 1984; Sieverding 1991). Consequently, the abundance of different types of propagule in the soil before disturbance may determine the impact of disturbance on mycorrhizal infection. If vegetation cover is lost, spores will become increasingly important as mycelium rapidly loses its infectivity, resulting in a shift in mycorrhizal populations after disturbance, in favour of those fungi which sporulated prior to the disturbance.

Effects of disturbance will vary with ecosystem. When Jasper, Abbott and Robson (1991) examined the impact of disturbance on soils removed from an annual pasture, forest and heathland growing in a mediterranean climate in south-west Australia, they noted that the extent of mycorrhizal infection on the roots of *Trifolium subterraneum* (subterranean clover) plants growing in the pasture soil was little affected by disturbance. In contrast, the extent of infection in both disturbed jarrah forest and heathland soils was reduced by almost half. Parallel soil dilution experiments indicated that VAM propagule numbers were much lower in the undisturbed forest and heathland soils than in the pasture. Jasper *et al.* (1991) inferred that, where propagule numbers were naturally low, as in the forest and heathland soils, disturbance would inevitably lead to a further reduction in the number of infective propagules and, as a consequence, a reduction in the soils' potential infectivity. However, in soils which harboured a large number of propagules, like the native grassland soils, disturbance even of a highly damaging nature might not reduce the overall number of VAM propagules below a level which would limit mycorrhizal development (see also Jasper, Abbott & Robson 1992).

The studies described above indicate that those ecosystems that support a high number of VAM propagules will be more resilient, and more likely to maintain infectivity and hence plant productivity after disturbance. However, it should be noted that, in these studies, the test plants were pre-germinated and were planted into the soils soon after disturbance, and grown in favourable conditions. The impact of disturbance on mycorrhizal infection in the field is likely to be greater, as plants will colonise disturbed ground more slowly and environmental conditions may be more severe. Both these factors will lead to a decline in inoculum infectivity and are likely to have an adverse effect on mycorrhizal infection of colonising plants. Continued monitoring of the recovery of the jarrah forest site indicated that mycorrhizal infectivity gradually recovered, but patches of high and low infectivity remained for several years. A uniform distribution of infectivity, equivalent to that of the undisturbed forest, was not achieved for seven years after vegetation was re-established (Jasper *et al.* 1992).

In ecosystems lacking robust VAM propagules (spores), disturbance can rapidly destroy mycorrhizal infectivity. Jasper *et al.* (1989) observed changes in VAM infectivity in jarrah forest soil on land disturbed by bauxite mining. Spores were not found in this soil before the disturbance. The proportion of root length on bait plants of *Trifolium* which became infected by mycorrhizal fungi declined from 21% before clearance to 5% one month afterwards (although soil disturbance was slight during this operation), and no mycorrhizal infection was found six weeks after the soil was stripped and respread on another site. It is likely that the cause of this extreme loss of infectivity was related to the absence of mycorrhizal spores in the original soil; consequently, infection was dependent upon mycelial and root fragments which were damaged during the processes of soil transfer.

Even slight surface erosion can have severe effects upon all types of mycorrhizal propagules, as they tend to be concentrated close to the soil surface (Abbott & Robson 1991). Erosion leads to a loss not only of surface soil particles and nutrients, but also much of the mycorrhizal population, thereby reducing the number of fungal propagules available for colonising plants.

Maintaining vegetation cover is important for mycorrhizal populations. Recent assessments of VA mycorrhizal propagule densities in semi-arid bushland of Somalia (Michelsen & Rosendahl 1989) have shown that, where there was good cover (of *Terminalia brevipes* forest), the concentration of propagules was 200 per 100 ml soil. In neighbouring bushland degraded by heavy grazing, logging and clearing for shifting agriculture, and where only 8% of the surface remained covered by vegetation, infective VAM propagule numbers were only 30 per 100 ml soil. The extent to which such damage can deplete semi-arid ecosystems of their active VAM inoculum, and the impact of such a reduction, was clearly displayed following disturbance of a western Colorado *Teucrium* (sage) community (Moorman & Reeves 1979). The root systems of test maize seedlings were 77% infected when grown in undisturbed soil but only 2% infected when harvested from adjacent disturbed soil.

In lowland tropical rainforests, spore numbers can be considerably lower than those found in tropical agronomic and grassland ecosystems (Redhead 1977; Louis & Lim 1987; Sieverding 1989; Musoko 1991), although there may be a greater diversity of species (Sieverding 1989). In normal circumstances, the high degree of vegetation cover found in such forests should ensure all-year-round access to external mycelium and mycorrhizal roots, and therefore little dependence upon the presence of spores. However, this heavy reliance on easily damaged infected roots and extramatrical hyphae means that the stable equilibrium between plant and soil microbes in undisturbed tropical moist forest can become greatly disrupted when the forest is opened for cultivating agricultural crops or forest trees.

In semi-deciduous moist forest at Mbalmayo, Cameroon, the extent of damage resulting from different methods of forest clearance was examined by following short-term changes in the VAM spore populations in plots subjected to manual canopy opening, partial or complete clearance by bulldozer, and an undisturbed control treatment. When the spore populations were initially examined, the study site was found to possess a homogeneous spore distribution. However, when spore numbers were subsequently re-assessed in samples taken six months later (three months after the different methods of site preparation had been applied), the picture changed considerably. Although seasonal effects appear to have led to a fall in spore numbers in all four treatments, the reduction in numbers was greatest in the completely cleared plot, which had received the most disturbance. It retained only 34% of its original spore numbers, while the undisturbed forest retained 73% (Musoko 1991; Mason, Musoko & Last 1992). Additional assessments of spore numbers, 18 months after the initial assessments, indicated that the decrease in spore numbers had been a short-term effect of logging, and that there had been a subsequent increase in numbers on the disturbed sites, so that they were higher than they had been originally. Results from a study of *Terminalia* plantations in Côte d'Ivoire (Wilson *et al.* 1992), which examined both undisturbed forest and forest which had been manually or mechanically cleared and replanted up to 23 years previously, indicated that forest clearance and replanting can result in long-term increases in spore numbers, lasting at least 16 years.

Decreases in spore numbers after logging have been reported from studies in Malaysian forest (Alexander, Ahmad & Su-See 1992), where there was a 75% reduction as a result of severe logging. Not only were spore numbers reduced, but most probable number (MPN) tests, and observations of root infection of plants along transects at the test sites both indicated that the overall inoculum potential of the sites was reduced where sites had been heavily logged, and adverse effects persisted for at least two years. Root systems of plants persisting on or colonising heavily logged forest were only 20–35% mycorrhizal, while those in the undisturbed forest were 70% mycorrhizal. Although there were large differences in species composition of the colonising plant species on the plots, which could affect the degree of mycorrhizal formation, comparisons of the extent of mycorrhizal infection on the few species which did occur in common between sites confirmed that mycorrhizal infection was lower on the plots which had been logged. Care must be taken with the interpretation of MPN tests because they themselves cause a lot of disturbance to inoculum; however, the root infection observations lend support to the view that logging reduced inoculum potential. It is likely that similar effects of logging on inoculum potential also occurred at Mbalmayo. Quantitative assessments (using field bioassays) of the impacts of logging on all sources of inoculum are needed to evaluate fully the effects in Cameroon, and complement the accumulated data on spore numbers. However, examination of the root systems of outplanted *Terminalia ivorensis* seedlings 18 months after plantation establishment did demonstrate that there were lower rates of mycorrhizal infection on the completely cleared plot, compared with the partially cleared plot (Musoko 1991). Survival of outplanted seedlings was also lowest on the completely cleared plot (Mason *et al.* 1989).

An additional facet of the studies in Mbalmayo, Cameroon (Musoko 1991; Mason *et al.* 1992), is that, when spores proliferated after logging, the balance of species was changed. On the completely cleared plot, numbers of *Glomus occultum*/*Acaulospora scrobiculata* increased six-fold after disturbance. By contrast, the least damaging method of site preparation (manual canopy opening) maintained a species distribution similar to that in the undisturbed control plot, where *Glomus etunicatum* was the dominant spore type. Because spores are likely to be important sources of infection in disturbed soil after root systems and fungal mycelium are disrupted, such changes in species composition may have an impact upon the subsequent development of vegetation. Soil samples removed from the root zones of a range of plant species from Mbalmayo Forest indicated that the change in species distribution of spores within the severely disturbed plots was related to the rapid invasion of the herbaceous weed *Chromolaena odoratum* (Siam weed), with which spores of *G. occultum* and *A. scrobiculata* were strongly associated (Musoko 1991). In Côte d'Ivoire (Lawson *et al.* 1991; Wilson *et al.* 1992), spore species diversity was increased by site disturbance, for at least 16 years, and long-term changes in species dominance occurred, which were most marked on the mechanically cleared plots.

The combination of information from infectivity bioassays in Malaysia (Alexander *et al.* 1992) and the above observations on changes in spore species composition and number indicates that forest clearance has major effects upon mycorrhizal populations which are likely to be significant for the sustainability of forest plantations. Further studies are needed to assess the impact of logging on all sources of inoculum in different tropical forest ecosystems. Although most bioassays are effected under controlled conditions in pots, more precise information on how logging affects the onset and spread of infection will be obtained from testing bait plants of target tree species in the field, thereby avoiding the further disturbance to inoculum caused by sample collection. These studies now need to be developed in order to assess the importance of the extent and nature of the VAM inoculum remaining after logging for the survival and growth of tropical tree seedlings, both in natural regeneration and plantations. In order to evaluate the consequences of changes in the species composition of mycorrhizal fungi, it is necessary to compare the effectiveness of different fungal species in promoting tree growth.

The importance of maintaining a highly effective population was demonstrated in Colombia, where *Manihot esculenta* is produced in either monoculture or rotational systems (Sieverding 1991). At one particular site, monoculture led to the build-up of a VAM spore population of which more than 50% were members of species considered to be inefficient, whereas, when *M. esculenta* was rotated with other crops, a smaller proportion of spores belonged to this group. Under monoculture, root yields were less than half those under rotation. Because chemical soil fertility was not a limiting factor, it was concluded that the composition of the indigenous VAM population was a crucial factor in determining the yield of cassava, which is obligately mycotrophic. Such observations have profound implications for forest management for both timber and non-timber species, and indicate that quantities of VAM propagules, the species composition, and their effectiveness need to be evaluated in much more detail.

Although it is possible to predict that those ecosystems which support a productive vegetation dominated by VAM plants, and which contain mycorrhizal spores in addition to other sources of inoculum, are more likely to maintain infectivity, even if disturbed, it is clear that many tropical ecosystems are likely to be highly vulnerable to damage, and therefore require careful management to ensure that mycorrhizal populations are maintained. The use of less destructive methods of site preparation to prevent damage occurring may be both economically and ecologically preferable to attempting to rectify the damage by inoculation or site manipulation.

MANAGEMENT OF VAM FUNGI

With improved understanding of the damaging effects of site disturbance, it may be possible in many cases to reduce the amount of damage to the natural mycorrhizal population that occurs during site preparation by selecting less damaging methods. However, where disturbance is unavoidable, or where indigenous VAM populations are already damaged, action to correct mycorrhizal deficiencies may be advantageous.

Two methods can be used to correct VAM deficiencies:

- manipulation of indigenous VAM fungi;
- inoculation with selected VAM fungi.

Indigenous populations can be manipulated to enhance the overall levels of inoculum at a site, or to enhance a particular mycorrhizal species, and to increase or decrease VAM species diversity. Inoculation can be used to improve nursery or outplanting performance, or both, with either single isolates, or mixtures.

Manipulation of indigenous VAM fungi

The use of suitable plant hosts to increase vegetation cover and restore VAM populations to their normal levels is a management practice which could be used as an alternative to inoculation (Dodd *et al.* 1990a).

Several studies have examined the effects of pre-cropping and crop rotation on VAM populations in agricultural systems (Schenck & Kinloch 1980; Howeler, Sieverding & Saif 1987; Jeffries & Dodd 1989; Dodd *et al.* 1990a, b). They indicate that cropping history can substantially influence the abundance and composition of the fungal community, and can be used to manipulate mycorrhizal populations in favour of the target agricultural crop. Methods of land management can have a major impact upon VAM species diversity, which declines with increasing intensity of land management (Sieverding 1989). Studies in forest plantations in Côte d'Ivoire indicate that VAM species diversity was positively correlated with herbaceous plant species diversity (Lawson *et al.* 1991).

There is little information relating to the use of revegetation programmes for restoring mycorrhizal populations in non-agricultural tropical ecosystems. However, in a severely disturbed savanna in southern Venezuela, where spontaneous recolonisation was very poor, revegetation with a range of plant species enabled the recovery of the VAM inoculum to an extent adequate to enhance plant growth (Cuenca & Lovera 1992). As a result, native plants were able to colonise the revegetated areas at a higher rate than the non-revegetated areas. These results indicate that revegetation programmes may be used to promote the recovery of VAM inoculum in order to aid recolonisation by native plants.

In the same vein, intercropping of perennials and annuals may possess the hidden advantage that woody perennials may maintain VAM populations of benefit to the annual crop. Studies of intercropping systems in Kenya have indicated that mycorrhizal infection of maize grown in soil taken from close (0.5 m) to *Cassia siamea* hedges is greater than when it is grown in soil taken from further away (2.0 m) (S McGreevy & K Wakanene Mbuthia, unpublished data), suggesting that trees may act as reservoirs of VAM inoculum. Whether the species of fungi maintained by the tree are beneficial to the crop remains to be investigated.

Inoculation with selected VAM fungi

There are many examples in the literature which indicate that inoculation of both tropical crops and trees can be very successful in promoting the growth of the host plant in short-term experiments. The majority of studies on trees have been targetted at fruit trees and at nitrogen-fixing species. Mycorrhizal inoculation has been found to be an effective tool for improving tree performance in the *Citrus* industry (Menge 1983), and has reduced the requirement for fertilizer. Sieverding (1991) lists studies by 28 authors in short-term nursery experiments in Central and South American countries. Practically all the tree species investigated responded positively to mycorrhizal inoculation.

Positive responses to VAM inoculation have been reported for seedlings of many leguminous tree species, many of which require effective VA mycorrhizas to supply P for nodulation and nitrogen fixation (Manjunath, Bagyaraj & Gopala-Gowda 1984; De la Cruz *et al.* 1988). *Acacia auriculiformis* (De la Cruz *et al.* 1988), *A. holosericea* (Cornet, Diem & Dommergues 1982), *A. mangium* (De la Cruz *et al.* 1988), *A. nilotica* (Michelsen & Rosendahl 1990; Reena & Bagyaraj 1990a), *A. scleroxyla* (Borges & Chaney 1988), *Albizia falcataria* (Ahmad & Maziah 1988; De la Cruz *et al.* 1988), *Calliandra calothyrsus* (Reena & Bagyaraj 1990a), *Cassia spectabilis* (Habte & Turk 1991), *Leucaena leucocephala* (Manjunath *et al.* 1984; Ahmad & Maziah 1988; Michelsen & Rosendahl 1990; Jagpal & Mukerji 1991), *Sesbania grandiflora* (Habte & Aziz 1985), *Sesbania sesban* (Jagpal & Mukerji 1991) and *Tamarindus indica* (Reena & Bagyaraj 1990b) have all been shown to be responsive to inoculation in short-term studies.

Reports among non-legumes are less frequent; however, several tree species from a wide range of tropical habitats have been found to respond positively to inoculation. They include species such as *Khaya grandifoliola* (Redhead 1975), *Terminalia superba* (Blal 1985) and *Theobroma cacao* (Chulan 1991). The list of Sieverding (1991) includes fruit trees such as *Citrus* spp., *Persea americana*, *Carica papaya*, *Psidium guajava*, *Annona muricata*, *Cyphomandra betacea*, *Passiflora* spp., *Solanum quitoense* and *Mangifera indica*, and forest trees such as *Hibiscus elatus*, *Cedrela mexicana*, *Ficus glabrata*, *Carludovica palmata*, *Terminalia oblonga*, *Genipa americana*, *Tabebuia* spp. and *Vitex cooperi*.

Results from a number of experiments in which different single-species inocula were compared demonstrate that there is considerable variation in effectiveness between fungal species and between isolates (eg Bagyaraj, Byra-Reddy & Nalini 1989; Reena & Bagyaraj 1990a, b). This evidence suggests that, where inoculation is required, there is the opportunity to screen and select those VAM fungi possessing greatest symbiotic efficiency. Criteria for selection include speed of colonisation, ability to take up nutrients and water, improvement of plant growth, persistence and competitivity with indigenous fungi, and production of large numbers of resistant propagules (Abbott, Robson & Gazey 1992). Selection may be exploited particularly effectively in a tree domestication programme where high-performing clones of trees could be matched with highly effective isolates of VAM fungi.

When inocula are selected, the researcher must have a clear perception of the conditions for which the inocula are being screened – is the aim to achieve growth responses in potted plants in the nursery (where comparisons may be made with non-mycorrhizal control plants grown in sterile soil, or unsterile soil containing a mixture of indigenous mycorrhizal fungi) or in plants grown in the field with a more dispersed root system and a background indigenous inoculum, or is the researcher hoping for growth responses in both the nursery and the field, despite the widely differing conditions encountered? Selection for improved growth under nursery conditions is easily achieved, as demonstrated by the many papers on this subject, but selection for long-term effects poses a far greater challenge which agricultural mycorrhizal researchers do not have to meet.

Persistent effects of inoculation on growth in the field have not yet been demonstrated convincingly. Long-term successful symbiotic relationships with trees will need to be effective under a range of environmental conditions, from nursery to outplanting site and maturing plantation (Wilson & Coutts 1985; Janos 1988), and with a changing background of indigenous fungi, which may have been deficient at planting, but which will recover as vegetation is re-established. Because of the changing conditions, and the diversity in VAM physiology (Brundrett 1991), a mixture of VAM fungi (as in natural soil inoculum of undisturbed sites) may be a long-term advantage for trees, enhancing their performance under a range of conditions, and reducing the variation in host response. As fungal species diversity is lower in intensively managed systems, it may increase ecosystem instability because of the more limited physiological range of the VAM fungi present, and the more intensively managed forest plantations may be in greater need of mycorrhizal management than the less intensively managed, more mixed plantations.

While the performance of fungal mixtures in comparison with single isolates does not appear to have been tested in long-term experiments, short-term studies have demonstrated that a mixture of indigenous mycorrhizal fungi was as effective in promoting growth of *Albizia falcataria*, *Gmelina arborea*, *Intsia palembanica* and *Leucaena leucocephala* as the best of seven introduced VAM species used as single-species inocula (Ahmad & Maziah 1988).

An important gap in the literature is information relating to performance of inoculated trees after outplanting. Practically all studies have been restricted to short-term observations in tree nurseries, where inoculation is frequently beneficial. The limited information that exists from field plantings indicates that inoculation can improve both survival and tree growth after outplanting, although this improvement has not been seen in all the experiments reported. Janos (1988) describes experiments in Costa Rica and Panama in which inoculated *Pithecellobium longifolium* seedlings had faster growth rates than non-inoculated seedlings in the nursery. After outplanting to over-grazed pasture, the inoculated seedlings maintained their superior growth rates for seven months before the growth rates of the non-inoculated plants caught up. In a further outplanting trial of non-inoculated and mycorrhizal seven-month-old *Inga edulis* planted on sites that had been cut three or 15 months previously and then allowed to regrow, the average height of mycorrhizal plants increased ten times faster than that of surviving non-inoculated individuals for eight months following transplanting on the more recently cleared land, and two times faster on land that had been cleared 15 months previously. The contrasting responses on these two sites may indicate the lower inoculum potential on the more recently disturbed site, compared with the older site where revegetation may have resulted in recovery of inoculum potential.

Dart, Umali-Garcia and Almendras (1991) have reported that *Acacia mangium* seedlings grew better in the nursery when inoculated with mycorrhizal fungi, and that all the non-inoculated seedlings had died two years after outplanting in the field. In Kenya, four tree species (*Acacia tortilis, Prosopis juliflora, Terminalia brownii* and *T. prunioides*) were pre-inoculated in the nursery with mixed VAM inoculants collected locally, and with rhizobia (Wilson *et al.* 1991; see also Milimo, Dick & Munro, pp210–219). Inoculated plants generally grew better in the nursery. Assessments made 30 weeks after outplanting to two different field sites indicated that inoculated plants survived better than non-inoculated plants, with the exception of *P. juliflora* at one site and *T. brownii* at the other. When averaged over the two sites, inoculated *Acacia tortilis*, *Prosopis juliflora*, *Terminalia brownii* and *T. prunioides* had survival rates at 30 weeks of 97%, 94%, 89% and 89% respectively, while those of non-inoculated plants were 79%, 88%, 81% and 57%. Further assessments two years after planting indicated that the beneficial effects of inoculation upon survival were sustained (Wilson *et al.*, unpublished data). However, while survival in the field was improved by inoculation, there were no substantial differences between treatments in the growth of surviving plants. Similarly, Cornet *et al.* (1982) found that, although inoculation improved the growth of *Acacia holosericea* in the nursery, and the absolute differences in height growth observed at planting were sustained for at least seven months after planting in the field, the relative differences between inoculated and uninoculated plants diminished. Ducousso and Colonna (1992) have also reported that, although inoculation improved the growth of *Acacia holosericea*, *A. senegal* and *A. raddiana* in the nursery, the beneficial effects of inoculation diminished after one or two years in the field. As mycorrhizal inoculation in the nursery often produces larger plants, differences in survival between inoculated and uninoculated treatments may result from the initial differences in plant size, from differences in mycorrhizal infection, or a combination of both, and data need to be interpreted with care. Furthermore, differences in growth rate can be misleading, when initial plant size is different.

The effects of inoculation on field performance will depend upon the quantity and efficacy of naturally occurring inoculum, which needs to be assayed at the time of planting and at intervals thereafter to interpret the performance of inoculated and control plants. Likewise, assessments of the extent of mycorrhizal infection on root systems before planting and at intervals after planting are desirable, although observations on field material are very difficult. Responses to inoculation are most likely to be found on sites which have low background availabilities of inocula, and with mycorrhizal-dependent tree species.

SYNOPSIS

Many tropical trees are highly dependent upon their mycorrhizal associations for growth and survival. Mycorrhizal fungi are major intermediaries between plant and soil, of particular importance in adverse environments, yet their role in tree domestication, and in developing sustainable forestry systems in the tropics, has been neglected.

Site preparation can have a great impact upon indigenous mycorrhizal populations, particularly those communities in which spore inocula have been relatively unimportant. The use of less damaging methods of site preparation results in less disturbance to mycorrhizal populations, and limited studies indicate that this factor is more favourable to mycorrhizal infection on the roots of planted tree seedlings. Where there is a choice in the method of site preparation to be applied, consideration should be given to using methods which retain much of the ecological diversity of the indigenous mycorrhizal flora, and which do not lead to its depletion, thereby providing a good source of inocula for planted trees and potential benefits in long-term sustainability. When sites are deficient in mycorrhizal fungi, they may be manipulated to enhance mycorrhizal populations, and, where specific tree/VAM fungal isolate combinations are to be exploited, plants may be inoculated in the nursery. Methodology is available for assessing the mycorrhizal status of sites, and the mycorrhizal dependency of plant species. These tools should be applied to determine appropriate strategies for the treatment of different sites and tree species.

Short-term studies of the effects of VAM fungi upon plant growth have demonstrated that the use of inoculants to improve seedling growth in the nursery is readily achievable for a wide range of tree species. The use of selected isolates of inocula can considerably enhance growth, and opportunities exist for the exploitation of tree clone/symbiont interactions, so that the domestication of trees could run in parallel with the domestication of mycorrhizal fungi. However, the use of fungal mixtures as inoculants may be preferable to the use of single isolates.

Inoculation can be used to improve survival rates during the establishment phase after tree planting. Longer-term effects on post-planting performance have yet to be realistically evaluated. The development of longer-term effects will depend upon the selection of inocula that are appropriate for the site conditions (which may not necessarily be those that are most beneficial in the nursery), and the availability of effective indigenous inocula on-site. Plants destined for disturbed, nutrient-poor sites, with low levels of background inocula, are most likely to benefit from the application of inoculants in the nursery. Results so far indicate that expectations of long-term cumulative effects on most sites should not be raised too high: the advantages of inoculation are most likely to occur during the establishment phase.

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Harnessing symbiotic associations: the potentials of nitrogen-fixing trees

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ABSTRACT

Nitrogen-fixing trees are of two general types: (i) those nodulating with single-celled bacteria – rhizobia – all but one of which are members of the family Leguminosae; (ii) those nodulating with the filamentous bacterium *Frankia*, which are found scattered in a range of families. *Potentially* these trees fix large amounts of nitrogen, and have multiple uses as crops (fuel, forage, etc) and for controlling soil degradation. However, if this potential is to be realised, host and symbiont genotypes must be selected and matched not only to each other, but to the environment in which they are grown. To illustrate both the problems and potentials of nitrogen-fixing trees, examples will be drawn from the dry and humid tropics, concentrating on legumes and the non-legume *Casuarina*.

INTRODUCTION

Of the approximately 18 000 species (in about 650 genera) in the family Leguminosae, the majority are tropical or subtropical, and most are trees. Many have the ability to form root nodules and fix nitrogen, but there are also numerous exceptions. Research into nitrogen-fixing legumes has been very heavily biased towards herbaceous crop species, such as soybeans and *Trifolium* (clover), and hence there is a tendency to regard these as the norm. Tree legumes may differ in almost all aspects of nodulation from their herbaceous relatives (Sprent 1989). Only the basic enzymology of the conversion of N_2 to ammonia and of ammonia assimilation appear to have been highly conserved during evolution. Thus, although the potential of leguminous trees for nitrogen fixation is being actively investigated in many countries, few facts are available, especially concerning mature trees. For this reason, no attempt will be made here to generalise, but rather selected examples are presented to guide an assessment of the potential for nitrogen fixation, and also to indicate how much work remains to be done.

Although numerically legumes account for most of the tropical nitrogen-fixing trees, there are two other non-legume genera of interest, namely *Parasponia* and *Casuarina*. *Parasponia* is a genus of the Ulmaceae and to date the only one outside the legumes known to nodulate with a single-celled bacterium belonging to the general category of rhizobia. *Parasponia* species are restricted to SE Asia and the Pacific islands. Their nodules can fix nitrogen at high rates, and thus they have considerable potential, but they only grow in a comparatively restricted area where daylengths are around 12 h and there is a high photon flux density with temperatures in the range 25–32°C. *Parasponia* spp. appear to be indifferent to both type and fertility of soils. The genus is not considered further here (for further details, see Trinick & Hadobas 1988; Becking 1992).

Of the disparate group of non-leguminous plants nodulating with the filamentous bacterium *Frankia*, *Casuarina* has been the most widely used in tropical areas. Other actinorhizal plants occur less commonly in tropical countries and tend to be shrubs rather than trees (see Schwintzer & Tjepkema 1990). The plants most commonly referred to as 'casuarinas' are members of the family Casuarinaceae, which has recently been divided into four genera, *Casuarina*, *Allocasuarina*, *Gymnostoma* and *Ceuthostoma* (Johnson 1988). All have traits such as reduced needle-like branches and cone-like fruits which make them superficially resemble conifers, although they are firmly located in the angiosperms, with affinities to some other actinorhizal groups (Mullin, Swenson & Goetting-Minesky 1990). They have proved to be useful in all tropical countries, being prized for fuelwood, construction and land rehabilitation. These uses have been well documented (National Research Council 1984; Diem & Dommergues 1990), as have their strategies for improving nitrogen fixation (Diem & Dommergues 1990).

Sanginga, Bowen and Danso (1990a) grew 11 provenances each of *Casuarina equisetifolia* and *C. cunninghamiana*, either with nitrogen fertilizer or inoculation with a mixture of *Frankia* strains (Table 1). Great variability in nodule mass produced was recorded; not all nodules were equally effective at fixing nitrogen, as the data for shoot nitrogen content show (Table 1). Some

Table 1. Variation in nodulation and nitrogen fixation amongst provenances of *Casuarina cunninghamiana*, inoculated with a mixture of *Frankia* strains (source: Sanginga *et al.* 1990a)

Origin of Provenance	Dry mass of nodules (mg plant^{-1})	N in shoot[1] of nodulated plants (mg)	N in nodulated shoots / N in fertilized shoots
1 Tenterfield, NSW[2]	148	71	1.54
2 Cabargo, NSW	133	53	1.04
3 Augathella, QLD	16	56	1.41
4 Morgan, QLD	133	62	1.21
5 Marega, QLD	42	38	0.71
6 Helenvale, QLD	132	37	0.78
7 Rollingstone, QLD	154	38	0.77
8 Uriana, ACT	160	40	0.87
9 Wauchope, NSW	181	46	1.16
10 Uriarna, ACT	44	38	0.82
11 Singleton, NSW	154	38	1.00

[1] Obtained by interpolation from histogram

[2] All from Australia: NSW, New South Wales; QLD, Queensland; ACT, Australian Capital Territory

of these effects may be indirect, resulting from different potential growth rates of the provenances under the conditions used (a glasshouse in Vienna). To allow for this factor, growth of nodulated plants was compared with growth of N-fertilized plants, although the form of N (ammonium or nitrate) was not specified. It can be seen that some provenances assimilated more N when fixing N, and some when using soil N. The former is usually true of plants with effective nodules (eg provenance 1), but the latter is not as well correlated with ineffective nodules. For example, provenance 11 had a large nodule mass, but little N in shoots of either nodulated plants or plants grown on fertilizer N. Provenance 7, with the same nodule mass and the same shoot N content in nodulated plants as provenance 11, grew much better on soil N. Unfortunately, we do not know how much N was used for root growth, a factor which could be very important for the ability of the provenances to cope with certain field environments (as described later for *Faidherbia albida*).

N FIXATION IN THE LEGUMINOSAE

Nodulation

A list of genera known to nodulate has recently been published (Faria *et al.* 1989). There have been new reports of nodulating species within these genera, and some new reports (mainly negative) on additional genera. However, the essential features of the list remain unchanged, as has the balance between nodulation in the different subfamilies (see also Allen & Allen 1981). In general, few caesalpinioid legumes can nodulate whereas most of the mimosoid and papilionoid legumes are able to do so. There are, however, notable exceptions in all groups. Even if a species has the potential to nodulate, it may not do so in all environments.

There are many legumes which have proven value or potential for domestication which cannot nodulate. Examples in the Caesalpinioideae are *Parkinsonia, Bauhinia, Caesalpinia* and *Cassia* (*sensu stricto*; the former section *Chamaecrista*, now a separate genus, can nodulate). It is possible to argue a case for using some of these in preference to nodulated tree legumes, as has been done recently for *Caesalpinia paraguariensis* (Aronson & Toledo 1992).

Of the more important mimosoid legumes, the pantropical genus *Adenanthera* (not to be confused with its nodulated relative *Anadenanthera*) does not nodulate. The nodulation status of *Parkia* needs very careful examination, as early positive reports have not been confirmed. Similarly, care is needed with *Acacia* spp., as some species, such as *A. brevispica* (Odee & Sprent 1992), may have lost the ability to nodulate.

A number of papilionoid trees appear unable to nodulate. They include some large trees of tropical America, such as *Vatairea* and *Vataireopsis*. The large pantropical genus *Pterocarpus* is unusual in that African, Asian and Venezuelan species nodulate, but Brazilian ones have so far proved negative. There are many genera, including some large trees from tropical West Africa (eg *Amphimas, Angylocalyx*) for which there is no information. Indeed, over 40% of all legume genera, mainly tropical ones, have not been examined for nodulation.

Rhizobia

The bacteria which nodulate legumes, collectively known as rhizobia, comprise at least three genera. Although all are grouped in the α subdivision of the proteobacteria, they are less closely related to each other than to a whole range of bacteria, including some animal pathogens (Young 1992). Although rhizobial genera may be categorised (see Table 2), they do not always fit easily into discrete categories. Growth may be fast, intermediate, slow or very slow. Slow growth may be combined with narrow host range, and fast growth with broad host range (Table 3).

In the work of Turk and Keyser (1992), bacterial isolates from tree nodules were classified as either *Rhizobium* or *Bradyrhizobium* according not only to their growth rate, but also to various standard cultural criteria such as acid production. The data selected for Table 3 are for those strains which, when inoculated on to the host species from which they were isolated, formed effective nodules (shown by bold italic type on the diagonal of the matrix). Considering first the

Table 2. Some characters of the three established genera of rhizobia known to nodulate legumes

Character	*Rhizobium*	*Bradyrhizobium*	Azorhizobium
1 Growth rate in culture	Fast	Slow	Fast
2 N_2 fixation *ex planta*	Absent	Some strains	Generic
3 Assimilation products of N_2 fixation *ex planta*	Absent	Absent	Generic
4 Major location for *nod, nif* genes	Plasmid	Chromosome	?Chromosome
5 Host range	Usually narrow	Often broad	*Sesbania rostrata*
6 Geographical distribution	Global	Mainly tropical	Tropical

Table 3. Range of hosts and effectiveness of nodules formed from rhizobia isolated from tree legumes. Headings of columns designate species as listed (source: Turk & Keyser 1992)

		Host species tested							
Host species of isolation	*Bradyrhizobium* or *Rhizobium*	Ll	Gs	Cc	Sg	Rp	Aa	Am	Pf
Leucaena leucocephala	R	***E***	E	e	O	I	O	I	I*
Gliricidia sepium	R	E	***E***	E	O	I	O	O	I
Calliandra calothyrsus	R	E	E	***E***	O	I	I	O	I
Sesbania grandiflora	R	O	O	O	***E***	I	O	I	I
Robinia pseudoacacia	R	O	O	O	O	***E***	O	O	O
Acacia auriculiformis	R	O	O	O	O	O	***E***	O	E
Acacia mangium	B	O	O	O	e	O	E	***E***	E
Paraserianthes falcataria	B	O	I	O	I	I	?	E	***E***

*E, effective; e, partially effective; I, ineffective; O, nodules not formed; ?, inconsistent response

rows in the Table, it can be seen that strains classified as *Rhizobium* vary greatly in the number of species, other than that from which they were isolated, that they nodulate. The formation of ineffective nodules on a number of hosts could lead to problems if these strains were used as inoculants for soils supporting a range of legume trees. The data set for *Bradyrhizobium* is less extensive, but also suggests variability. The isolation of large numbers of *Rhizobium* strains from tropical trees, now found in many laboratories, counters the conclusions of some early workers that tropical rhizobia are principally slow-growing forms (see, for example, discussion in Allen & Allen 1981).

In this study, *Leucaena leucocephala* nodulated only with strains isolated from itself, *Gliricidia sepium* or *Calliandra calothyrsus*. This corner of the Table appears very tidy, but we should note that *Gliricidia* is a papilionoid genus, whereas the other two are mimosoids. Taxonomically, *Gliricidia* is closely allied to *Sesbania* and *Robinia*; strains from these genera do not nodulate the *Leucaena/Gliricidia/Calliandra* species tested, although the converse situation sometimes leads to ineffective nodules. The most specific association in this work is that between *Robinia pseudoacacia* and its isolates, but even here ineffective nodules were formed with isolates from several other genera.

It should be emphasised that the data in Table 3 represent only the tip of the iceberg. Some tropical trees can nodulate with strains of both *Rhizobium* and *Bradyrhizobium*. A further complication is that trees may be nodulated by strains from crop plants and *vice versa*. The most widely studied example is the newly designated species *Rhizobium tropici*, which forms nodules with *Phaseolus vulgaris* and *Leucaena* spp. (Martinez-Romero *et al.* 1991). Finally, it should be noted that inconsistent results are not uncommon in this type of work. In a comprehensive study recently carried out in Kenya (D W Odee *et al.*, unpublished data), four seedlings each of a range of tree species were grown in soil from 12 different parts of the country. Nodulation among these four seedlings was often very variable, from zero to large numbers of nodules formed. This could result from genetic variation in the host, a point which will be considered later.

FACTORS AFFECTING NODULATION AND NITROGEN FIXATION

Although most of the examples in this section are taken from legumes, similar arguments can usually be made for *Casuarina*. There are two major problems in attempting to estimate nodulation and N fixation in the field. First, finding nodules, even if they are present, may be difficult for various reasons:

- the weak connection to the subtending root in many species, especially *Acacia*, means that nodules readily become detached during excavation;
- nodules may be deep in the soil, especially in arid areas (see Johnson & Mayeux 1990).

Second, there is no universally applicable method of measuring N_2 fixation in the field for trees of any size. Seedlings and young plants are different from mature trees, because N balance and ^{15}N dilution methods can be used (see Giller & Wilson 1991). The only feasible method for mature trees is to use ^{15}N at natural abundance levels. The methodology has been reviewed several times in recent years, eg by Shearer and Kohl (1986). Recently, the method has been successfully applied to trees in a range of different environments, from arid (Mariotti, Sougoufara & Dommergues 1992 for *Casuarina equisetifolia*; Johnson & Mayeux 1990 for *Prosopis glandulosa*) to the Amazon floodplain (Martinelli *et al.* 1992 for unspecified mimosoid legumes).

Space precludes an assessment of all factors likely to affect nitrogen fixation. Experiments are most easily carried out in pots, and a range of factors are known to affect N fixation under these conditions (Table 4). Rather surprisingly, there has been comparatively little work on the effect of combined N on N fixation by tree species. It is generally assumed that the 'normal' situation for crop species applies, namely that combined N inhibits both nodulation and N fixation, but that some 'starter N' may be beneficial. There is a further tacit assumption that legumes prefer nitrate to ammonium as an N source, but this is not necessarily true. In *Acacia auriculiformis*, a rapidly growing Australian species being used in Brazil and elsewhere (see Booth & Turnbull, pp189–194), plants grew very poorly on nitrate, becoming chlorotic, whereas on ammonium they grew and nodulated well (Goi *et al.* 1993).

Table 4. Some factors which may affect estimates of nitrogen fixation potential in pot-grown plants. For access to relevant literature, see Sprent and Sprent (1990) and Giller and Wilson (1991)

Age of plant	Weeks Months Years
Growth conditions	Temperature Photosynthetically active photon flux density Water supply
Soil factors	Physical Chemical Biotic Endosymbiont *(Frankia*, rhizobia) Helper and other bacteria

A further complication which may be found when plants are grown on different sources of N concerns the allocation of resources between root and shoot. N M Gitonga of the University of Dundee is studying *Faidherbia albida,* and has measured root growth and plant dry mass when seedlings were given various forms of N. This species is well known for its ability to produce deep tap roots which may penetrate to the water table – where, according to Dupuy and Dreyfus (1992), there may be plenty of compatible rhizobia – as well as producing its leaves in the dry season. After eight weeks' growth in a Dundee greenhouse, tap roots were almost 1 m in length (Table 5), with those plants given nitrate being slightly shorter than control, ammonium-grown or nodulated plants. Note that this length of tap root was achieved over an almost two-fold range of root dry mass. In plants given no N, shoot dry mass was very low, being less than a third of those grown in ammonium. These differences in response led to a range of values for root/shoot ratios and suggest that caution should be used when assessing a plant's ability to fix N by reference to shoot N content alone (see below).

Table 5. Growth of *Faidherbia albida* on different sources of nitrogen (N), eight weeks after planting (source: unpublished data of N M Gitonga)

Treatment*	Length of tap root (mm)	Shoot dry mass (mg)	Root dry[1] mass (mg)	Root/shoot
O	948b[2]	134a	303a	2.26
N_2	966b	259b	397b	1.53
NO_3-	866a	210b	307a	1.46
NH_4+	958b	419c	537c	1.28

*O, control, uninoculated, no added N; N_2, effectively nodulated; NO_3-, 5 mmol nitrate-N; NH_4+ 5 mmol ammonium-N

[1] Tap root plus laterals

[2] Values within a column with the same letter are not significantly different ($P<0.05$)

Obviously, before using a plant for its ability to fix N, its nodulation potential in the soils where it is proposed to grow must be examined. A recent study of this type assessed 44 legume species on two soils (one acid, one neutral) in Chile (Aronson, Ovalle & Avendaño 1992). Several species known to nodulate did not do so, and others nodulated only poorly, which suggests that, if these species are to be grown in Chile, they should be inoculated, a topic considered below. Many of the species studied by Aronson, Ovalle and Avendaño (1992) which nodulated well were considered to be potential weeds and therefore excluded from further trials. This opens up the contentious matter of introducing exotic species into new areas. A risk/benefit analysis of such procedures has been made by Hughes and Styles (1989). Introduced species often produce large numbers of seeds, and in the absence of predators they can spread rapidly. Invasive N-fixing plants may seriously affect nutrient cycling in natural vegetation (Witkowski 1991).

Not surprisingly, plants vary greatly in their ability to fix N under adverse environmental conditions. Reports are now beginning to appear for tree species. For example, Marcar, Dart and Sweeney (1991) studied three Australian species of *Acacia* and ranked their salinity (NaCl) tolerance in the order *A. ampliceps* > *A. auriculiformis* > *A. mangium*. Perhaps N-fixing plants will be even more useful under increased atmospheric CO_2 concentrations: Norby (1987) found that *Robinia pseudoacacia* and two actinorhizal plants (*Alnus glutinosa* and *Elaeagnus angustifolia*) grew more rapidly and nodulated more when grown at twice the ambient CO_2 concentration.

Table 6. Variation within rhizobia isolated from *Robinia pseudoacacia* nodules (source: Batzli *et al.* 1992)

Factor	Range found
6 phosphogluconate dehydrogenase (nmol NADPH min^{-1} mg^{-1})	6–394
pH reaction in culture	Acid, neutral, alkaline
Mean generation time (h)	3.4–17.8
Tolerance to NaCl	No growth on 120 mol m^{-3} to growth on 256 mol m^{-3}

Table 7. Shoot N content in three provenances each of two legumes inoculated (I) or grown with added fertilizer (N), harvested at 12 or 36 weeks after planting (source: Sanginga *et al.* 1990b)

Legume species	Shoot N (mg $plant^{-1}$)			
	12 weeks		36 weeks	
Provenance	I	N	I	N
Leucaena leucocephala				
A	68	88	289	287
B	36	54	214	188
C	46	63	363	232
Faidherbia (Acacia) albida				
A	25	30	107	96
B	20	38	80	97
C	23	32	60	79

GENETIC VARIATION

Variation in rhizobia

This topic has been studied for many years and some aspects have already been considered for tree symbionts (see Table 3). In another recent study, Batzli, Graves and van Berkum (1990b) examined genetic diversity in 186 effective isolates from *Robinia pseudoacacia*, all obtained from two sites in Allegany County, Maryland, USA (Table 6). Clearly, in spite of the host specificity found by Turk and Keyser (1992) (Table 3), the rhizobia nodulating *R. pseudoacacia* are very varied.

Variation in host genotype

A number of studies on various species have been carried out at the International Atomic Energy Authority's laboratories in Vienna. Data were obtained by Sanginga *et al.* (1990b) from three provenances each of *Leucaena leucocephala* and *Faidherbia albida* (Table 7), which showed that harvests made after 12 and 36 weeks were different because some provenances nodulated slowly initially. However, there is clear variation among provenances of each species, especially for inoculated plants harvested at 36 weeks. In *L. leucocephala,* variation was also found between provenances grown on combined N (type unspecified). Plants had greater shoot N content when inoculated. Whether this result reflects greater total N content or is a consequence of altered root/shoot ratio (see Table 5) is not known.

Another study considered *Gliricidia sepium* (Sanginga, Manrique & Hardarson 1991). The provenances were obtained from the Oxford Forestry Institute and some were the same as those used for a molecular study of variation by Chalmers *et al.* (1992) (Table 8). Considerable variation can be seen both in the mass of nodules produced and in the amount of N fixed (again based only on shoot N content). The amount of N fixed per unit dry mass of nodules was very similar in the lower three populations in Table 8 (0.47, 0.46 and 0.43 mg, respectively). However, the amount fixed by the Nicaraguan

Table 8. Variation in nodulation and nitrogen fixation and genetic differences in populations of *Gliricidia sepium* (source: data from Sanginga *et al.* 1991; Chalmers *et al.* 1992)

Origin of population	Dry mass of nodules (mg $plant^{-1}$)	N2 fixed[1] (mg $plant^{-1}$)	Genetic similarity[2]	Polymorphic loci[3]
Managua, Nicaragua	56	38	0.78	24
Mariara, Venezuela	84	23	0.93	3
El Roblar, Costa Rica	64	30	0.85	15
Playa Tamarindo, Costa Rica	48	22	0.78	24
Pedasi, Panama	72	31	0.94	2

[1] Based on shoot N only

[2] Based on number of shared DNA fragments within a population

[3] Sum of polymorphic loci detected by nine oligonucleotide primers $plant^{-1}$

population was higher (0.67) and by the Venezuelan lower (0.27). The authors commented that the coefficients of variation for their data were much higher for inoculated than for N-fertilized plants. All these data suggest considerable variation between and within populations of *G. sepium* in their ability to nodulate and fix N.

Individuals from a provenance may vary greatly in their ability to nodulate in the same soil. This pattern is not obtained with highly selected cultures of crop legumes. Because tree species are generally grown from unselected seed (when vegetative propagation is not employed), it is perhaps not surprising that individual plants vary widely. Further, as nodulation requires the matching of genotypes from two diverse populations, it is not surprising that the coefficient of variation for N-fixing plants is greater than for plants grown on combined nitrogen. How, then, can we attempt to select host genotype/rhizobial strain combinations for trees, bearing in mind the problems of assessing variation and breeding of woody plants?

Assessment of variation may be greatly simplified by use of modern molecular methods. The data in the two right-hand columns of Table 8 are based on the technique known as RAPD (randomly amplified polymorphic DNA). This technique was used by Chalmers *et al.* (1992) to examine within- and between-population variation in *Gliricidia sepium* and *G. maculata.* Of the populations shown, those from Venezuela and Panama were genetically relatively uniform, and therefore perhaps not good candidates for trying to select for improved N fixation. On the other hand, the Nicaraguan population, which had the most efficient nodules, also displayed the most genetic diversity, and is therefore a more promising source of material for improvement. These studies are currently being extended to look for genetic markers more closely related to N fixation. Within the next few years, large-scale screening of woody germplasm for N-fixing potential (and, of course, many other traits) should be possible. All we then have to do is to match good host germplasm to effective, efficient and competitive rhizobia. This matching is likely to be difficult. Inoculation, particularly of promiscuous genotypes, is fraught with problems. Now that the basis of recognition between hosts and rhizobia is being elucidated (see Brewin 1991 for a review), at least for a few crop species, we have the possibility of genetically engineering rhizobia for particular host genotypes.

CONCLUSION

There is great potential for domestication of N-fixing trees. Before this potential can be realised, basic studies on the relationships between host, endosymbiont and the environment are needed. Modern molecular techniques should aid in the selection of host material and in matching it to suitable rhizobia/*Frankia*. Targeting one or two selected species for an intensive study might be most effective in defining ways for screening populations, avoiding the time- and labour-consuming processes of factorial host genotype/rhizobial (or *Frankia*) strain experiments.

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Case studies

Capturing and managing the genetic variation in *Prosopis* spp. for economically useful characters

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ABSTRACT

Self-incompatibility in *Prosopis* spp. results in obligately outcrossed trees whose progeny from a single parent tree may vary by a factor of 100% or more in the production of pods or total biomass. Asexual propagation is, therefore, required in order to capture genetic variation in *Prosopis* spp. Despite ten years of research on three continents, tissue culture of *Prosopis* spp. has not proved useful. Rooting of stem cuttings is the most effective technique for mass propagation of clonal material, but requires intensively managed stockplants. A solar-powered mist system for the propagation of stem cuttings has been developed for use in the tropics where power supplies are often intermittent. Rooting of cuttings from mature trees is difficult, which hinders the capturing of elite, proven genotypes identified in the field. Although air layering is effective in this respect, grafting techniques are preferable and often 100% successful. Clones of various *Prosopis* species are available that produce large (25 cm), nutritious (44% sugar content) pods; grow in 3.2% NaCl (seawater); are thornless, high biomass producers; and are non-browsed. These clones could be used: (i) directly in high biomass-producing fuelwood plantations; (ii) as scions to upgrade existing stands for greater pod production and thornlessness; (iii) to create clonal seed orchards; or (iv) for grafting on to rootstocks with a tolerance of high alkalinity or salinity.

INTRODUCTION

In self-incompatible (Simpson 1977), obligately outcrossing genera such as *Prosopis*, the genetic variability in progeny is extremely large. While it is useful to conserve genetic variability to meet future needs, such as an outbreak of pests or disease, it has been found that the variability within any batch of seedlings is so high that it limits the commercial exploitation of many individual traits. To overcome this problem, and to capture the attributes of individual genotypes, some form of asexual propagation is necessary. It would allow the vegetative multiplication of elite individual trees found growing in natural stands or in field trials.

The four basic types of asexual propagation for trees, namely tissue culture, rooting of stem cuttings, air layering and grafting, have been evaluated with respect to *Prosopis* spp. Despite considerable effort by several laboratories, a reliable tissue culture protocol for *Prosopis* spp. has not developed to the point where it can be used even for research-scale production of clonal material. In contrast, rooting of stem cuttings, air layering and grafting techniques have now been developed to the stage where they could be used operationally. However, each of these methods has its advantages and disadvantages, which are considered here in the context of a genetic improvement programme.

TECHNIQUES OF ASEXUAL REPRODUCTION

Tissue culture

Laboratories in Chile (Jordan & Balboa 1985), England (Batchelor *et al.* 1989), India (Goyal & Arya 1981; Ramawat & Nandwani 1991; V Dhawan, personal communication) and Texas (Green, Tabone & Felker 1990; Tabone *et al.* 1986) have been working to develop tissue culture propagation methods for *Prosopis*. While budbreak and shoot growth have been achieved from *Prosopis* explants, in no case were shoots produced other than from the initial explant. That is, shoots could not be excised from the original mother explant and successfully subcultured.

Our laboratory has found that, while 95% of the axillary buds produce 2 cm long shoots in six weeks, these shoots senesced and died by the 12th week in culture (the explants are subcultured every three weeks) (Tabone *et al.* 1986). The shoots begin to yellow and die from the terminal tip. The young leaves are the first to die, followed by the older leaves. This symptom is typical of a deficiency of an immobile plant nutrient, such as calcium, for whole plants growing in soil. However, increasing the calcium concentrations in the media failed to overcome the senescence.

After having developed a reasonable cytokinin/auxin concentration to stimulate shoot production, Tabone (1986) examined all 20 inorganic nutrients and vitamins at low (20%), normal (100%) and high (500%) concentrations of the basal Murashige–Skoog media, but found no striking nutrient deficiency that could account for this necrosis. Coconut milk, liquid corn endosperm, charcoal, ascorbate, sulfhydryl reagents and polyvinylpyrrolidone were added to the cultures without avail (Green 1989). To test the possibility that gases such as ethylene were produced that inhibited shoot development, a humidified air exchange system was constructed in side-arm flasks. Air exchange did not prevent the mortality of the shoot explants (Green 1989).

Mature *Prosopis* trees secrete gums at the ends of cut branches, probably to reduce the incidence of secondary infections. Similar gums may develop during *in vitro* culture, forming a barrier that prevents nutrient uptake. Trimming brown surfaces from the explants has been found to stimulate the growth of the explants for about a week (R Schmidt & P Felker, unpublished data). Further research is needed on nutrient uptake by explants, if tissue culture of *Prosopis* spp. is to become an effective tool for routine asexual propagation.

Rooting of stem cuttings

Rooting of stem cuttings can produce greater numbers of asexual propagules than any other technique: for example, only about eight hours' labour is required to take 2000 cuttings. Felker and Clark (1981) reported the rooting of stem cuttings of a number of *Prosopis* species, and noted a strong seasonality in rooting ability, with cuttings rooting well in the spring but not in the late fall. Klass *et al.* (1985) examined the environment for rooting cuttings in a growth chamber, and found that optimum temperatures were about 35°C and that irradiances greater than 500 μmol m^{-2} s^{-1} were required. They observed a photoperiod effect, with cuttings rooting best when stockplants and cuttings received a daylength of 12 h and 18 h, respectively. Souza (1986) examined the rooting of stem cuttings under plastic bags, under mist of varying frequencies and with fog systems, and found that almost no cuttings rooted under fog, whereas high rooting percentages (around 70%) were obtained under mist.

Following studies by Felker and Clark (1981) and Klass, Wright and Felker (1987), it became clear that one of the most important factors influencing rooting was the growth environment of the stockplants. If shoots of the *P. alba* stockplants were growing rapidly (50 cm lengths in three weeks) and free from insect damage, the cuttings rooted without hormones or fungicides. Even with high light intensities and air temperatures, there was occasionally a decline in the rooting percentage of *Prosopis* cuttings. Souza and Felker (1986) examined the influence of nutrient application regimes on carbohydrate contents, N contents and percentage rooting of *Prosopis alba* cuttings, and found optimal rooting was obtained when stockplants received 500 mg l^{-1} N twice a week. Under intensive management, *Prosopis alba* stockplants produced about 50 two-node cuttings per month.

In contrast to the ease with which cuttings rooted when taken from intensively managed juvenile stockplants grown in a glasshouse, it has been difficult to root cuttings from mature field-grown trees. Typical success rates have been less than 1%. The development of propagation techniques which enable material from mature trees to be rooted successfully is, therefore, a high priority.

In 1988, a company named Plantclone Inc was formed in Kingsville, Texas, to produce *P. alba* clone B2V50 commercially by mist propagation, for sale as ornamentals. Commercially viable mist propagation systems were developed, using 80 stockplants in 20 litre pots, that routinely produced about 1000 rooted cuttings per month from June through October. This period coincided with air temperatures >32°C and high (>1000 μE m^{-2} s^{-1}) light intensities. Propagation of clone B2V50 was discontinued in 1991 because of severe damage of outplanted trees by temperatures of −12°C.

Prosopis spp. are an important source of fuelwood and fodder in many less-developed countries, and clearly offer great potential for domestication by vegetative propagation and clonal selection, if appropriate propagation techniques can be developed. Sandys-Winch and Harris (1991) reported a technique for rooting cuttings that did not require electricity. This technique required placing large (1–2 cm diameter and 30 cm long) cuttings without leaves in an enclosed environment. After 22 weeks of twice-daily watering, these cuttings had 97% rooting success. Similarly, the low-technology non-mist system described elsewhere in this volume (see papers by Leakey, Newton & Dick, pp72–83; Mesén, Boshier & Cornelius, pp249–255; Ladipo *et al.*, pp239–248), which does not require an electrical or piped water supply, has also been used successfully for the propagation of *Prosopis juliflora* (see Leakey *et al.*, pp72–83, and references therein). Wojtusik, Boyd and Felker (1993) recently developed a solar-powered mist system that yielded 90% rooting success on location in Haiti. A water supply with a minimum pressure of 1.5 MPa was required for the mist nozzles. This system used a solar panel to charge a 12V car battery, which operated a solenoid valve when the moisture evaporated from a stainless steel 'leaf' under the mist system.

Air layering

Air layering techniques for mature *Prosopis* spp. have been developed in the Rajasthan desert (Solanki, Kackar & Jindal 1986). A branch about 70 cm long is girdled where it is about 1 cm in diameter. The bark is removed from a section about 2 cm long, auxin powder is applied, and moist peat moss is wrapped tightly around the girdled branch with clear plastic. Roots appear through the plastic after six to eight weeks. Some of the leaves are stripped from the severed branch prior to potting. In the USA, 20–30% success has been achieved using this technique on mature trees. The technique is, therefore, useful for obtaining the first asexual propagule from mature field-grown trees. However, it is not appropriate for mass propagation because of the low multiplication rate.

Grafting

Wojtusik and Felker (1993) recently examined four graft types for *Prosopis* spp. and found that cleft and whip grafts were equally successful, while side-veneer grafting was less useful, and T-bud grafts failed completely. Graft compatibility between North American (*P. glandulosa* and *P. articulata*), South American (*P. alba* and *P. chilensis*) and tropical species (*P. juliflora*) was nearly 100%. The opportunity to use grafting to capture mature elite genetic material for further multiplication was demonstrated by its successful application in Texas on *P. alba* rootstocks, using scions from five fast-growing, erect, non-browsed and thornless *P. juliflora* trees in a five-year-old Haitian field trial (Wojtusik *et al.* 1993).

A significant rootstock effect on biomass production was noted in graft compatibility trials (Wojtusik & Felker 1993). Scions of all species had greater biomass production when grafted on to *P. alba* or *P. chilensis* rootstocks than when grafted on to themselves.

USEFUL GENETIC CHARACTERISTICS OF *PROSOPIS* SPP.

The 44 species of *Prosopis* native to North and South America, Africa, and Asia have great variability with regard to environmental tolerances and useful economic characters. Burkart's (1976) monograph provides the most comprehensive description of variation in morphological traits. *Prosopis* species grow from sea level to 4000 m elevation (*P. ferox* in Argentina), and from the equator to 48°S latitude in Argentina. Some species are prostrate shrubs (*P. strombulifera*), while others can grow into trees 20 m tall (*P. juliflora* and *P. alba*). Some species have horny and thornless individual trees. Thornless *P. alba* trees were much more susceptible to damage from goat browse than *P. juliflora* from Peru in Haitian field trials with 70 open-pollinated families (Lee, Russell & Felker 1991). These trials also demonstrated great variation in the number of mainstems produced and in the presence of erect form.

In a progeny trial in the California Imperial Valley, over a 100-fold range in the biomass accumulation of 55 families of different *Prosopis* spp. was observed after two years' growth (Felker *et al.* 1983). *P. alba* and *P. chilensis* displayed higher growth rates than the Californian or Arizonan native *Prosopis* species. The slowest-growing species was *P. tamarugo* from the Chilean salt deserts. The largest individual trees in this trial were subsequently cloned by rooting stem cuttings.

There is also considerable range in tolerance of *Prosopis* spp. to temperature. Most *Prosopis* spp. tolerate air temperatures of over 40°C, if water is available. However, the species vary greatly in their tolerance to absolute minimum temperatures (Felker *et al.* 1981). *Prosopis juliflora* from the Caribbean or Peru is a truly tropical species which is completely killed by temperatures of –4°C. These temperatures are tolerated without damage by *P. alba* and *P. chilensis*, although they are killed by extended periods of –12°C (P Felker, unpublished data). In contrast, Texas native *P. glandulosa* var. *glandulosa* tolerates 5 h of –18°C without damage. However, *P. glandulosa* appears to require sustained 30°C temperatures for budbreak and temperatures of 35°C for optimal growth.

There is great variation in the resistance of *Prosopis* spp. to attack by psyllid insects. The young tender growth of *P. glandulosa* var. *torreyana* from the California desert is very susceptible to psyllid damage, while the South American species *P. alba* and *P. chilensis* are much more resistant (P Felker, unpublished data). It should be noted that this is not the same psyllid that damages *Leucaena leucocephala*, which is 100% resistant to the psyllids that attack *Prosopis* spp. (P Felker, unpublished). Considerable variation in psyllid resistance has also been noted among the algarrobos in plantations in the Chilean salt deserts. In this case, resistant individuals could have been grafted on to susceptible trees.

When *Prosopis* spp. native to the hot (42–48°C) California desert were planted in a cooler (32–38°C), but higher-humidity environment in Texas near the Gulf of Mexico, all 100 trees died from attack by stem cankers within three years (P Felker, unpublished data). *Prosopis velutina* from Arizona and *P. flexuosa* from the interior deserts of Argentina were similarly affected but to a lesser extent. In contrast, the Texas native *P. glandulosa* var. *glandulosa* and the Argentine species *P. alba* and *P. chilensis* appeared to be canker-resistant.

The variation in *Prosopis* pod production and chemical characteristics is large. The mean pod production per mother tree from a five-year-old California trial ranged from 7.1 kg tree^{-1} to 0.0 kg tree^{-1} (Felker *et al.* 1984). Perhaps even more striking was that, within the family with the greatest mean production, the pod production ranged from 3.2 to 12.2 kg tree^{-1}. Pod sugar and protein contents in a California field trial ranged from 10% to 40% and from 10% to 17% respectively (Oduol *et al.* 1986). In spite of high analytical values for pod sugar content of the trees, some trees have a bitter after-taste while others are relatively mild and sweet. While most *Prosopis* pods are about 15 cm long, some in Brazil are nearly 50 cm long. Thus, there is great opportunity for selection for pod size, sugar and protein content, and for lack of astringency.

There is also considerable variation in *Prosopis* spp. response to soil factors. Rhodes and Felker (1987) exposed 100 seedlings of nine open-pollinated families to high salinity in a greenhouse environment, and found individuals of *P. alba, P. flexuosa, P. chilensis* and *P. juliflora* that could grow in 3.2% NaCl, the same salinity as seawater. Individual trees that continued to grow in this salinity have been repotted and could be asexually propagated for use as salt-tolerant rootstock. When some of these clones were examined in saline but waterlogged field conditions in southern Pakistan, they grew poorly (P Felker, unpublished data). The very thorny *P. articulata* and *P. juliflora* appear to be the *Prosopis* species with the greatest tolerance of waterlogging. Singh, Abrol and Cheema (1989) found that *P. juliflora* was able to grow in sodic soils with a pH as high as 10.4, if the soils were amended with zinc, gypsum and barnyard manure. Without these amendments, *P. juliflora* was able to grow in soils with a pH of 9.0.

In a greenhouse trial examining nitrogen fixation in 13 *Prosopis* species, Felker and Clark (1981) found ten-fold differences in the rates of N fixation for these species. The N fixation rates were highly correlated with biomass production in two-year-old field-grown trees. It is unclear whether the greater N fixation caused greater growth, or whether greater growth provided more photosynthate to make more N fixation possible.

Attributes of *Prosopis* species that are generally overlooked are the beautiful orange/red colour of the wood and its technical qualities for fine furniture and flooring manufacture (Tortorelli 1956; Weldon 1986). It should not be surprising, given the beauty and excellent technical properties of other tropical legumes such as *Dalberghia sissoo* (Indian rosewood) and *Pterocarpus* spp. (cocobolo). The wood of *Prosopis* spp. is somewhat harder than species such as *Quercus* (oak), *Prunus* (cherry), and *Juglans* (walnut), but its real advantage is that its volumetric shrinkage (3–4%) is among the lowest of any species in the world. When solid furniture is moved from high- to low-humidity environments, the wood contracts or expands depending on the air humidity. Having one of the world's lowest values for volumetric shrinkage, *Prosopis* has much less of a tendency to expand and contract than other fine hardwoods. *Prosopis alba* from Argentina (Tortorelli 1956) and *P. glandulosa* (Weldon 1986) from Texas also have low values for volumetric shrinkage.

The practical implication of these technical qualities is that *Prosopis* timber should command a price of about \$400–800 m^{-3} (700 kg) which is nearly five to ten times greater than its value for firewood. Thus, where economic development issues are important, the development and management of *Prosopis* spp. for fine furniture wood could be considered. Value-added manufacture of fine furniture or flooring would further increase the value of this resource.

USE OF CLONAL MATERIAL IN THE GENETIC IMPROVEMENT PROCESS

To capture the first asexual propagule from proven field trees, it is necessary to use either grafting or air-layering techniques, or pollarding to produce juvenile material. Grafting produces many more individuals with less effort than air layering, although many more individuals can be produced from stem cuttings if the tree resprouts copiously after pollarding. After clonal stockplants have been obtained, the resulting shoots can either be used to provide rooted cuttings for transplanting to the field, additional stockplants, material for clonal seed orchards, or scions for grafting on to existing trees.

Where fuelwood plantations are desirable, clones which produce high biomass will obviously be most useful. When rooted cuttings of *Prosopis alba* were used to establish plantations for fuelwood, productivities of 21 Mg ha^{-1} dry biomass were obtained in the third growing season (Felker *et al.* 1989). There are many other applications where clonal material may also be of value. For example, the mature trees in the 1000 ha *Prosopis alba/flexuosa/chilensis* plantations in northern Chile appear to vary greatly in pod colour, size and production, and in resistance to stem cankers and psyllids (P Felker, unpublished).

Grafting could be used to circumvent the numerous problems that prevent successful tree establishment in semi-arid regions. Well-established seedlings arising from natural regeneration could be cut off above the browse line and superior, thornless material could be grafted on to them. This would reduce the requirements for nurseries, the transportation of seedlings to the field, and the costs of labour and maintenance. The hybridisation of geographically distant trees could be greatly facilitated by grafting the desirable parents on to the same tree or at least grafting all possible parents into the same field plot. The need to survey dates of pollen shed, and the difficulties in transporting live pollen to conduct the crosses could then be avoided. It would also be useful to explore the influence of grafting on processes such as flowering, dwarfing, date of budburst, and cold hardiness, that are known to be influenced by the rootstock in other tree species.

Some of the most intriguing rootstocks would be those found by Singh *et al.* (1989) to tolerate pH values of 10.4 and those of Rhodes and Felker (1987) that grew in 3.2% NaCl. Our casual observations suggest that *P. articulata*, which is extremely spiny, may be one of the most tolerant *Prosopis* spp. to conditions which are both saturated and saline. Unfortunately, the pods of *P. articulata* have some of the lowest sugar contents of all *Prosopis* species, and the trees have such long and profuse thorns that they would be extremely undesirable in almost all circumstances. The *P. juliflora* in India that tolerates pH 10.4 conditions is not as spiny as *P. articulata*, but the pods are quite bitter and not nearly of the same value as other *P. juliflora* or *P. alba*. Thornless clones of *Prosopis alba* and *P. juliflora* with abundant high-sugar pods could be grafted on to rootstock which, other than its tolerance to severe edaphic conditions, would be completely useless.

Salt-tolerant clones could be of immense value in areas such as southern Pakistan, where irrigation mismanagement has destroyed hundreds of thousands of hectares of land that is now too saline and too waterlogged to grow arable crops. Foresters in Gujarat, India, have begun to manage *Prosopis* spp. as one of the few plants capable of growing in the saline groundwater resulting from seepage from the ocean. R Ahmad (unpublished) at the University of Karachi, Pakistan, has irrigated *Prosopis* spp. with highly saline water along the coasts of Pakistan, to provide windbreaks for controlling sand dune movements on to roads and villages.

In some instances, rooted cutting technology may be viewed as too technologically advanced, in which case it would be desirable to use seeds even if the full genetic potential of clones were not achieved. There has been a considerable demand for *Prosopis* seed that would produce thornless trees, and it would be advantageous to use superior thornless clones in a seed orchard to produce genetically improved seed. Naturally occurring thornless trees produce seed that results in thorny and thornless trees due to outcrossing with wild thorny trees. Thus, there is an opportunity to combine thornless clones in an isolated seed orchard to produce seed which produces thornless plants, that also possess improved growth rates, improved pod production, greater salt tolerance, etc. Because *Prosopis* is self-incompatible, a seed orchard of a single clone would probably result in infertile seed. Thus, multiple thornless clones would be required in the seed orchard. Heterosis should occur in these seed orchards resulting in greater growth rates in the progeny than either of the parents. Mating schemes for clonal seed orchards have been described in detail. Before any long-term investment in clonal seed orchards, the mating designs should be reviewed carefully.

This author has frequently observed large plants of *Prosopis* spp. being used around homes for shade trees in south-western USA, Haiti, Mexico, Chile and Argentina. In the United States, pod production in yards is highly undesirable and trees with minimal pod production would be preferred. In contrast, in developing countries, where abundant forage for animals would be an added advantage to shade, use of thornless *Prosopis* clones with a propensity for producing long sweet pods would be most desirable. These clones could be produced by rooted cuttings and grown in 20 litre polyethylene bags typical of nursery stock, or existing wild trees could be grafted.

CONCLUSIONS

A suite of asexual propagation technologies is now available to capture the qualities of outstanding elite genotypes and to multiply these clones rapidly for use in genetic improvement programmes, to produce clonal seed orchards, or for direct use in plantations. Grafting techniques now offer the possibility of combining trees with a resistance to adverse edaphic conditions, such as high salinity, with trees with other useful characteristics, such as thornlessness or pod production. Imaginative use of these techniques offers great potential for reforesting arid lands.

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Domestication of lesser-known tropical tree species: the Australian experience

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ABSTRACT

The CSIRO Australian Tree Seed Centre has played a major role in domesticating tree species for over 25 years. This paper describes recent work carried out by the Centre's staff and other researchers in Australia, Zimbabwe, Kenya, Pakistan, Indonesia, Thailand and China. The work, which is being supported by the Australian Centre for International Agricultural Research, has assessed the potential of lesser-known Australian species for multipurpose use. This paper provides a brief description of the major phases in the domestication process, including species selection, seed collection and distribution, nursery practice, species and provenance trials, species/site matching, tree improvement, tree management and utilisation. Progress with the domestication of *Acacia auriculiformis* is described as a detailed case study.

INTRODUCTION

Libby (1973) outlined strategies for the domestication of forest trees in which he recognised six levels of tree improvement. He noted that the utilisation of most tree species still follows a pattern established by neolithic societies. Wild seeds are used to establish plantations and these are the source of seed for expanding the plantation resource, with little or no attempt to improve seed quality. Only a small number of Australian species have advanced beyond this lowest rung of the domestication ladder, although in some of these species (such as *Eucalyptus grandis*) the domestication process is well advanced (Table 1). There are dramatic improvements in productivity to be gained, even in the early stages of tree improvement (see Table 1). For example, an economic evaluation of the tree introduction programme in China supported by the Australian Centre for International Agricultural Research (ACIAR) indicated internal rates of return on investment in the range 27–45%, which were largely due to the correct selection of provenances (McKenney *et al.* 1991).

Table 1. Increasing productivity of *Eucalyptus* plantations in Brazil due to silvicultural treatments (source: Campinhos 1991)

Period	Silvicultural practices	Mean productivity (m^3 ha^{-1} yr^{-1})
1966–70	Low genetic quality seeds and fertilizer use	17.4
1971–75	Genetically pure seeds (unimproved) and fertilizer usage	22.3
1976–80	As in previous stage, but from selected stand	35.0
1981–85	Improved seeds and vegetative propagation	44.9
1986–90	As in previous stage and additional selection	60.0

This paper outlines only the first stages in the domestication process, and in particular those leading to the selection of the most suitable provenances for use in a specific area. The stages considered are: species selection, seed collection and distribution, nursery practice, species and provenance trials, species/site matching, tree improvement, tree management and utilisation. The latter stages of domestication described by Libby (1973) are an iterative process of tree improvement based around clones. Each stage uses a set of 'clonal' seed orchards, clone-holding orchards, 'seedling' seed orchards, clone evaluation plantings, and general evaluation plantings. Clonal approaches are not discussed further here (see papers in this volume by Foster & Bertolucci, pp103–111; Felker, pp183–188; Leakey, Newton & Dick, pp72–83; Ladipo *et al.*, pp239–248; Mesén, Boshier & Cornelius, pp249–255; Milimo, Dick & Munro, pp210–219).

The paper draws examples from two main areas of work. The first is an eight-year programme of collaborative research into the domestication of 'lesser-known' Australian trees, such as *Acacia,* *Casuarina, Melaleuca, Grevillea* and *Sesbania* species. The programme was co-ordinated by ACIAR and involved researchers in national institutes in Zimbabwe, Kenya, Pakistan, Indonesia, Thailand and China, as well as Australia. The second is the 25-year experience of the Australian Tree Seed Centre (ATSC) based at CSIRO's Division of Forestry. The main objective of the Centre is to support the collection, distribution and improved use of the genetic resources of Australian trees. The Centre responds to over 2000 enquiries every year and dispatches about 15 000 seedlots from over 600 species to researchers in 100 countries. A major part of the Centre's funds are provided by the Australian International Development Assistance Bureau (AIDAB).

GENERAL METHODS

Species selection

The first stage of any domestication process is to decide which species will be evaluated. This decision will depend on the needs which are to be met and the number of species which a programme can examine. In April 1983, ACIAR organised a meeting of foresters and botanists to identify 'lesser-known' Australian tree and shrub species with potential for multipurpose use. Turnbull (1986) summarised the selection criteria as follows:

- plants capable of providing products and services in addition to fuelwood;
- adaptable plants that are easily established and maintained;
- plants capable of growing in extreme environments, including arid and humid tropical zones, infertile soils, heavy clays, saline, highly alkaline or waterlogged or exposed coastal situations.

Other desirable characteristics noted were an ability to fix atmospheric nitrogen, a capacity for rapid growth, an ability to coppice, and good burning properties. Using these criteria, 108 species were selected from 170 initially suggested. As this was to be a large programme of research, the selection criteria were broad and numerous species were chosen. If resources allowed only a small number of species to be examined, then the selection criteria would have to be more specific.

When the species have been chosen, existing information about them can be collated. For the ACIAR programme, a book was produced summarising the characteristics of 100 of the species (Turnbull 1986). It included the botanical name, common names, family, main attributes, botanical features, geographical distribution, physiography (ie where it is found in the landscape) and soils, vegetation type, utilisation, silvicultural features, pests and diseases, limitations, related species, research contacts and references. The two-page description also included a map, showing the species distribution and a photograph of a typical specimen. Scant information was available for many of the 'lesser-known' species. However, the collation of information served to highlight gaps in knowledge which could be filled during the course of the programme. (Though a book may not be produced by smaller projects, a similar format could be followed.)

Seed collection and distribution

The availability of high-quality and well-documented seed is a prerequisite for any research underpinning a domestication programme. Securing the seed may involve detailed planning over several years and a substantial investment of resources. Tree seed centres play an important role in this activity. Their basic role is to collect, document and distribute authenticated seed.

The objective of first seed collections is to sample some of the genetic variation within and between populations. For each species, seed should be collected from at least two provenances in contrasting environments, but the sampling strategy may vary according to the variability of the environment in which the species occurs and the extent of its natural distribution. If possible, seed samples should be collected from several widely spaced (>100 m apart) trees at each site. However, if the seed crop is small, it may be necessary to bulk the seedlots. The techniques used in the ACIAR collections have been described by Searle (1989).

It is important to record information about the stand of trees and the environmental conditions at the sampling site. The ATSC uses a standard seed collection data sheet which includes essential entries such as species, seedlot number, provenance name (to be used in a data base), location name, latitude, longitude and altitude. If possible, information on factors such as aspect, slope, soil texture, pH, geology and vegetation associations are also added, as well as mensurational data such as height, diameter, habit and crown dimensions. The data sheet indicates whether botanical voucher specimens, photographs and bulk or individual tree samples were taken. Space is also provided for seed viability assessments made in the laboratory.

Nursery practice

It is pointless expending great effort to collect seed if they cannot be stored effectively, and then used to raise seedlings of a size suitable for planting. Doran (1986) and Ryan *et al.* (1987) have summarised some of the techniques used in the ACIAR programme. They describe pre-sowing treatments, optimum temperature, moisture and light conditions for germination, choice of seedling containers, soils, use of fertilizers and insecticides, soil sterilisation, inoculation with symbiotic organisms, time of sowing, transplanting, shade, shelter, watering, weed control, root pruning and hardening off. They also consider tree establishment, including site preparation, spacing, time of planting, transport of plants to the field, planting method, fertilization, weed control and pest protection.

Relatively few Australian trees have 'recalcitrant' seeds, but storage is a problem with many tropical species. For example, difficulties may be experienced with storing many dipterocarp species for more than a few weeks. Chin (1990) provides a general review of recalcitrant seeds which cannot be successfully stored under cold dry conditions (see also Tompsett, pp61–71).

Species and provenance trials

Arboreta containing a few individuals of many species have demonstration value, but are no substitute for well-designed replicated trials. Boland and Turnbull (1989) summarised some of the design decisions behind the ACIAR species trials. The project initially used a randomised complete block design, with square plots of 24 or 36 trees and with three or four replications. The design was largely determined by the objective of the project, which was to assess the growth and survival of about 25 lesser-known Australian species at each site over a period of six to ten years. The large plot sizes provided some buffering between plots and allowed for thinning, which was required in some cases at three years. Later in the project some trials were established using incomplete block designs with five to ten tree line plots. Such trials have a short life (2–3 years), but are comparatively inexpensive to set up. They are well suited to adverse environments, where planting may need to be repeated over several years to study the effects of erratic climatic conditions.

Training in statistical design and analysis was an important output from the ACIAR project. A book entitled *Design and analysis of field trials in forestry* is in preparation, and Matheson (1990a, b) has provided a brief introduction to the subject. The Australian Tree Seed Centre has produced a more general guide to nursery practice and the establishment of species/provenance trials (Carter 1987), which has been widely distributed and translated into several languages.

As it was desirable to establish the species trials over a range of relevant climatic and soil conditions, the initial ACIAR trials were located in Australia, China, Kenya, Thailand and Zimbabwe, on sites located in areas where there was a perceived need for the species being tested. Accessibility and security were major concerns. Assessment procedures were standardised as far as possible. The MPTDAT microcomputer data base system developed by the United States Agency for International Development (USAID) in its Forestry and Fuelwood Research and Development Project (F/FRED) and by the CSIRO Division of Forestry provides a useful framework for storing data from trials.

Species identified in the ACIAR trials as having good potential were further tested in range-wide provenance trials (Gwaze 1992). Some of these provenance trials used individual progenies, so that there was the potential to convert the trial into a seed production area.

Species/site matching

Establishing, maintaining and assessing trials is an expensive operation. It is important to make the most of information from these trials, so the capability of other sites can be assessed. Recent developments in interpolating climatic data have greatly improved the ability to assess the potential of sites in different regions, countries or throughout the whole world. New methods to predict where and how well different species and provenances may grow in different environments have been summarised by Booth (1991).

Tree improvement

The application of the results of species and provenance trials is dependent on the availability of seed. Some native species may come from areas which are not readily accessible. In the case of exotics, seed may be available from the country of origin, but ultimately it is desirable that a seed source is developed in the country where the seed will be used. Species such as *Acacia crassicarpa, Casuarina junghuhniana, Eucalyptus grandis* and *E. urophylla* have been identified in species/provenance trials as having potential for wider planting, and seed orchards have been established for these species. In some cases, the seed orchards have been developed as provenance/progeny trials, from which poorly performing progenies can be culled. This procedure can accelerate the production of high-quality seed, but it must be done carefully and represents only the first step in tree improvement.

Matheson (1990a, b) has provided a brief introduction to tree improvement methods. He notes that a worthwhile breeding strategy requires:

- a breeding population;
- methods of selecting superior material;
- a method of regenerating and upgrading the breeding population (by open or controlled pollination); and
- a method of transferring material from the breeding population to the planting site (a

seed orchard, nursery cuttings or a tissue culture laboratory).

He outlines some alternative approaches, including simple mass selection methods or more complex recurrent selection strategies. He also provides seven examples of strategies being used for different species in different parts of the world.

It is important to develop breeding plans at an early stage in the domestication process, so that staff and financial resources can be allocated efficiently. Research to understand the reproductive biology of the species, including levels of inbreeding, is an integral part of any tree breeding programme. Breeding plans for *Acacia mearnsii* and *Eucalyptus globulus* have been prepared by Raymond (1987, 1988) and ACIAR has supported research on the reproductive biology of both species. Vegetative propagation can also be used for the mass propagation of the products of a tree improvement programme. ACIAR has supported research on cuttings and micropropagation of tropical acacias, and some practical techniques have been developed (Carron & Aken 1992).

The genetic engineering of tree species to add characteristics, such as partial resistance to insect defoliation or herbicides, may be an increasingly important part of tree improvement in the future. However, the first requirement is to ensure that transformed trees are reproductively sterile. This will prevent the 'escape' of foreign genes into native forests.

Tree management

To realise the full potential of any species, research into tree management, including nutrition, weed control, spacing, coppicing and thinning, should proceed in parallel with tree breeding (see Table 1). Where appropriate, the nutrition research should include work on symbiotic organisms, which may dramatically affect productivity, particularly on poor sites (Reddell, Rosbrook & Ryan 1989; Dart, Umali-Garcia & Almendras 1991). ACIAR has supported research on ectomycorrhizal, *Rhizobium* and *Frankia* associations aimed at selecting effective symbionts and developing low-cost appropriate technologies.

Utilisation

All the work described in the preceding sections aims to produce effective management systems, but they are useless if the trees do not provide the product(s) required by the grower. Whether the desired products include sawn timber, pulp, fuelwood, fodder, tannin, honey or some other output, the appropriate parts of the trees must be evaluated to ensure that a satisfactory product can be produced (see, for examples, resource evaluation and utilisation papers in Boland 1989 and Turnbull 1991).

DOMESTICATION CASE STUDY: *ACACIA AURICULIFORMIS*

The domestication of *Acacia auriculiformis*, a fast-growing nitrogen-fixing tree from Australia, Papua New Guinea and Indonesia, began about 50 years ago. The original seed introductions to most countries were haphazard, in the sense that no records were kept of seed origin or genetic quality. Initial introductions were for ornamental purposes and were undoubtedly collected mainly from planted trees, with easy accessibility being the chief selection criterion.

A. auriculiformis was introduced into Thailand in 1935 and is now planted widely; in India it has become a major plantation species since its introduction into West Bengal in 1946; and in China since 1961 over 50 000 ha of plantations and 3000 km of roadside plantings have been established. It has been planted on a lesser scale elsewhere in Asia, Africa and South America. The early plantings of *A. auriculiformis* demonstrated its wide adaptability in the humid and subhumid tropical lowlands. It generally formed a crooked, multistemmed and heavily branched tree, which could be used for fuelwood and small items of furniture, or for shelter and amenity purposes.

In 1982, the Food and Agriculture Organisation was stimulated, by the recognition of *A. mangium* in Malaysia as a fast-growing species capable of providing timber and pulpwood, to assess the potential of other tropical acacias for wood production (Turnbull *et al.* 1983). In 1984, a planning workshop of the International Union of Forestry Research Organizations (IUFRO) recognised the potential for increasing the productivity of *A. auriculiformis* in Asia, and recommended a programme of tree improvement and silvicultural research (IUFRO 1984). The recommendation was implemented in a programme of co-ordinated research supported by the United States Agency for International Development (USAID), through its Forestry/Fuelwood Research and Development Project (F/FRED) in Asia, and the ACIAR forestry research programme in Asia and East Africa.

Pulping studies showed that the wood of *A. auriculiformis* was suitable for chemical pulping and comparable with some of the commercially accepted high-quality *Eucalyptus* (Logan 1987). The major drawback to its utilisation for this purpose was its crooked stem form and multiple-leader habit. The natural stands of this species occur primarily in sparsely populated regions with poor road access, so exploration of the genetic resource was difficult and expensive. However, when it was accomplished, tall straight trees were found in Papua New Guinea and northern Australia, and it appeared likely that the introduction of this genetic material into a domestication programme would extend the utilisation potential to poles and industrial wood.

Seed collected in a systematic way throughout the natural distribution of *A. auriculiformis* was critical to the domestication process, and provided the material for subsequent research. The collections were undertaken by CSIRO's Australian Tree Seed Centre in co-operation with the Papua New Guinea Department of Forests; between 1987 and 1990, about 3000 seedlots were distributed to researchers (Gunn & Midgley 1991). The field collections provided information on the natural distribution and ecology of the species (Boland *et al.* 1990), and the seeds were used for genetic studies, provenance trials, physiological screening, and the establishment of seed orchards.

Provenance variation of the species was confirmed in glasshouse trials (Pinyopusarerk, Williams & Boland 1991) and through isozyme studies (Wickneswari & Norwati 1991), and the striking degree of genetic diversity has been demonstrated in field trials. In China, after two years, the fastest-growing provenance, which was from Papua New Guinea, was over 5 m tall. It was 20% taller and 42% greater in stem diameter than the local source of *A. auriculiformis* (Yang Minquan, Bai Jaiyu & Zeng Yutian 1989). The single Queensland provenance (Springvale Holding) included in this trial had the best stem form, with a high percentage of straight single-stemmed trees. Subsequent and more comprehensive trials in China and Australia have confirmed the overall superiority in stem form of the Queensland provenances. Other international trials have yet to be assessed and reported.

The best growth rates of *A. auriculiformis* are attained on deep, slightly acidic soils in the higher rainfall areas of the humid tropics. Recent trials have indicated that at least some provenances have considerable potential for growing on degraded lands. In Zimbabwe, there has been satisfactory growth on a site with low rainfall (600 mm yr^{-1}) (Gwaze 1992). In addition, relatively high levels of alkalinity have been tolerated (McKinnell & Harisetijono 1991), and there have been some promising results on sites with a low-to-moderate salinity level where seasonal waterlogging is a factor (Marcar *et al.* 1991). Preliminary physiological studies show major differences between provenances in water use efficiency, and this knowledge may provide the basis for selecting more drought-tolerant provenances or clones (K C Woo, personal communication).

Information on the reproductive biology and vegetative propagation of *A. auriculiformis* is a prerequisite to tree improvement through seed orchards, hybridisation and the multiplication of selected clones. Research in Australia, Malaysia and Thailand has provided insights into flowering, seed production, inbreeding, stem cuttings and tissue culture. The results are reported in ACIAR workshop proceedings (Turnbull 1991; Carron & Aken 1992).

Adequate nutrition is essential for optimising the early establishment and growth of trees, especially on degraded lands. It is particularly important that the gains from tree breeding are not squandered by inadequate cultural techniques. Research on the role of symbiotic micro-organisms and the application of inorganic fertilizers in the nutrition of *A. auriculiformis* has been conducted in Australia and the Philippines. Effective strains of *Rhizobium* have been isolated which have given large growth responses in the field (Dart *et al.* 1991), and mycorrhizas have been found to be beneficial in enhancing establishment and growth (De la Cruz *et al.* 1988).

This programme of research to domesticate *A. auriculiformis* stimulated the production of a comprehensive annotated bibliography on the species (Pinyopusarerk 1990), and results are being published as they become available. The research will provide a firm basis on which to improve the species' productivity and utilisation. Seed orchards have already been established in Australia (Harwood *et al.* 1991) to provide seeds for planting in Asia and elsewhere, until local seed production areas are operational.

CONCLUSIONS

Australian species have provided some of the most successful examples of domesticated trees. There is no doubt that many species with great potential for domestication around the world await discovery and development. Through training and co-operative research programmes, the Australian experience can help realise the potential of this 'bag of uncut diamonds'. The economic and social benefits of international co-ordinated approaches, as illustrated by the *A. auriculiformis* programme, to realise the potential of fast-growing, adaptable and useful tree species in tropical developing countries are likely to be very substantial. It is hoped that the international collaborative model for research developed between F/FRED, ACIAR, CSIRO and national research agencies in Asia and Africa will be applied to other potentially important tree species.

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Domestication of lesser-known species of the genus *Leucaena*

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ABSTRACT

The genus *Leucaena* (Leguminosae: Mimosoideae) is known worldwide by the cultivated and fully domesticated species *L. leucocephala* (Lam.) de Wit. It is a premier forage and fuelwood multipurpose (MPT) tree, but its acceptance is limited by factors such as its intolerance of highly acid soils and susceptibility to psyllid insects. In the genus *Leucaena* Benth. there are 15 other species, which offer solutions to these limitations. Most of these species are partly domesticated, and some have been important ethnobotanically. Two of these lesser-known species, *L. diversifolia* and *L. pallida*, and their interspecific hybrids with *L. leucocephala*, have given superior yields in international yield trials and appear to deserve wide evaluation. The domestication status and future prospects for these lesser-known species are reviewed.

Domestication of the lesser-known *Leucaena* species began in Latin America for fuelwood, food and forage, and has expanded greatly in the past three decades through genetic improvement. Germplasm collection is well advanced, with all 16 species represented by 1875 seed collections in the three major germplasm banks (University of Hawaii, Australia's Commonwealth Scientific and Industrial Research Organisation, and the UK's Oxford Forestry Institute). Most of these collections have been evaluated during the past two decades in long-term trials, and all but one of the *Leucaena* species have been hybridised experimentally in Hawaii. Of the 232 hybrid combinations tested, over half (141) produced viable seed, leading us to the view that the entire genus can serve as a germplasm resource for future genetic improvement. Several species hold direct promise for domestication as multipurpose trees for the tropics and subtropics. Eight activities that are seen to have a major influence on domestication of leucaenas are demonstration, genetic improvement, germplasm protection, yield evaluation, quality evaluation, clonal propagation, communication and large-scale seed production. An emerging international network (LEUCNET) and the journal *Leucaena Research Reports* (founded in 1980) enhance rapid exchange of knowledge and germplasm and will play significant roles in the domestication process in the future.

INTRODUCTION

The genus *Leucaena* (Leguminosae: Mimosoideae) is a richly polymorphic complex of 16 species of leguminous trees and shrubs endemic from Texas in North America to northern Peru in South America (Brewbaker 1987a, b; Brewbaker & Hutton 1979; Brewbaker & Sorensson 1990; Hughes 1989). The genus is of ethnobotanical importance as a human food in Latin America, as well as in parts of SE Asia, and the Mexican state of Oaxaca was named after it (after the Aztec word 'huaxin'). It became known internationally, however, following the apparently casual transfer of one self-pollinated variety of the species *L. leucocephala* (Lam.) de Wit subsp. *leucocephala* from Mexico to the Philippines in the 16th century. This 'common' variety (ipil-ipil, kubabul, koa haole, lamtoro) became one of the most versatile and useful nitrogen-fixing trees in tropical agroforestry. It is currently being replaced by even more vigorous arboreal types known as 'Salvador' or 'Hawaiian giants' (L. *leucocephala* subsp. *glabrata;* Brewbaker 1987b).

Domestication of a plant species normally involves adoption by growers for specific uses, and *L. leucocephala* is an example of a species where this process is well advanced. Ultimately, this process results in the careful collection, protection, characterisation, evaluation and increase of germplasm of the species (Smith *et al.* 1992). The adoption and use of a lesser-known species as a resource for genetic improvement of trees such as *L. leucocephala,* however, lead to many of the same results. Important examples include species such as the wheat relative *Triticum tauschii* (*Aegilops squarrosa*), the barley relative *Hordeum spontaneum,* and the sugarcane relative *Saccharum spontaneum.* In the genus *Leucaena,* opportunities exist for the direct domestication of a few species. However, as reviewed here, the opportunities for use of *Leucaena* species are even greater through hybridisation and genetic transformation. These opportunities for both direct and indirect use have prompted the collection, evaluation and hybridisation of all lesser-known species in the genus. This paper considers the status of domestication of these species and the processes that may play significant roles in their further domestication.

COLLECTION AND EVALUATION OF *LEUCAENA* GERMPLASM

There are three major world collections of *Leucaena* germplasm, held respectively by the University of Hawaii (UH), the Oxford Forestry Institute (OFI) and the Commonwealth Scientific and Industrial Research Organisation of Australia (CSIRO). Together, these include about 1875 accessions, including duplicates, and at least half have been increased by seed production. Table 1 gives details for the 16 *Leucaena* spp. Domestication status (DomSt) is indexed on a 1–5 scale (1 high, 5 low), and information is summarised on botany, forage biomass and other traits. Botanical descriptions of all taxa are given in Appendix 1. Passport data on these accessions are available from the respective institutions.

All 967 accessions in the UH collection (Table 1) have been grown and evaluated. They represent 15 species, and slightly over half are of *L. leucocephala*. Most of these accessions were collected during botanical expeditions into Latin America by the senior author and colleagues. Major expeditions occurred in 1967, in 1978 (with A J Oakes, Germplasm Resources Center, USDA), in 1985 (under support of the International Bureau of Plant Germplasm Resources (IBPGR) with S Zarate, R Van Den Beldt, C Sorensson and N Glover), and in 1988 (with C Hughes and C Sorensson). The UH collection also includes trees obtained from CSIRO (42 lines) and OFI (23). Cultivar K8 was released in 1968 and an accession collected in 1978; *L. leucocephala* K636 (PI 443740) is being submitted for release in 1993.

CSIRO's collection of 815 accessions (Table 1) includes many from R Reid's botanical expeditions between 1979 and 1981 (adding 183 new accessions, mostly of lesser-known species) and in 1985. Two superior lines from these collections are *L. diversifolia* CPI46568 (a Guatemalan diploid, = K749) and *L. pallida* CPI 84581 (= K748). Most individual accessions in the UH and CSIRO collections are composed of seeds bulked from several trees, although about 25% of the *L. diversifolia* (tetraploid) and *L. leucocephala* accessions were from individual elite trees (both taxa are self-pollinating). The CSIRO collection also includes trees obtained from UH (23 lines) and other institutions.

OFI has conducted Latin American expeditions for woody legumes since the mid-1980s, largely under C Hughes (Hughes 1991a). The OFI collections are provenances based on seed composited from trees harvested separately at each site. The 93 provenances (Table 1) represent 991 half-sib families, collected in adequate quantity for extensive field evaluations and selection. Initial provenance evaluations (Stewart, Dunsdon & Hughes 1991) identified two taxa that have attracted interest in Central America, *L. salvadorensis* and *L. shannonii* subsp. *magnifica*.

The first *Leucaena* evaluation in Hawaii was planted in 1963 at the Waimanalo Research Station (sea level, 21.2°N 157.5°W) and the 86 accessions (numbered K1–K86) included four species (Gonzalez, Brewbaker & Hamill 1967). Subsequent Waimanalo trials were planted in 1966 (K87–K112), 1971 (K113–K338), 1978 (K339–K600), 1979 (K1–K316), 1980 (K317–K678), 1983 (K682–K695), 1985 (K742–K893) and 1990 (K903–K996). Seeds were freely distributed by

Table 1. Domestication status and descriptive data for 16 *Leucaena* species

	Domestication			Psyllid	Elevation	Mature		No. of lines[2]		
Species	status[1]	$2n$	Biomass	tolerance	range (m)	Height (m)	Dbh (cm)	UH	CSIRO	OFI
L. collinsii	3	52,56	Med	High	400–800	15	20	37	10	5 (113)[3]
L. cuspidata	5	–	V.low	–	1800–2000	5	5	–	2	2 (2)
L. diversifolia	3	52	High	High	700–2500	17	17	76	16	12 (80)
L. diversifolia	2	104	High	Med	700–1500	20	30	42	11	7 (88)
L. esculenta	2	52	Med	High	700–2000	15	27	55	13	3 (48)
L. sp. 'glossy'	4	112	V.low	Med	1900–2400	7	15	2	4	5 (5)
L. greggii	5	56	Low	Med	1200–1800	7	13	32	9	3 (50)
L. lanceolata	4	52	Med	Low	0–800	13	25	47	41	7 (83)
L. leucocephala	1	104	High	Low	0–900	20	40	541	590	19 (78)
L. macrophylla	4	52	Low	Med	400–1500	8	13	17	19	4 (30)
L. multicapitula	5	52?	Med	Low	0–200	17	30	3	–	2 (20)
L. pallida	2	104	High	High	1500–2100	13	15	20	15	6 (50)
L. pulverulenta	3	56	Med	Low	0–1500	20	35	18	45	3 (33)
L. retusa	4	56	Low	High	500–1400	5	5	18	13	1 (10)
L. salvadorensis	4	56	Med	Med	400–700	15	30	3	–	6 (123)
L. shannonii	4	52,56	Med	Med	0–900	15	30	33	12	6 (136)
L. trichodes	5	52	Low	Low	0–600	12	17	23	15	2 (50)
Total								967	815	93 (991)

[1] Rated on a 1–5 scale (1 = fully domesticated).

[2] UH, University of Hawaii; CSIRO, Commonwealth Scientific and Industrial Research Organisation; OFI, Oxford Forestry Forestry Institute

[3] Numbers in parentheses are of half-sib families

UH and the Nitrogen Fixing Tree Association, and several species were entered into international *Leucaena* psyllid trials (Glover 1988). Most of these trials were designed with small plots of 14–20 trees planted at 1 m x 1.5 m spacing, and maintained for at least six years. About half of the 15 species were also tested after 1980 at high-elevation sites on Haleakala, Maui (850 m) and Mealani, Hawaii (900 m). Prior to 1986, 12 species had been field-tested extensively in Hawaii, leading us to identify them as valid species; most of the 40 other published epithets in the genus were identified as synonyms (Brewbaker 1987a). Subsequent field expeditions have led to recognition of four additional taxa, namely *L. cuspidata, L. multicapitula, L. salvadorensis* and the as-yet unpublished polyploid *L.* sp. 'glossy' (see Appendix 1).

The CSIRO collections were initiated in the 1950s, but the entire collection was first planted out in 1978 at the Lansdown Research Station near Townsville, Queensland (sea level, 19.2°N, 146.5°W), and characterised by Bray (1984). Subsequent trials were established at five sites in Queensland (Bray *et al.* 1988) and were managed for the identification of superior forage types. Initial field evaluations of many OFI provenances were made in collaboration with two Honduran forestry agencies at Comayagua, Honduras (500 m, 14.3°N, 87.4°W) (Hawkins & Ochoa 1991; Stewart *et al.* 1991), and *L. salvadorensis* has recently been grown for seed production and evaluation in several Central American countries.

Many germplasm collections held internationally are dominated by the cultivar 'common' of *L. leucocephala* (subsp. *leucocephala*) that appears to lack any significant genetic variability (W Sun, University of Hawaii, unpublished). Collections that include significant resources of lesser-known *Leucaena* spp. include those of Centro Internacional de Agricultura Tropical in Colombia, the International Center for Research in Agroforestry in Kenya, the International Institute for Tropical Agriculture in Nigeria, the International Livestock Center for Africa in Ethiopia, the Taiwan Forest Research Institute, and the Universidad Nuevo Leon in NE Mexico. Additional lines are maintained at a state research centre in the Yucatan, Mexico, the National University of Mexico in Mexico City, the Escuela Agricultura Panamericana in Honduras, the Sta. Ana Research Station in El Salvador and the University of the Philippines at Los Baños. All of these field trials have been observed by the senior author.

DOMESTICATION STATUS OF *LEUCAENA* SPECIES

The 16 *Leucaena* species are classified in five groups in Table 1 on the basis of their current domestication status. Full domestication (Class 1) characterises only *L. leucocephala*, which is widely planted and utilised throughout the tropics. Species placed in Class 2 include *L. esculenta* and *L. pallida* that serve as human food in Mexico (Zarate 1982), and *L. diversifolia* that is now planted in many places in the tropics and subtropics. Most species are viewed as intermediate in domestication (Table 1), while four species are considered undomesticated (Class 5). All leucaenas appear to provide attractive browse forage and fuelwood, and they are normally known by name to indigenous peoples. All are nitrogen-fixing (*Bradyrhizobium* spp.), mycorrhizal (vesicular–arbuscular), and of potential importance as companion trees in the reforestation and stabilisation of degraded lands throughout the tropics.

The current status of domestication in *Leucaena* spp. (Table 1) does not necessarily reflect our perception of the potential for full domestication, as can be seen for individual species in Appendix 1. The most promising are *L. diversifolia* and *L. pallida*. The tetraploid form of *L. diversifolia* is a self-pollinator that grows into a columnar tree at cooler sites where soils can be more acidic than those preferred by *L. leucocephala* (Hutton 1990; Bray & Sorensson 1992). It is being planted in the highlands of E Africa and S Asia. The self-sterile tetraploid, *L. pallida*, and its hybrids have shown superior forage performance when under heavy psyllid pressure. Most diploid species are rated less highly for domestication potential.

INTERSPECIFIC HYBRIDISATION

Interspecific hybridisation of leucaenas in regions of endemism has been precluded by the ecological and geographical separation that characterises most species, and possibly reinforced by floral preferences of pollinating insects and differences in the timing and lengths of flowering seasons (Sorensson 1993). Hybrid swarms are unknown *in situ* and the few hybrids found appear to reflect agricultural movement of *L. leucocephala*, the suspected pollen parent of most natural hybrids. Thus, domestication of lesser-known species cannot depend on naturally occurring hybrids.

Interspecific hybridisation among *Leucaena* species became a major thrust of research in Hawaii soon after it was started by Gonzalez *et al.* (1967), and continued under Pan and Brewbaker (1988); Sorensson (1993) intercrossed 15 species in practically all combinations (232 of 240 possible matings of a 16 x 16 matrix). Over 75% of these crosses have been partially or fully seed-fertile, and 99 hybrids have been grown from the 141 combinations producing viable seed. Several hybrids are promising for direct production, but many more appear valuable in breeding (Brewbaker & Sorensson 1990). These results lead us to the view that the entire genus provides a genetic base for future improvement research, and suggest that all species warrant further collection, protection and evaluation.

Most *Leucaena* breeding is based at present on tetraploid species (Table 1) and their interspecific hybrids, often with impressive growth and adaptability (Brewbaker & Sorensson 1990). *Leucaena pallida* has been the major source for psyllid resistance and low seediness (owing to its self-sterility), and tetraploid *L. diversifolia* for cold tolerance. Triploid hybrids between tetraploid and diploid taxa have been of particular interest, and were studied by Hutton (1981, 1990) as a genetic source of acid soil tolerance for *L. leucocephala.* Many triploids (Sorensson 1993) were fully seedless, a trait of great interest in improving acceptability for reforestation and wood yields (Brewbaker & Sorensson 1990). Many hybrids are interesting for gene introgression into *L. leucocephala,* a process that has been accelerated by the use of unreduced gametes from diploid parents (Sorensson 1988). Colchicine-induced polyploids also hold promise for the conversion of superior diploids to the tetraploid level, facilitating gene transfer and the synthesis of new amphidiploids.

GENETIC EXPLOITATION OF LESSER-KNOWN SPECIES

Leucaena is a richly polymorphic genus that displays extensive variability for nearly all important traits under study (Brewbaker 1987b). However, much of this genetic polymorphism resides in lesser-known species. Full exploitation of the genus is thus dependent on the successful management of these taxa. Important traits of lesser-known taxa include the following.

- *Psyllid tolerance.* Well over 50% of the *Leucaena* species have tolerance or resistance to psyllids (Homoptera: *Heteropsylla cubana*) (Table 1) (Sorensson & Brewbaker 1987). *Leucaena pallida* has been used to incorporate resistance into *L. leucocephala.*
- *Cold tolerance.* Most species are of highland or subtropical origin (Table 1) and exhibit better tolerance of cool weather than lowland-adapted *L. leucocephala.* Species that have been used for this purpose include *L. diversifolia* (Bray & Sorensson 1992), *L. pallida,* and *L. pulverulenta* (Gonzalez *et al.* 1967). Other species of promise include frost-tolerant taxa (next section), the tetraploid *L.* sp. 'glossy' and three diploids: *L. cuspidata, L. esculenta* and *L. greggii.*
- *Frost tolerance. Leucaena retusa* is well known for frost resistance and *L. pulverulenta* for partial resistance. Ongoing trials in New Mexico and Texas, USA, have shown that *L. greggii* is also frost-tolerant, as *L. cuspidata* may be.
- *Acid soil tolerance.* A highly sought trait in leucaenas internationally is tolerance of soil acidity (Hutton 1981, 1990; Oakes & Foy 1984). Diploid *L. diversifolia* provided useful tolerance genes in Hutton's programme, and other species that looked promising to him included *L. esculenta, L. pallida* and *L. shannonii.*
- *Mimosine content and forage quality.* About half of the species contain less of the toxic amino-acid, mimosine, than *L. leucocephala,* some with about 75% less. Species known to be very low in mimosine are *L. diversifolia, L. esculenta* and *L. pulverulenta* (Bray 1983); others that are quite low include *L. collinsii* and *L. pallida* (Brewbaker 1987b). Mimosine is fully degraded by a bacterium *Synergistes jonesii* in ruminants, and therefore is considered a problem only for non-ruminants, as are the dihydroxypyridine breakdown products. Nutritional quality as measured by intake and digestibility is generally high but varies widely among the species (Austin *et al.* 1991).
- *Wood density and lumber quality.* Leucaenas have fairly dense heartwood, with specific gravities ranging from 0.45 to 0.85 (Brewbaker 1987b). The 'leadtrees' *L. pulverulenta* and *L. retusa* have high wood density (the former was widely used in railway construction). *Leucaena salvadorensis* ('sepia') is valued in Central America as poles for its high density and dark-coloured heartwood (Hughes 1988), as are some *L. collinsii* populations.
- *Drought tolerance.* Most species tolerate drought very well, although none has been shown conclusively to tolerate drought better than *L. leucocephala.* Following one of the worst extended droughts on record, the CSIRO germplasm collection at the Lansdown Station in N Queensland was observed by the authors, and some lines of *L. lanceolata* looked superior in drought tolerance. This species colonises some very arid Mexican coastal soils. Other species occurring in arid regions include *L. collinsii, L. greggii, L. macrophylla, L. retusa, L. salvadorensis* and *L. trichodes.*
- *Genetic diversity of tree form.* The genus *Leucaena* is distinguished by unique, heritable intraspecific diversity in tree form. Many species range in habit from forest ideotypes (tall, columnar, clear bole) to shrubs or spreading small trees, and all are highly tolerant of coppicing, providing growers with great flexibility in sustainable

agricultural systems (Brewbaker & Shelton 1993). The variation is well known in *L. leucocephala,* as it distinguishes 'common' cultivars from 'giant' or 'Salvador' types. Similar variation occurs in *L. diversifolia, L. lanceolata* and *L. pallida. Leucaena trichodes* (small tree) and *L. multicapitula* (arboreal) are related taxa that also fit this scenario.

- *Waterlogging tolerance.* Species such as *L. diversifolia* and *L. multicapitula* occur in high-rainfall areas and need more thorough evaluation for waterlogging tolerance. The diploid *L. diversifolia,* such as those naturalised in Indonesia, should also be tested.

DOMESTICATION PROCESSES

Eight activities that appear especially important in domesticating the lesser-known species of *Leucaena* and similar multipurpose trees are described below.

i. *Demonstration.* Demonstration is a *sine qua non* to promoting interest in lesser-known tree species. After three decades of research on *Leucaena,* Brewbaker (1987b) concluded that most people have no real understanding of their growth capability. Under most favourable conditions, replicated yields achieved by leucaenas include 100 tonnes of total fresh biomass ha^{-1} yr^{-1} and 50 tonnes edible biomass ha^{-1} yr^{-1}. These extraordinary values are not easy to grasp, and the average grower must be shown to believe. Such demonstrations are often under-financed and mismanaged, and are most effective when treated with care similar to that given to a high-value fruit tree.

ii. *Genetic improvement.* Superior but unselected germplasm will rarely meet growers' demands in the 21st century. Superior F_1 species hybrids are known that greatly outyield *L. leucocephala* var. Cunningham and K8, two great cultivars of the 1970s, when grown for forage under psyllid pressure. Major advances are occurring with simple recurrent selection in broad-based germplasm. Although breeding is often a slow process, it must be emphasised that the generation time of most leucaenas is about 18 months, and large populations can be screened at the densities common for forage production (75 000–150 000 per hectare). Without genetic improvement it is unlikely that any of the self-sterile species can be advanced in domestication status.

iii. *Germplasm protection.* Almost all natural populations of leucaenas in Latin America are under continuing pressures from man and grazing animals. Some *in situ* germplasm protection occurs for this genus in national parks and preserves, notably in Costa Rica, Honduras and Panama, but more is needed. The option of developing *ex situ* germplasm conservation deserves consideration.

iv. *Yield evaluation.* Most research trials have involved only *L. leucocephala,* and yield evaluations of other species and provenances in diverse agroecosystems are thus of high priority. Acid soil tolerance provides a useful example of the need for thorough characterisation of lesser-known species in soils that vary in pH and in concentrations and forms of aluminium, manganese, calcium and phosphorus. Progress in pest resistance breeding is only likely to occur when evaluations are made under heavy and uniform infestations. Much can be learned even from two-year trials as small as 0.05 ha (adequate for a fully replicated design with 20 entries, three replications, and rows 5 m long). Seedling selection may be effective for some traits (Sorensson 1993).

v. *Quality evaluation.* Domestication leads to plants tailored to specific uses and management; this will not occur in *Leucaena* without careful evaluations of quality. Quality components needing study are those of forage (eg intake, digestibility, tannins, lignins, saponins, mimosine, protein) and of wood (eg density, fibre length, wood colour, ease of pulping). Quality evaluation and breeding research must be closely linked, to ensure that yield improvement does not occur at the expense of quality.

vi. *Vegetative propagation of specific genotypes.* It is routine to find superior trees among breeding populations of outcrossed *Leucaena* spp. Rapid genetic gains comparable to those in *Pinus* and *Eucalyptus* can be predicted using quick and reliable clonal propagation methods. With such methods, cloning of seedless triploid or aneuploid hybrids could emerge as a predominant force in domestication in the genus (Brewbaker & Sorensson 1990). Propagation *in vitro* holds promise, but explants have been difficult to sterilise and shoots grown from callus often fail to root or to survive transplanting. Some grafting techniques are used regularly for propagating seedless aneuploids in Indonesian coffee orchards, but it is probable that grafting will not meet commercial-scale propagation needs. Studies in Taiwan, India and Hawaii indicate that certain *Leucaena* genotypes can be rooted quickly and reliably from semi-woody cuttings, but genetic selection for this trait may be essential.

vii. *Communication.* The distances involved among *Leucaena* workers, many of them in developing countries, often prevent personal exchange of information. Effective written communication is essential. One journal has been devoted since 1980 to the genus, namely *Leucaena Research Reports* (LRR). The 13 volumes (1440 pp) have been sent to about 1500 associates of the Nitrogen Fixing Tree Association (NFTA: Paia, Maui, Hawaii). The LRR has been a favoured outlet for reports on efforts to domesticate lesser-known taxa, although many important trials are unreported to the international community.

viii. *Large-scale seed production.* Seed increase of the self-pollinating polyploid leucaenas presents no major obstacles. However, seed production from self-sterile parents of seedless hybrids and synthetics requires further reproductive and developmental studies, especially where parents must be cloned and flowering dates differ. Onset of flowering may be controllable by managing irrigation water, coppicing, or growth hormones. The production of seeds from different hybrids in the same orchard is possible, reducing costs to seedsmen (Sorensson 1993).

CONCLUSIONS

Domestication of leucaenas is viewed here as a process that must involve demonstration, genetic improvement, germplasm protection, yield evaluation, quality evaluation, clonal propagation, communication and seed production of released cultivars. An international *Leucaena* research and development network (LEUCNET) has been proposed by the Universities of Hawaii and Queensland, with an initial planning workshop to be held in 1994. The network would seek to co-ordinate diverse teams of international scientists and streamline the activities essential to domestication.

The genus *Leucaena* exemplifies the diverse domestication processes affecting tropical trees. Prior to the 1500s, domestication was based on food use by indigenous Americans, notably of *L. leucocephala* (Gomez-Pompa 1987) and the large-seeded *L. esculenta* (Zarate 1982). During the 16th century, a single genetically uniform line of *L. leucocephala* (cv Common) was brought to SE Asia and dispersed worldwide. Domestication of giant forms of *L. leucocephala* in the late 1900s greatly expanded the acreage under *Leucaena,* and spurred interest in agroforestry systems such as alley farming. The international movement of the psyllid since 1984 has brought special attention to other species of the genus. Interest in domesticating lesser-known species of *Leucaena* started with Dutch efforts in the 1920s to use *L. diversifolia* and *L. pulverulenta* as shade in highland Indonesian plantations. Progress in domestication has expanded with the collection, characterisation, and yield evaluation of many species and interspecific hybrids. All studies confirm the superiority of the genus as a woody legume for forage and green manure use and fully justify future research to domesticate these lesser-known species (Brewbaker 1987b).

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APPENDIX

Botanical description of the 16 *Leucaena* species

The 16 recognised *Leucaena* species are discussed below in alphabetical order with a brief description of their botany, distribution, uses and potential for domestication (see also Table 1).

1 ***Leucaena collinsii* Britton and Rose** (COLL), in *North American Flora*, **23** (2), 126. 1928. Type: Collins & Doyle 157, Tuxtla Gutierrez, Chiapas, Mexico. 1907. Field variants include a southern population in Guatemala, subsp. *zacapana*, and a northern population with larger trees and flowers (to 13 m) in Chiapas, Mexico, subsp. *collinsii* (Hughes 1991b). This species is a hardy spreading tree of dry hilly midlands with a distinctive shape like *Ulmus* spp. Leaves are large, to 20 cm, with 8–15 pairs of pinnae and small (3–7 mm) leaflets. Flowering heads are small, to 18 mm, and white, pods 16–20 mm x 12–18 cm, seeds 6–8 mm. It is self-sterile but produces heavy pod set under most conditions, often with seedless pods that ripen very slowly, about 300 days in Waimanalo. It is often found dominating the calcareous soils at low to mid-elevations (eg 300–800 m in the Grijalva and Motagua River basins). *L. collinsii* is of some local importance for shade and is lopped for fuel. The wood is dense and used for small construction, but it is not widely fed to animals. Its high psyllid and drought tolerance make this species valuable for gene transfer, while domestication *per se* may offer little.

2 ***Leucaena cuspidata* Standley** (CUSP), in *Contributions from the United States National Herbarium*, **20**, 189, 1919. Type: USNH Purpus 5183, San Luis Potosi, Mexico. Little is known of this apparently rare and endangered species. Morphologically it resembles *L. greggii*, a small multistemmed shrub (to 5 m height), native to high-elevation areas that may receive frost, yellow coloration in the inflorescence, long peduncles (to 3.5 cm), strikingly long stipules (to 4 mm), long and narrow woody pods, squarish seeds and small coriaceous leaflets. Its inflorescence is smaller and lighter yellow than that of *L. greggii*, however, and its leaflets are cuspidately tipped, hence its name. Like *L. greggii*, it occurs in Nuevo Leon, where the two species are separated geographically by the large San Luis Potosi valley which lies west of the Sierra Madre Oriental. *L. cuspidata* also extends south into Hidalgo, also at high elevations (about 2000 m), and these populations may be morphologically distinct (Zarate 1982, 1984). It is summer-flowering and autumn-seeding. It appears to have no indigenous use.

3 ***Leucaena diversifolia* (Schlecht.) Benth.** (DIV2, DIV4), in *Journal of Botany*, **4**, 417, 1842. Type: Shiede, Jalapa, Veracruz, Mexico. This species is widespread, and occurs as two distinct subspecies *diversifolia* (2*n*=104) and *trichandra* (2*n*=2) (Bray & Sorensson 1992). The type specimen was of subspecies *diversifolia*. It occurs as highly variable

shrubs or trees, 5–18 m in height, with a distinctive dark bark. Leaflets are very small (3–6 mm) on leaves (8–18 cm) with 15–30 pairs of pinnae. The flowers are conspicuously reddish, small (8–12 mm) in diploid *L. diversifolia*, larger (to 15 mm) in tetraploid *L. diversifolia*. Pods are reddish, fairly small (1–1.5 cm x 12–18 cm), with small dark seeds (to 5 mm). The diploid subspecies is self-incompatible and morphologically diverse, while the tetraploid subspecies is self-compatible, with limited outcrossing. Several published taxa are considered synonyms (Brewbaker 1987a). The diploids range from Oaxaca in Mexico south to Nicaragua between 800 m and 2000 m, while the tetraploid is largely found in Veracruz, Mexico. The diploids appear less restricted to calcareous sites, and have been used by Hutton (1981, 1990) in breeding acid tolerance. *Leucaena diversifolia* trees are lopped for fuelwood and occasionally grown or protected for shade (coffee plantations) and in fencerows. Yield trials under cooler temperatures in Queensland, Hawaii and Nepal show this species and its hybrids to be much superior to *L. leucocephala* (Bray & Sorensson 1992).

4 ***Leucaena esculenta* (Moc. and Sesse) Bentham** (ESCU), in *Transactions of the Linnaean Society of London*, **30**, 442, 1875, as *Acacia esculenta* Moc. and Sesse, in *De Candolle*, **2**, 470, 1825; no type specimen existed of this taxon, but type locality was given as 'Mexico'. Subspecific variation includes a rounded-branch variant at lower elevations in W Mexico (subsp. *matudae*). No synonyms occur, although *L. pallida* has been incorrectly referred to it. *Leucaena esculenta* is an attractive tree that is easily distinguished from all other species. It is large, to 20 m in height, with basal diameter to 60 cm and a distinctively thick, corky, whitish bark marked by horizontal scars on older trees. Branches are sharply angulate. Leaves are very large (to 40 cm) with large numbers (to >12 000) of tiny leaflets (3–4 mm), on 30–50 pairs of pinnae. Flowers are large and white, while pods are reddish and among the largest of the genus (to 2 cm x 25 cm) and seeds are large and squarish (7–9 mm). Flowering occurs in the autumn. This species is distributed widely in the midlands of Mexico. The large pods are marketed at physiological maturity and normally eaten green, and are of ethnobotanical importance (Zarate 1982), although the mimosine and dihydroxypyridine content will preclude frequent cultivation for this use. Trees are occasionally planted on farms or used in agroforestry cropping systems with interplanted crops. Establishment is rapid and yields are high in forage trials, but IVDMD digestibility values for this species are the lowest among leucaenas (Austin *et al.* 1991). The species is virtually immune to the leucaena psyllid (Table 1). Gum exudation from some hybrids has been of interest because the gum resembles gum arabic (Brewbaker & Sorensson 1990). It is a most interesting species as a genetic resource.

5 ***Leucaena* sp.** 'glossy' (GLOS) (syns. L. *cuspidata* subsp. *compactiflora*, *'confertiflora'*). This small tree, common to San Pedro Chapulco and other mountain villages in Puebla and Oaxaca, Mexico, was treated as *L. cuspidata* subsp. *compactiflora* var. *adenostricta* by Zarate (1984), but should be treated under a new epithet. It was shown by Sorensson (1989) to be a self-compatible polyploid with 112 somatic chromosomes (confirmed by R A Bray, unpublished) and occurs south of the volcanic axis, whereas *L. cuspidata* occurs north of it. The inflorescence is reddish, small (about 1.5 cm diameter) and open, containing only about 75 florets (comparable to *L. pulverulenta*). Leaves are glossy, hence the temporary name *L.* sp. 'glossy'. Leaflets are small and rounded, and the leaf gland is subcylindrical. Zarate (1984) noted that it was occasionally cultivated and that its pods were sold in regional markets by villagers.

6 ***Leucaena greggii* S. Watson** (GREG), in *Proceedings of the American Academy of Arts and Sciences*, New Series XV, Whole Series XXIII (May 1887–May 1888). Series XVIII. *Contributions to American Botany*, 249–272. Type USNH 2636386. A small tree of the midlands of NE Mexico extending from Linares, Nuevo Leon, into the hills westward and northwards to Coahuila. Leaflets are finely divided, about the size of *L. leucocephala*, but waxy and coriaceous. Leaves have conspicuous subcylindrical glands at the base of each pinna, as in *L. retusa*. Flower heads are golden in colour, on long peduncles to 6 cm long. Pods are narrow, long and woody, and seeds are squarish, as in *L. retusa*. It withstands occasional frosts and extended dry seasons. Roadside trees are regularly lopped for cut-and-carry fodder for goats, and provenance evaluations for use in reforestation are ongoing in NW Mexico.

7 ***Leucaena lanceolata* S. Watson** (LANC), in *Proceedings of the American Academy of Arts and Sciences*, **21**, 427, 1886. Type: E. Palmer 6, Batopilas, Chihuahua, Mexico, 1885. Evident subspecific variation includes a widespread shrubby phenotype and two

populations of arboreal variants in Oaxaca, one that has been treated as subsp. *sousae* (eg K952). This species has the widest distribution of any species in the genus, from Sonora to Chiapas, Mexico, and is taxonomically complex with a number of synonyms. It commonly occurs as a shrub in dry, often calcareous lowlands, normally growing to 7 m, although the arboreal form reaches 16 m. Leaves range from 10 to 25 cm, with only 3–6 pairs of pinnae and 6–7 pairs of large (2–4 cm) leaflets. Flower heads are large (to 25 mm), white and heavily scented. Pods are 16–25 mm wide and 15–30 cm long, with seeds like those of *L. leucocephala* (a probable amphiploid derivative of *L. lanceolata*). It is used for forage and fuelwood but seems to be planted. Some accessions show unusual drought tolerance in Australia, and high growth rates. This species could be of great interest for drought-prone areas.

8 ***Leucaena leucocephala* (Lam.) de Wit** (LEUC), a taxon fully described in the literature (Brewbaker & Sorensson 1989; Smith *et al.* 1992).

9 ***Leucaena macrophylla* Benth.** (MACR), in *Botany of the Voyage of HMS Sulphur. . . ,* **90**, 1844. Type: Hinds 1841, Acapulco, Mexico. Hughes (1991a) identified two subspecies, *macrophylla and nelsonii.* This is a small tree (4–8 m) of dry midlands in W Mexico and has very large leaflets (30–70 mm) in leaves ranging to 25 cm, with only 2–3 pairs of pinnae. The white flower heads are small (9–14 mm) and dense, and pods are 1.5 cm x 15–20 cm, with seeds of 7–8 mm. Flowering is late and synchronous with *L. esculenta. Leucaena macrophylla* occurs from coast to dry midlands and from Oaxaca north to Sinaloa in W Mexico. Pods are seasonally marketed as 'guaje verde' in a manner similar to that of *L. esculenta,* and trees are protected but not commonly planted.

10 ***Leucaena multicapitula* Schery** (MULT) (syn. *L. multicapitulata*), in *Annals of the Missouri Botanical Garden,* **37**, 303–304, 1950. Type: P. White 135, Canal-zone, Miraflores, Panama. This species is related to *L. macrophylla* and *L. trichodes,* all with large leaflets, small inflorescences, and few seeds per pod. *Leucaena multicapitula* is distinguished by its tall arboreal habit (to 20 m), by a distinct geographical distribution in Panama and Costa Rica, and by semi-paniculate inflorescences, broad cupulate petiolar glands and 16-grain polyad pollen (Sorensson 1993). The inflorescence has relatively few florets (about 50–70) and is quite fragrant. It is autumn-flowering and winter-seeding. Pods are short (about 12 cm) and wide (to 3 cm). This fine tree is found in high-rainfall areas, and has much promise for domestication (Robustiano & Sorensson 1987).

11 ***Leucaena pallida* Britton & Rose** (PALL), in *North American Flora,* **23**, 126–127, 1928. Type: Rose 2359, Huejuquilla, Jalisco, Mexico, 1897. Several taxa are synonymised with this species, including four designated by Britton and Rose and the *L. esculenta* subsp. *paniculata* of Zarate (1984). Shrubby and arboreal forms segregate in this species, and are found in dry highlands in Mexico. It was shown by Pan and Brewbaker (1988) to be a probable amphidiploid hybrid of *L. esculenta* and *L. diversifolia,* and closely resembles the diploid hybrid of those species (Sorensson 1993). Leaves range from 15 cm to 40 cm, with 10–20 pairs of pinnae. Flower heads are large (to 20 mm), pinkish and with many florets. Pods are variably long (10–18 cm) and wide (12–16 mm). It is sporadic in the central midlands of Mexico as a backyard or fencerow tree coppiced for fuel, fodder or food. It is of great importance for the genetic improvement of other species in psyllid tolerance and rapid seedling growth.

12 ***Leucaena pulverulenta* (Schlecht.) Bentham** (PULV), in *Journal of Botany,* **4**, 417, 1842. Basionym: *Acacia pulverulenta* Schlecht., *Linnaea,* **12**, 571. Type: Schiede, Berlandier 288, San Antonio, Veracruz, Mexico. This distinctive tall tree has no synonyms. It grows to 18 m with basal diameters reported >50 cm. Bark and leaves are greyish, leaves ranging from 15 cm to 25 cm with 10–20 pairs of pinnae and 15–30 pairs of small (3–6 mm) leaflets. Flower heads are small and open, white, with few (50–75) florets. *L. pulverulenta* is distributed on dry, often calcareous soils, from Veracruz north into S Texas, where frost often reduces the tree height. It is known as 'tepeguaje' or 'leadtree', and is widely retained and protected through its range as a shade and fuelwood tree, but rarely planted. Trees are often found in fencerows and are routinely lopped for fuel. Fast-growing hybrids (2*n*=80) with *L. leucocephala* were produced in Hawaii (Gonzalez *et al.* 1967) and even named in Indonesia, from which sterile segregants were used as coffee shade. This species deserves great interest as a domesticate.

13 ***Leucaena retusa* Bentham, ex Gray** (RETU), in *Plantae Wrightianae Texano-Neo-Medicanae,* **1**, 64, 1852. Type: C. Wright 171, Rio Nueces, Texas, 1849. This is a distinctive, yellow-flowered, subtemperate shrub. It grows to 5 m in height, and leaves range up to 15 cm, having only 3–4 pairs of pinnae and 4–8 pairs of large (15–30 mm)

reticulated leaflets. Blooming heads are attractively golden, ranging to 3 cm, with 150–200 florets, while the pods are narrow, 10 mm, and long (20–25 cm). It occurs in SW Texas and NE Mexico (Coahuila, Chihuahua) and favours limestone soils. It is slow to nodulate, possibly with unique rhizobial affinities. It is the most cold-tolerant species of the genus, surviving snow and heavy frosts and ranging to 2000 m elevation. *Leucaena retusa* is known as 'littleleaf leadtree', and is grown as an ornamental. It is often browsed by cattle and goats. It is probably the best genetic source of frost tolerance genes; it has high drought and heat tolerance and high-density wood that encourage further domestication.

14 ***Leucaena salvadorensis* Standley ex Britton & Rose** (SALV), in *North American Flora,* **23**, 125, 1928; Type: Calderon 2031, Jocoro, Morazan, Salvador, 1924. Hughes (1988) rediscovered and developed major collections of this species. It is an erect and tall tree (that can exceed 18 m) with leaves ranging from 16 cm to 24 cm, with 4–7 pairs of pinnae and 15–25 pairs of long thin leaflets (4 mm x 20 mm). The white flower heads are 12–22 mm in diameter, and the pods are large and heavily thickened, 18–30 mm x 15–22 cm. Pod ripening is extremely slow (as in *L. collinsii*). It is sparsely distributed from Salvador into Nicaragua in dry foothills, and is known by the common name 'sepia' in reference to the dense, dark wood. It makes straight poles valued in house construction, and is lopped for fuelwood. Foliage is relatively sparse but browsed by animals. The species has been promoted by OFI for greater domestic use in Central America.

15 ***Leucaena shannonii* Donn. Smith** (SHAN), in *Botanical Gazette,* **57**, 419, 1914. Type: Shannon 5032, Cuscutlan, Cojutepeque, Salvador, 1892. No synonyms. Hughes (1991b) formally described and named two subspecies, *shanonnii* (shrubby, to 8 m) and *magnifica* (arboreal, to 14 m), and corrected the specific epithet from the collector's *'shannoni'* to conform to taxonomic traditions. The two subspecies mimic the 'common' and 'giant' forms of several other species. Leaves range from 15 cm to 25 cm, with 4–5 pairs of pinnae and large leaflets (18–25 mm). Flower heads are heavily scented, white, 10–15 mm in diameter, and pods are small (1 cm x 12 cm) and usually velutinous. This is a shrub or small tree of dry, often calcareous lowlands from SE Mexico to Nicaragua, with subsp. *magnifica* as a tree in Guatemala. It serves throughout its range as a fencerow, fuelwood or shade tree and as lopped fodder. It is native in drought-prone areas, and the vigour of subsp. *magnifica* makes it attractive for breeding.

16 ***Leucaena trichodes* (Jacq.) Bentham** (TRIC), in *Journal of Botany,* **4**, 417, 1842. Type: Vienna Herb. as *'Mimosa trichodes* Jacq.' 32049, Brazil. At least five epithets are considered synonyms (Brewbaker 1987a). This small tree resembles *L. macrophylla and L. multicapitula* (Table 1), with which it is cross-fertile, but differs in several important features, including pollen (Sorensson 1993). The leaflets are very large (20–50 mm) and have 2–4 pairs of pinnae. The flower heads are white, aromatic and very small (7–12 mm), and pods are 2 cm x 10–15 cm, glabrous, with small seeds (6–7 mm). *Leucaena trichodes* colonises dry coastal areas to 300 m elevation from northern Peru through Ecuador and Colombia to Venezuela. Throughout this range it is known as a hardy fuelwood tree, but is rarely planted. Like so many *Leucaena* spp., this one is of questionable value as a domesticate except as a possible genetic reservoir.

Domestication of *Sesbania sesban* for agroforestry systems in eastern and southern Africa

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ABSTRACT

Sesbania sesban has potential for soil improvement and pole production when grown in short-rotation fallows or as scattered trees in cropland. Examples of the domestication of *S. sesban* by farmers are presented, together with research results from field trials by the International Centre for Research in Agroforestry (ICRAF). Results from two field trials in western Kenya indicated that variation in growth rate and crown form among and within provenances is considerable. Genetic gains in height growth based on progeny performance at two-location trials are reported to range from 14%, when the mean of the best ten families is used, to 61%, when the mean of the best five trees in the trial is used, for the Maseno location. Growth and reproductive phenology also displayed significant variation, offering further possibilities for genetic improvement.

Above- and below-ground characteristics of *S. sesban* which constitute an ideotype for a specific agroforestry technology are discussed, together with techniques for the grading of superior trees. Parallel research on tree genotype x *Rhizobium* strain specificities and on the rooting pattern of *S. sesban* is described.

INTRODUCTION

With the current emphasis on integrated land management practices such as social forestry and agroforestry, many hitherto 'lesser-known' (or 'Cinderella') tree and shrub species are receiving increased research attention. In the past ten years, information/data inventories, tree improvement and management research have been initiated in many parts of the world, with an emphasis on the multipurpose tree and shrub species that have the potential to provide a combination of products and services (Burley & von Carlowitz 1984; Burley 1984). Some priority multipurpose tree species for agroforestry development in humid and subhumid parts of tropical Africa that have been identified are currently the focus of research at the International Centre for Research in Agroforestry (ICRAF) (Maghembe 1989; Owino 1991).

One such species is *Sesbania sesban*, which has been shown to enhance soil fertility (Rao, Gill & Abrol 1989; Onim *et al.* 1990) when grown in short-rotation fallows. At the same time, this species provides the farmer with fodder and poles. Indeed, with the elimination of its prevalent large stem knots leading to weak poles, and problems with pests and nematodes, *S. sesban* could be an excellent species for agroforestry development in the humid and subhumid tropics of Africa. It is with this background that *S. sesban* has been identified as a priority species for ICRAF's tree improvement research programme.

ECOLOGY AND NATURAL VARIATION

Sesbania sesban (Leguminosae) is common in natural vegetation and in cultivated fields in central, eastern and southern Africa (Lewis 1988). It is a fast-growing and often heavily branched tree, which attains 3–8 m height at maturity. Actively growing parts of the stem are characteristically pinkish. It closely resembles *S. bispinosa* in gross morphology but for the pinkish stem colour. Some forms resemble the slender and sparse-foliaged *S. macrantha*.

Within natural vegetation, *S. sesban* is commonly found on sites with permanent or seasonal swamps. Over a long period of time, farmers in western Kenya have favoured *S. sesban* trees with higher growth rates and good (knot-free and straight) stems in the fallows and cultivated fields (authors' personal observation). Although the extent of genetic improvement through farmers' practices has not been analysed, this may represent an example of tree domestication by farmers.

On good sites, *S. sesban* grows about 3 m in height per annum for the first two years, after which the growth rate declines rapidly. Terminal dieback occurs at about four years of age, so the species is only briefly perennial. Plants flower and fruit at an age of two months in the nursery and three months in the field. Flowering starts shortly after the onset of the rains. In areas with two rainy seasons in a year, it flowers and sets fruit twice, coinciding with the rainy periods (Figure 1).

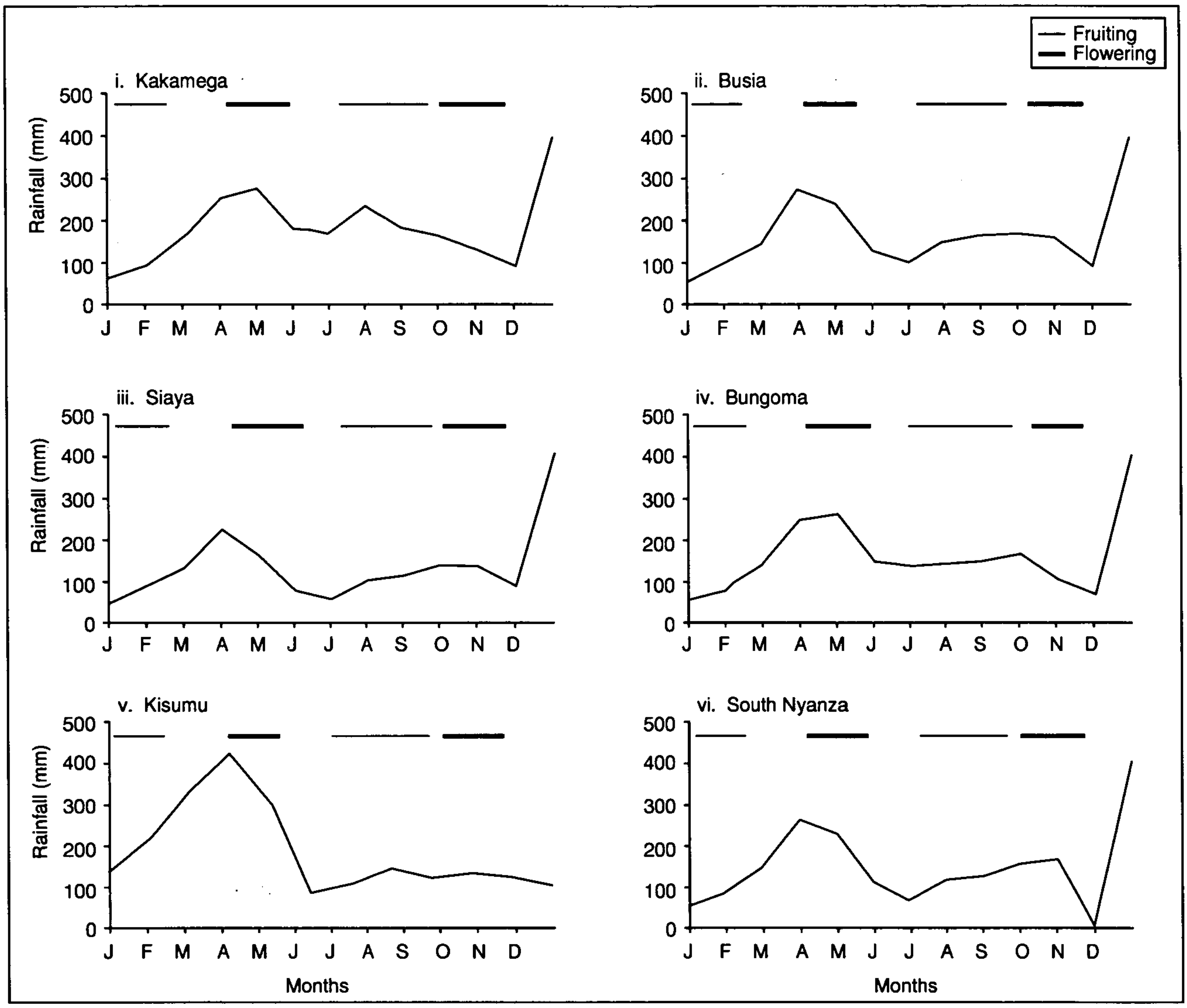

Figure 1. Flowering and fruiting calendar of *Sesbania sesban* in western Kenya, 1990. Data collected by authors during plus-tree selection in 1990; observations based on plus-trees and their neighbours (n>5 per region)

Field trials have revealed significant differences in growth rate among local landraces. An analysis of height growth of 22 half-sib families at two sites (Kisii and Maseno, Kenya) indicated that the Kisii landrace (K7 series) showed superiority at both sites, whereas the Kakamega and Kisumu landraces (K1 and K5, respectively) showed intermediate performance (Figure 2). Great variation in crown form and branching habit was also recorded among the half-sib families. The Kisii landrace was characterised by strong apical growth and limited lateral branching, whereas the Kakamega landrace was much more highly branched (Figures 3 & 4). Furthermore, early results from progeny trials indicated a strong genetic basis to the observed variation (narrow sense heritabilities of height for Maseno, Kisii and combined sites were 0.4, 0.64 and 0.52, respectively). This pronounced variation in growth rate and crown form offers an opportunity for selecting the most desirable genotypes for farmers by further genetic improvement research.

POTENTIAL OF *S. SESBAN* IN AGROFORESTRY SYSTEMS

S. sesban has greatest potential when managed in short-rotation fallows. On favourable sites, it can provide valuable poles and improve soil fertility within a period of about six months (Oduol, Akunda & Wambugu 1993). Furthermore, it is a valuable source of green manure (Evans & Rotar 1987). For example, in one experiment at Maseno in Kenya, *S. sesban* added 448 kg N ha^{-1} yr^{-1} to the soil when used as a source of green manure (Onim *et al.* 1990). Natural regeneration in cultivated fields is prevalent and the species rarely becomes a difficult weed to eradicate as farmers have relatively little trouble in removing mature trees during field preparation.

The appropriate period of tree growth in fallows or on cropland will depend on the specific combination of products and services required. For the combination of poles, fuelwood and soil fertility improvement, one to two years of tree growth would be ideal on favourable sites (Dutt & Urmilla-Jamwal 1989; Weerankoon 1989). For the combination of fuelwood and soil fertility improvement, a six-month rotation (followed by clearing and replanting) might be more appropriate (Yamoah & Getahun 1989; Rao *et al.* 1989).

TREE IMPROVEMENT RESEARCH INITIATIVES FOR *S. SESBAN*

Given the great potential of *S. sesban* for agroforestry in humid and subhumid parts of Africa, ICRAF initiated a germplasm improvement research programme for the species in 1990. The first phase of this research was the evaluation of a wide range of germplasm accessions collected by the International Livestock Centre for Africa (ILCA) planted at one site (Maseno) in western Kenya. Results from this field evaluation indicated that a landrace from Kenya (Kakamega provenance) was superior in growth rate and

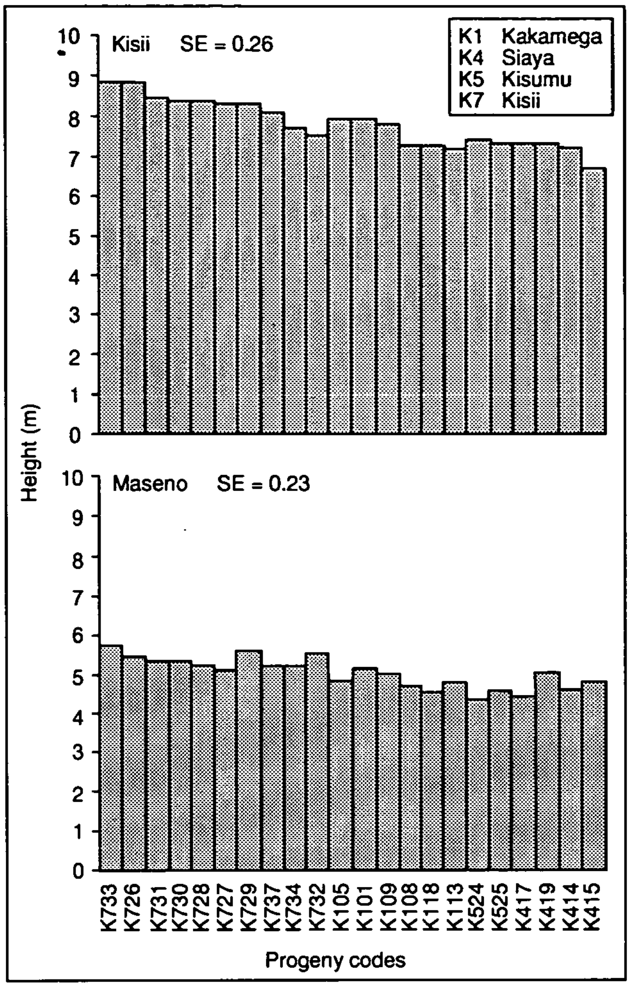

Figure 2. (left) Mean heights of 22 *Sesbania sesban* half-sib families at Kisii and Maseno, Kenya, after one year

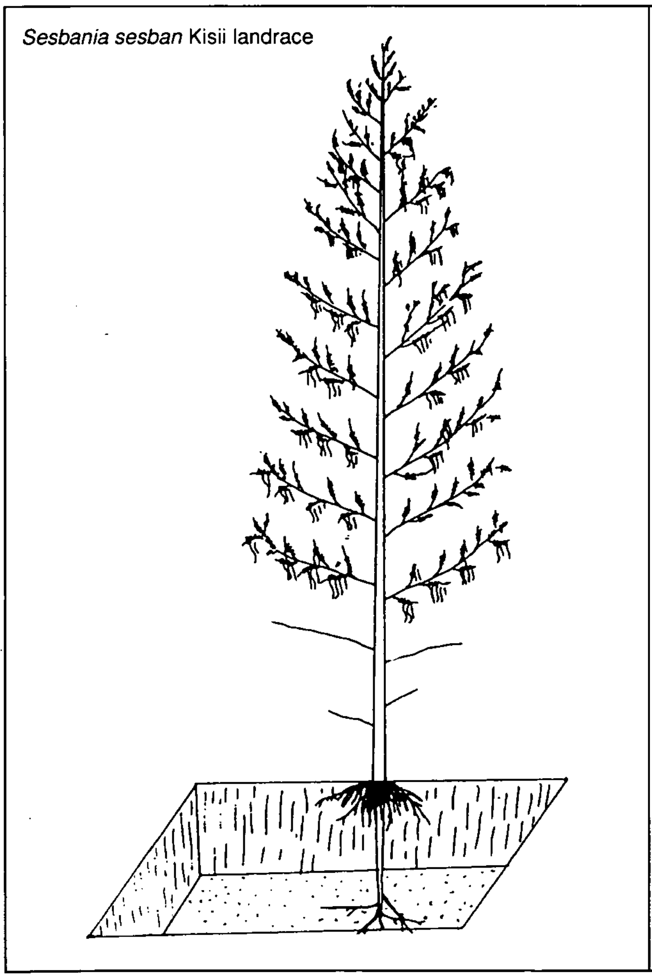

Figure 3. (below left) Diagrammatic representation of a typical *Sesbania sesban* tree from the Kisii landrace

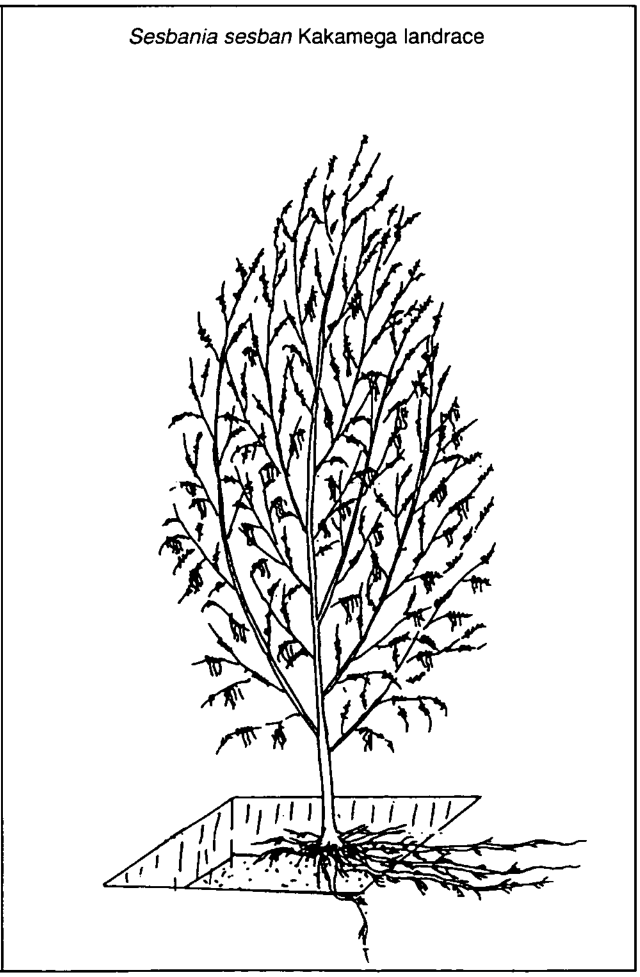

Figure 4. (below) Diagrammatic representation of a typical *Sesbania sesban tree* from the Kakamega landrace

total above-ground biomass production. The Kakamega provenance also proved superior in two other provenance trials in Burundi and Rwanda (unpublished data). It was, therefore, decided to select phenotypically superior trees for evaluation and breeding research from within the Kakamega provenance.

The next step involved the definition of the ideal ideotype towards which selection and breeding research should concentrate. The ideotype was defined in relation to the agroforestry technologies with the greatest potential for the region. The three most promising technologies within which *S. sesban* could play important roles are (i) short-rotation tree fallows, (ii) relay fallows with trees grown together with crops in hedges, and (iii) scattered trees on cropland. For these technologies it is considered that *S. sesban* should have:

- high growth rate in terms of height;
- straight stems with few large knots;
- narrow crowns to minimise competition with companion crops;
- sparse foliage to facilitate light penetration;
- branching architecture which maximises pole quality (ie small evenly spaced branches);
- narrow and deep rooting patterns to minimise competition with companion crops;
- freedom from pests and diseases (including root diseases and nematodes);
- copious nodulation and high rates of fixation of atmospheric nitrogen.

Most of the above tree characteristics can be combined in a single phenotype, as exemplified by an eight-month-old tree of the Kisii landrace at the Kakamega site in Kenya (Figure 5).

The practical challenge for *S. sesban* improvement research is, therefore, to reduce primary and secondary branching and increase apical growth, while at the same time selecting for a deep and narrow rooting pattern (as depicted in Figure 3) and confirmed potential for N fixation. Consequently, initial selections of superior phenotypes have been made on the basis of height growth, stem diameter, branch density, crown diameter, foliage density, stem straightness, branching architecture, and freedom from pests and diseases. This initial mass selection began in Kenya in mid-1990. To date, 38 phenotypically plus-trees have been selected and their progeny are under field-testing as half-sib families. The target is to extend the range of search into Uganda and to assemble an initial breeding population of some 100 genetically plus-trees.

In collaboration with staff at the Department of Soil Science, University of Nairobi, a parallel research initiative has been studying tree genotype x *Rhizobium* strain interactions. More recently, rooting pattern studies at four sites in Kenya involving 22 half-sib families have been completed. Observed trends from these below-ground tree characteristics will be reported elsewhere.

ESTIMATES OF GENETIC GAINS FROM FIRST-GENERATION SELECTION

Data from one-year-old progeny trials of *S. sesban* at two sites in western Kenya were used to estimate genetic parameters and genetic gains (Table 1). Variance components for family and within-family were estimated *via* expected mean squares in an analysis of variance. Narrow-sense heritabilities (h^2) were calculated using intra-class

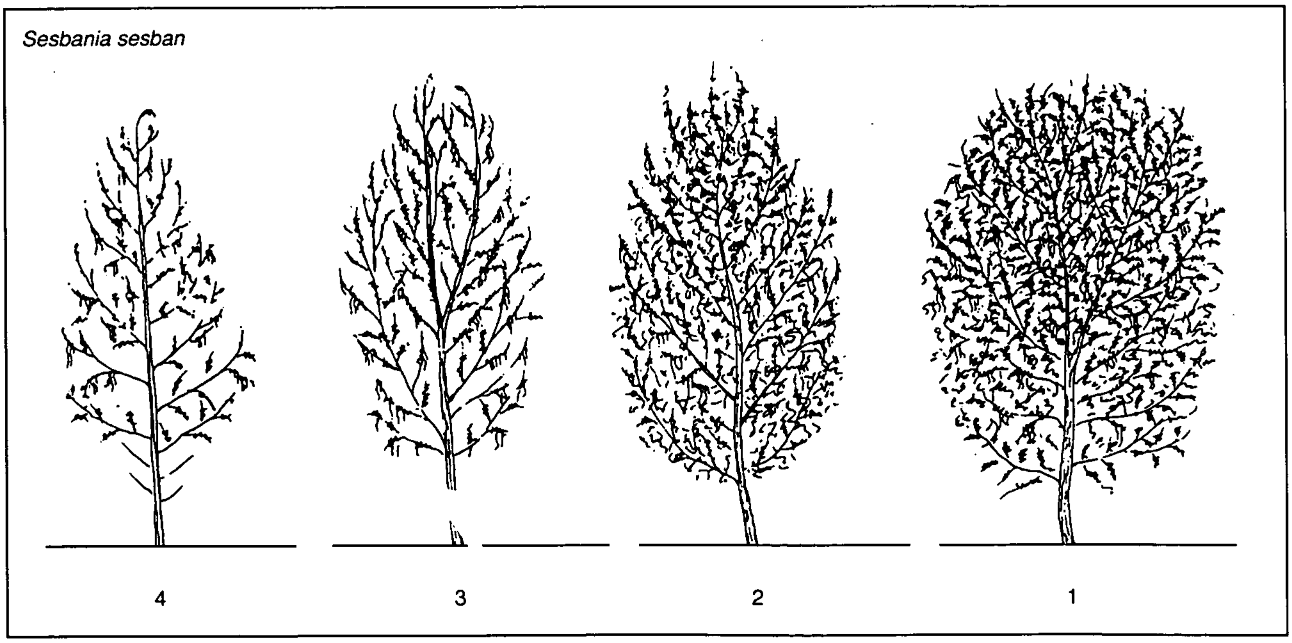

Figure 5. Diagrammatic representation of contrasting ideotypes of *Sesbania sesban*

correlations (Falconer 1981) as follows:

$$t = \frac{\sigma^2 b}{\sigma^2 b + \sigma^2 w}$$

where t = intra-class correlation; $\sigma^2 b$ = between-family variance; and $\sigma^2 w$ = within-family variance.

The intraclass correlation (t) is an estimate of the correlation of family values and can be used to estimate narrow-sense heritability (h^2). For half-sibs, $t = 1/4\ h^2$. Estimated values of h^2 for height growth from Maseno, Kisii and combined progeny trials were 0.4, 0.64 and 0.52, respectively.

Table 1. Genetic gains[1] (%) calculated from *Sesbania sesban* progeny trials for height growth at Maseno and Kisii sites in Kenya

	Percentage genetic gain		
Selection method/intensity	Maseno[2]	Kisii[2]	Maseno/Kisii[3]
Mean of best five trees in the trial irrespective of family	61	127	174
Mean of best ten trees in the trial irrespective of family	54	116	165
Mean of best five families	20	49	32
Mean of best ten families	14	34	22

[1] Formula for genetic gain used: selection differential x narrow sense heritability (h^2)

[2] Based on progeny test results at separate sites

[3] Based on combined progeny test results at two sites

CONCLUSIONS

Results from progeny trials with *S. sesban* have confirmed large differences between half-sib families in stem growth rate and quality, with narrow-sense heritability estimates for height growth ranging from 0.4 to 0.64. Substantial gains can be made through selection and breeding for these traits. Research is on-going to improve understanding of the nature and amount of genetic variation in the species.

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Domestication of trees in semi-arid East Africa: the current situation

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ABSTRACT

In East Africa, pastoralists in the dry savannahs rely heavily on trees and shrubs for browse, fodder, shade, fencing and firewood, etc. This review focuses on the use of non-industrial trees and shrubs, and discusses the role of domesticated indigenous trees in agroforestry systems.

To date, much attention has been paid to matching species to different ecoclimatic zones, especially with regard to drought tolerance. More recently, specific studies have been initiated on provenance variation, for example in *Acacia* species, and low-technology vegetative propagation techniques have been developed for a number of species. Multipurpose tree species offer numerous opportunities for genetic selection and domestication, such as improvements in survival, growth rate and yield, as well as various quality attributes associated with different forest products.

Mycorrhizal inoculation has been found to enhance greatly the survival of trees planted in degraded areas, which have low mycorrhizal inoculum potential. Inoculated trees have been used to restore the soil inoculum and have been shown to enhance the growth of interplanted agricultural crops. Studies in progress in Kenya are screening for the effectiveness of indigenous rhizobial strains associated with N-fixing tree species. There are opportunities to exploit tree/crop symbiotic associations further in agroforestry systems, using trees selected both for their own attributes and for soil-improving qualities.

INTRODUCTION

Africa is faced with the serious problem of not being able to feed its population or supply it with wood fuel. Production of more than one crop plant by each farmer is a common feature of traditional farming systems in Africa (Sanginga, Mulongoy & Swift 1992), and plant species that provide more than one product are favoured for planting (Konuche & Milimo 1989). Multiple cropping systems usually involve the use of multipurpose trees and shrubs, including legumes, in intimate association with seasonal and perennial food crops and livestock. The success of these systems lies in a high overall biomass yield, good nutritional value of the edible products, and a wide diversity of products. This diversity also reduces the chances of complete crop failure (Torquebiau 1992).

In East Africa, pastoralists in the dry savannahs rely heavily on trees and shrubs for browse, fodder, shade, living fences and windbreaks. These species are also important as sources of wood (firewood, poles, posts) and non-wood products (gums, resins, fruits, food, medicines) and for maintaining soil fertility (Table 1). Certain decorative woods, especially the black ones (*Diospyros* spp., *Dalbergia melanoxylon*, etc), are also commercially very important for carvings for the tourist trade.

This review focuses on the non-industrial trees and shrubs in semi-arid East Africa which could be selected for use in agroforestry systems. The multipurpose nature of trees and shrubs in agroforestry poses difficulties for tree improvers, such as whether single or multipurpose characteristics should be selected when breeding or selecting improved lines of multipurpose trees (see Owino, Oduol & Esegu, pp205–209; Simons, MacQueen & Stewart, pp91–102). This paper covers progress in three stages of the domestication process:

i. species selection;

ii. propagation and intraspecific genetic selection, and

iii. the incorporation of these selections into sustainable management systems.

In East Africa, a start has been made with these processes by screening species for adaptation to different climatic/edaphic conditions (Table 2), the evaluation of provenance variation and the creation of a small number of clones. In addition, investigations are in progress to examine the role of symbiotic soil micro-organisms, including inoculating trees with vesicular–arbuscular mycorrhizal fungi (VAM) and nitrogen-fixing bacteria (rhizobia).

Table 1. Tree and shrub species listed by their common uses in East Africa

Poles and posts	Fuelwood	Erosion control	Carving
Acacia albida	*Acacia nilotica*	*Acacia albida*	*Acacia albida*
A. nilotica	*A. polycantha*	*A. elatior*	*A. polycantha*
A. tortilis	*A. saligna*	*A. senegal*	*A. tortilis*
Azadirachta indica	*A. seyal*	*A. tortilis*	*Balanites aegyptiaca*
Balanites aegyptiaca	*A. tortilis*	*Albizia coriaria*	*Commiphora* spp.
Callitris glauca	*Azadirachta indica*	*A. lebbeck*	*Croton megalocarpus*
Cassia siamea	*Balanites aegyptiaca*	*Cajanus cajan*	*Delonix elata*
C. spectabilis	*B. orbiculans*	*Cordia sinensis*	*Diospyros scabra*
Casuarina equisetifolia	*Callitris glauca*	*C. ovalis*	*Dobera glabra*
Cordia sinensis	*Cassia siamea*	*Croton megalocarpus*	*Erythrina* spp.
C. ovalis	*Casuarina equisetifolia*	*Combretum micranthum*	*Hyphaene ventricosa*
Croton megalocarpus	*Combretum micranthum*	*Dalbergia melanoxylon*	*Terminalia brownii*
Delonix elata	*Cordia sinensis*	*Euphorbia tirucalli*	*Ziziphus mauritiana*
Eucalyptus camaldulensis	*Croton megalocarpus*	*Lannea alata*	
E. tereticornis	*Diospyros scabra*	*Lantana camara*	
Hyphaene ventricosa	*Eucalyptus camaldulensis*	Leucaena leucocephala	
Leucaena leucocephala	*E. tereticornis*	Prosopis chilensis	
Melia azedarach	*Leucaena leucocephala*	P juliflora	
Melia volkensii	*Melia azedarach*	Salvadora persica	
Prosopis chilensis	*Parkinsonia aculeata*	*Tamarix aphylla*	
P juliflora	*Prosopis chilensis*	*Ziziphus* spp.	
Salvadora persica	*Salvadora persica*	*Ziziphus mauritiana*	
Tamarindus indica	*Syzygium cumini*		
Terminalia brownii	*Ximenia americana*		

Windbreaks	Ornament	Hedges	Human food	Human food
Acacia albida	*Acacia albida*	*Bixa orellana*	*Adansonia digitata*	*Manilkara butugi*
A. nilotica	*A. nilotica*	*Cassia edulis*	*Annona chrysophylla*	*Mimusops fruticosa*
A. polyacantha	*A. polycantha*	*C. grandiflora*	*Azanza garckeana*	*Phoenix reclinata*
A. tortilis	*A. tortilis*	*Caesalpinia decapetala*	*Balanites glabra*	*Rhus natalensis*
Berchemia discolor	*Adansonia digitata*	*C. pulcherrima*	*Bequaertiodendron natalense*	*R. vulgaris*
Cassia siamea	*Adenium obesum*	*Chrysophyllum albidum*	*Berchemia discolor*	*Sclerocarya birrea*
C. spectabilis	*Berchemia discolor*	*Duranta repens*	*Borassus aethiopum*	*S. caffra*
Croton megalocarpus	*Cassia siamea*	*Dovyalis caffra*	*Canthium gueinzii*	*Sorindeia obtusifoliolata*
Delonix elata	*C. spectabilis*	*Opuntia dellenii*	*Carissa edulis*	*Strychnos decussata*
Diospyros scabra	*Croton megalocarpus*	*Pithecellobium dulce*	*Cordia sinensis*	*Syzygium guineense*
Euphorbia tirucalli	*Delonix elata*		*C. somaliensis*	*Vangueria apiculata*
Ficus sycomorus	*D. regia*		*Cordylogyne africana*	*V tomentosa*
Leucaena leucocephala	*Diospyros scabra*		*Diospyros mespiliformis*	*Vitex payos*
Schinus molle	*Erythrina abyssinica*		*Ficus glumosa*	*Ximenia americana*
Tamarindus indica	*Ficus sycomorus*		*F urceolaris*	*X. caffra*
	Melia azedarach		*F vallis-choudae*	*Ziziphus abyssinica*
	M. volkensii		*Flacourtia indica*	*Z. mucronata*
	Panax fruiticosa		*Grewia ectasicarpa*	
	Phyllanthus roseoptia		*Hirtella zansibarica*	
	Schinus molle		*Hyphaene coriacea*	
	Terminalia spinosa		*Lannea alata*	

SPECIES SELECTION

Until recently, when it became government policy in Kenya to promote the replanting of indigenous rather than exotic tree species, most of the work on the selection of trees of semi-arid lands in Kenya was with exotic fast-growing species. For example, a trial with Australian *Acacias* on two semi-arid Kenyan sites (Marimanti and Lanchiathurio) at 18 months indicated that *Acacia holosericea, A. cowleana, A. plectocarpa, A. leptocarpa* and *A. brassii* were promising (Chege & Stewart 1991). In other trials in the Embu/Meru/Isiolo project, species showing promise were *Acacia albida, A. cyanophylla, A. nilotica, A. polycantha, A. victoriae, Atriplex nummularia, Atriplex semi-baccata, Balanites aegyptiaca, Melia volkensii, Prosopis juliflora, Terminalia spinosa* and *Ziziphus mauritiana* (Armstrong & Lugadiru 1986). Subsequently, the performance of exotics was compared with indigenous species but seldom with a wide range of provenances. Comparative results of 58 exotic and indigenous tree and shrub species at

Table 2. Tree and shrub species listed according to site requirements

	Ecoclimate and rainfall zone[1]	Geomorphology[2]	Soils[3]	Soil/water regimes[4]
Acacia albida	1–4	1	1,2	1,2
A. gerrardii	3–4	1,2	1	3
A. mellifera	2–3	0	1,2	3
A. nilotica	1–4	0	1	3
A. polyacantha	4	1,0	1,2	3
A. senegal	1–4	1	3	2,3
A. seyal	2–4	2	3	3
A. tortilis	1–4	1,0	1,3	1,2,3
Adansonia digitata	2–4	1,2	1	3
Azadirachta indica	2–4	2	1	1,3
Balanites aegyptiaca	1–4	0	1,3	3,0
Berchemia discolor	3–4	1,0	3	3
Boscia angustifolia	2–3	0	1,3	3
B. coriacea	2–3	0	1,3	3
Boswellia hildebrandtii	2–3	2,0	1	3
Carissa edulis	3–4	1,2	1	3
Combretum molle	3–4	2,0	1,3	3,0
Commiphora africana	2–3	2	1,3	3
Conocarpus lencifolius	3–4	1	1	1,3
Cordia sinensis	1–3	1,2	1,3	1,3
Croton megalocarpus	4	2	1	3
Dalbergia melanoxylon	2–4	2	1	3
Delonix elata	1–3	2,1	3	3
D. regia	4	0	1	3
Diospyros mespiliformis	3	0	1,3	3
D. scabra	1–3	1	1,3	3
Dobera glabra	2–3	0	1,2	2,3
Dodonaea viscosa	4	3,0	2,3	3
Euphorbia tirucalli	2–4	0	2,3	0
Grewia villosa	2–3	0	2	3
Hyphaene ventricosa	1–3	1	2	1
Melia azedarach	3–4	0	2	3
M. volkensii	3–4	1	2	3
M. stenopetala	3–4	1	2	1
Parkinsonia aculeata	2–3	0	1,2,3	0
Piliostigma thonningii	4	0	2,3	3
Pithecellobium dulce	4	2	2	3
Populus ilicifolia	2–4	1	1,2	1
Salvadora persica	1–3	1,0	2	0
Syzygium cumini	2–4	1	1,2	1

[1] 1, 150–350 mm; 2, 300–350 mm; 3, 450–900 mm; 4, 600–1100 mm

[2] 1, depressions/river banks; 2, plains; 3, hills/slopes; 0, not specific

[3] 1, clays; 2, loam, sand, groundwater alluvial; 3, rocks, gravel, hardpans

[4] 1, dependent on groundwater; 2, tolerates seasonal inundation; 3, requires moist, well-drained soils; 0, not specific

two years of age at Loruk (Kenya) are reported by Kimondo (1991). From these results, the Australian *Acacias* generally were superior in height growth, but had poor survival with only three out of the 15 species achieving greater than 80% survival (Table 3), compared with nine out of 12 of the indigenous species. The indigenous *Sesbania sesban* was the tallest, but had only 25% survival. Of the other indigenous species tested, the height and survival of *Acacia seyal* and *Melia volkensii* were acceptable (Kimondo 1991).

Similarly, trials with exotic (25) and indigenous (16) species have also formed part of the objectives of the Baringo fuel and fodder project based near Lake Baringo in Kenya. Mortalities less than 50% occurred with only *Acacia tortilis* and the exotics *Prosopis pallida, P. chilensis, Acacia aneura, Cassia sturtii, Gleditsia triacanthos, Prosopis tamarugo, Acacia albida, Simmondsia chinensis, Azadirachta indica* and *Atriplex canescens.*

In order to facilitate domestication, it is necessary to determine the tree and shrub characteristics desired by a particular community, and to identify genetically outstanding natural populations and individuals for propagation by seed or vegetative techniques. In semi-arid areas, there is considerable variation in soil types, rainfall (quantity, frequency, duration of dry

Table 3. Mean height and survival of Australian *Acacia* spp. and 12 other species indigenous to Kenya at two years of age at Loruk, Kenya (500 mm mean annual rainfall) (source: Kimondo 1991)

Species	Country of origin	CSIRO seedlot number	Mean height (m)	Survival (%)
Acacia holosericea	Australia	14660	2.8	85
A. holosericea	"	14632	2.8	93
A. farnesiana	"	–	2.6	55
A. torulosa	"	14888	2.6	33
A. plectocarpa	"	17207	2.5	74
A. brassii	"	15480	2.4	15
A. difficilis	"	14623	2.4	51
A. ampliceps	"	14668	2.4	74
A. ampliceps	"	14631	2.3	55
A. shirleyi	"	14622	2.2	26
A. cowleana	"	14885	2.1	35
A. cowleana	"	14683	2.1	32
A. julifera	"	14656	2.1	44
A. raddiana	"	–	1.7	82
A. trachycarpa	"	15767	1.6	18
A. nilotica	India	–	2.8	78
Tamarindus indica	Kenya	–	2.9	97
A. nilotica	"	–	1.9	82
A. nubica	"	–	1.0	23
A. tortilis	"	–	1.6	99
Cordia sinensis	"	–	1.6	91
Dalbergia melanoxylon	"	–	1.5	97
Terminalia brownii	"	–	1.3	95
A. mellifera	"	–	1.1	98
Croton megalocarpus	"	–	1.1	94
Berchemia discolor	"	–	1.1	74
Sesbania sesban	"	–	3.2	25
Balanites aegyptiaca	"	–	0.9	68

season, reliability, etc), proximity to water table, pH, salinity, and topography. Thus, there is a likelihood that wild tree populations will have adapted to their environments on a local scale. In addition to this small-scale variation, there are superimposed regional gradients of increasing aridity. Species trials in Kenya at Hola, Ramogi, Baringo, Kibweze, Lodwar, Embu and Meru have screened more than 500 different exotic and indigenous tree and shrub species for their adaptation to different ecological zones. In East Africa, therefore, it is clear that there has been considerable genetic testing at the species level. This testing now needs to be extended to a study of the genetic variation between provenances, as well as the likely variation within different populations.

INTRASPECIFIC GENETIC SELECTION

International provenance trials with dry-zone *Acacia* spp. are currently in progress, co-ordinated by the Oxford Forestry Institute (Fagg & Barnes 1990). Four African *Acacia* species (*A. tortilis, A. nilotica, A. senegal* and *A. albida* [now called *Faidherbia albida*]) with wide geographical distributions, which include East Africa, were identified as having particular potential as producers of a range of products and as being suitable for planting on arid, degraded sites. As a prerequisite to the successful establishment of provenance trials, a study was made in 1987–90 of:

- morphological and phenological variation of the tree species and of their rhizobial symbionts throughout their natural range;
- the breeding systems of the species.

In addition, a sampling strategy was developed and utilised to provide the basis for genetic exploration, evaluation and conservation as a basis for subsequent domestication (Fagg & Barnes 1990).

In the second phase of this project (1990–93), *A. eriloba* was added to the project and the above research was extended and seed collections were made. These collections were for distribution to collaborators in the establishment of international provenance trials. In addition to superior performance in terms of growth, these trials are intended to test other characteristics, such as nutritional value, fodder production, and gum quality and productivity (Fagg *et al.* 1990).

By 1991, over 30 provenances had been deposited in the UK Forestry Commission's seedbank at Alice Holt, Surrey, England. For a number of these provenances, seed collections were made from individually sampled trees for more detailed studies of genetic variation and breeding systems. Leaf collections were also made for studies on peroxidase activity and nitrogen fixation assessments. Wood samples were collected for dendrochronology studies, and gum samples were taken for chemical analysis. In a parallel study funded by the European Commission, further seed collections of *Faidherbia albida* have been made from East Africa for a collaborative study between institutions in the UK, France and Senegal on its reproductive biology, and its genetic variability in agroforestry characteristics and in its isoenzyme patterns (Lockhart, Fagg & Barnes 1990).

In another study, 30 families within three provenances of *Melia volkensii*, in which seeds were collected along a sharp climatic gradient, were established on three sites in Kenya (Embu, Bura and Malindi) in 1990. Preliminary results have indicated pronounced variation at the family level, but not at the provenance level, in growth, drought tolerance, root architecture, branch density and size, leaf phenology and resistance to spider mite attacks. These results have important implications for the selection of genotypes for dry and wet season fodder production, the provision of shade for livestock, and for intercropping with agricultural crops (P Milimo, unpublished data).

In other areas of semi-arid Africa, studies are in progress on species also indigenous to East Africa. In two different experiments involving *F. albida*, provenances raised from West African seed had generally smaller shoots compared with those from South Africa, under moist soil conditions (Wanyanja, Mills & Gwaze 1991; Vandenbeldt 1991). In the drier West African plots, all provenances of *F. albida* from South Africa had 100% mortality at the end of the second year, while survival of both provenances in South Africa was the same. In South African plots, local provenances outperformed the West African ones in height growth. The South African provenances had greater shoot dry biomass compared with those from the West African provenances, which allocated 20% more dry matter to the roots. These results indicate that, in this instance, local provenances were better adapted to the prevailing conditions than introduced ones.

A detailed study of variation between 75 provenances of *Sesbania sesban* has been made by the International Centre for Research in Agroforestry (see Owino *et al.*, pp205–209). A further component of the study with this species is to select individual and contrasting phenotypes for their apparent suitability for producing poles, fodder and biomass. These will be propagated vegetatively to assess their potential for maximising productivity of a particular product by selecting single-purpose clones of this multipurpose species (P Oduol, personal communication; see also Owino *et al.*, pp205–209).

Variations between and within species in their capacity to resist drought are likely to be a major characteristic influencing the survival and growth of trees in the semi-arid lands of East Africa. Although stable performance of a provenance over a wide range of environments is generally regarded as desirable, past attempts to identify and select trees for semi-arid areas have resulted in a wide range of responses among species and provenances to different environments, as would be expected. This has been demonstrated in progeny/provenance tests of *Melia volkensii* and *M. azedarach* established on three sites with 400 mm, 950 mm and 2000 mm annual rainfall, in northern Queensland, Australia. Results from these studies show marked variation within and between species in leaf phenology, survival and above-ground dry mass production (P Milimo, unpublished data). Thus, given the range of soil types and water availability in these conditions, genotype/ environment interactions are almost certain to prevent the selection of a widely acceptable provenance.

The detection of early indicators of good field performance is a valuable step in tree improvement. In hot dry sites, high water use efficiency, and the absence of photo-inhibition, may be determined by examining morphological and physiological characteristics. This examination, however, is likely to be more successful at the clonal rather than the provenance level. Success would depend on the capacity to use juvenile tissues to predict the responses of mature trees to drought conditions. However, because mature trees are more likely to be able to utilise water deep underground, drought tolerance is probably much more important in seedlings and young plants.

Most of the indigenous trees of semi-arid East Africa could be selected for a range of genetic traits. Thus, selection in multipurpose tree species could include not only the typical, forestry-related characteristics such as growth rate and stem form, but also selection for resistance to drought, salinity, alkalinity; fodder and pod yields and quality (nutritive value, digestibility, freedom from alkaloids, thornlessness, etc); yields and quality of gums, resins and pharmaceuticals (see Waterman, pp42–48); firewood and charcoal quality (high wood density, presence of oxalates (Prior & Cutler 1992), etc); as well as for nitrogen-fixing ability in the leguminous species. The problems associated with selection of multipurpose species are considered by Simons *et al.* (pp91–102): see also Felker (pp183–188) for studies on *Prosopis* spp.

PROPAGATION BY SEED

Although propagation by seed is the main method of plant multiplication in E Africa, availability of quality seed is a major constraint affecting planting (Shakacite 1987; Shehaghilo 1987; Wate 1987; Milimo 1987). Problems that prevent the use of seed can be broadly classified as irregular or infrequent flowering and seed inviability and/or dormancy.

Fruit-bearing species like *Ziziphus mauritiana*, *Diospyros scabra, Balanites aegyptiaca* and *Dobera glabra* have well-defined seed collection periods, although their viability declines rapidly with time (Zumer-Linder 1983). However, seedlings of many of the popular wood-producing indigenous tree species cannot be propagated easily by seed because they exhibit dormancy. Amongst these are *Melia volkensii* (Milimo & Hellum 1989a, b), *Terminalia* spp. (Specht & Schaefer 1990) and *Hyphaena coriacea* (Zumer-Linder 1983). The techniques that have been used to break dormancy are not practical for large-scale seed production, and therefore more research on this aspect is needed. Insect damage is a major constraint on seed availability in some genera, eg *Balanites* and *Acacia.*

VEGETATIVE PROPAGATION

Vegetative propagation is becoming increasingly important in forestry and agroforestry for the multiplication of limited seed material and for the production of genetically uniform stock for planting. The value of vegetative propagation to multiply selected planting material and to capture genetic potential has long been known (Libby 1973; Zobel & Talbert 1984; Leakey 1987). Vegetative propagation gives the tree improver the ability to multiply, test, select from and utilise the large genetic diversity present in most tree species. In this way, selected, highly productive but unrelated clones can be used commercially for reforestation and agroforestry (Leakey 1991).

Studies to determine the best propagation environment for semi-arid species have indicated that a non-mist propagation system is generally more effective than conventional mist propagation (Dick, East & Leakey 1991). In particular, the better rooting of cuttings in non-mist propagators seems to be related to a lower susceptibility to rotting and consequent mortality (Figures 1 & 2). The low-technology non-mist propagator currently used in Kenya has been described by Leakey *et al.* (1990) (see also Ladipo *et al.*, pp239–248). This design does not require electricity or piped water, and is therefore particularly suitable for rural areas in the tropics. Several groups working in Kenya have successfully utilised this technology to root a variety of species (Table 4).

Trials have started in Kenya to determine protocols for the larger-scale propagation of semi-arid zone species. Initial work has shown that *Acacia tortilis* and *Prosopis juliflora* both root well from pollarded material. Three months after pollarding *P. juliflora* trees 1 m above ground

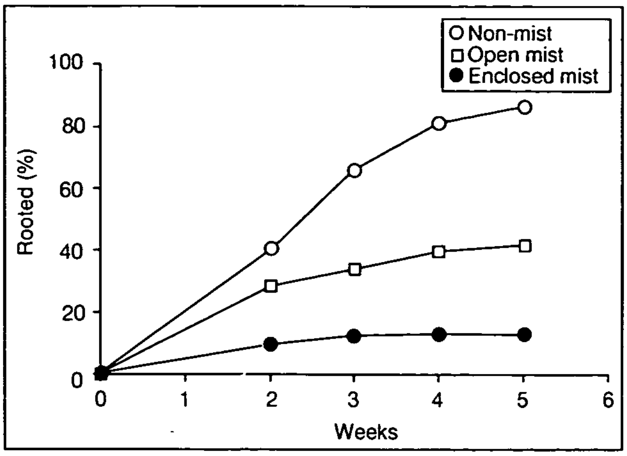

Figure 1. Effect of three propagation environments: (i) a low-technology non-mist propagator, (ii) an open mist system, and (iii) a mist system enclosed in polythene, on the percentage of *Prosopis juliflora* cuttings forming adventitious roots

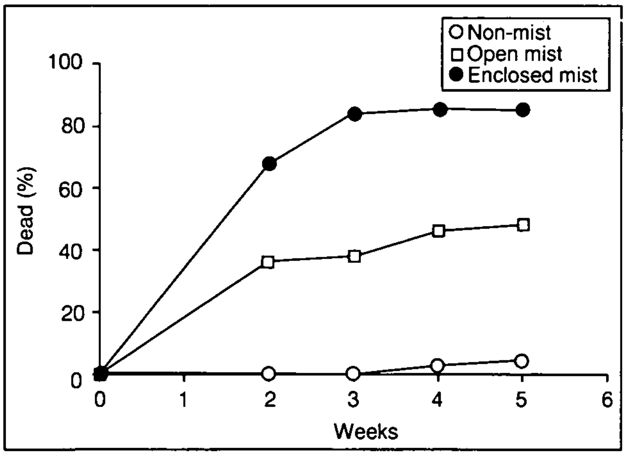

Figure 2. Percentage mortality of *Prosopis juliflora* cuttings in three propagation environments

level (to avoid grazing by goats), between 50 and 250 cuttings were harvested and transported the same day to the propagators in Nairobi, four hours' drive away. Two-node cuttings (approximately 5 cm length) were taken from each shoot after discarding the very soft 10 cm at the tip. The cuttings were dipped in a commercial rooting powder 'Seradix 2' (May & Baker Ltd, active ingredient 0.8% indole-3-butyric acid, IBA), and placed in the non-mist propagators. The number of cuttings rooted was assessed five weeks later when 43% and 96% rooting had occurred in *A. tortilis* and *P. juliflora*, respectively. Three harvests were collected from one tree of *P. juliflora* pollarded in December 1988; cuttings were collected in February, August and November 1989, with rooting success of 43%, 56% and 83%, respectively. The differences in rooting success are probably attributable to the stage of growth of the resprouted material when collected, rather than to season. Older, more lignified tissue was collected in the first two harvests and is less likely to root than younger material.

It is clear that the system developed in Kenya has great potential for practical implementation in semi-arid areas with species which coppice. The ability to root tropical trees from leafy stem cuttings depends upon many factors, such as the physiological state of the stockplant, the propagation environment and the treatment applied to the cutting prior to propagation, eg the leaf area and the concentration of applied auxins (Leakey 1985). A good understanding of these factors is necessary to sustain output from vegetative propagation systems (Leakey, Newton & Dick, pp72–83).

The state of the leaf on the cutting is an important factor in determining the rooting potential of a cutting. For example, leaves on cuttings of *Terminalia spinosa* trimmed to 30 cm^2 produced roots in a shorter period than those trimmed to only 7.5 cm^2 (Newton, Muthoka & Dick 1992), whereas leafless cuttings did not root. The mean length of the longest root increased with increasing leaf area (0, 7.5, 15 and 30 cm^2), which is almost certainly important for subsequent cutting survival and establishment in the nursery. Large-leaved cuttings were droughted, displaying the lowest foliar relative water content. In response to this drought, these cuttings closed their stomata and thus had the lowest stomatal conductance, and displayed the highest rate of leaf shedding (Newton *et al.* 1992). These self-regulated changes in leaf area resulted in cuttings with optimal leaf area for rooting in the environment tested.

Stockplant management is also critical for sustained, successful rooting. The light

Table 4. Dry zone species propagated by vegetative stem cuttings at ITE, Edinburgh, National Museums of Kenya and Baringo fuel and fodder project

Acacia albida
A. karoo
A. polyacantha
A. senegal
A. tortilis
Balanites aegyptiaca
Carissa edulis
Cassia siamea
Combretum heroense
Cordia sinensis
Dalbergia melanoxylon
Diospyros mespiliformis
Dobera glabra
Faidherbia albida
Ficus sycomorus
Leucaena leucocephala
Melia volkensii
Prosopis juliflora
Sclerocarya birrea
Sesbania sesban
Tamarindus indica
Terminalia brownii
T. prunioides
T. spinosa
Vangueria infausta
V. madagascariensis
Ximenia americana
Ziziphus mauritiana
Z. mucronata

environment to which stockplants are subjected also influences rooting potential of cuttings. In *Acacia tortilis* grown under different light qualities at constant irradiance (150 μmol m^{-2} s^{-1}) in controlled environment conditions, stockplants grew tallest in light with a red/far-red ratio (R:FR) of 0.61, rather than at 1.09, 3.14 or 4.48 R:FR (Dick & East 1992). Cuttings from shoots harvested from plants grown at low R:FR (0.61 and 1.09) rooted better (77–79%) than those from R:FR 3.14 (63%) or R:FR 4.48 (22%). This response is similar to that of other tropical trees (see Leakey *et al.*, pp72–83).

TREE ESTABLISHMENT AND SUSTAINABLE MANAGEMENT

The value of domestication in capturing a range of genetic potential is lost if, when the selected material of multipurpose trees is planted out in the field, they either do not establish or grow poorly. Such problems have often occurred when reforesting drylands where soil moisture and nutrients are limiting (Wood 1989; Armstrong & Lugadiru 1986; Chege & Stewart 1991; Chirchir & Stewart 1989), or when the seedlings have been inadequately protected from grazing animals. The change in environmental conditions experienced by the plants during transplanting may be severe, and may result in severe droughting of the plants, which can be at least partly alleviated by irrigation (Newton, Munro & Wambugu 1993). Although the application of water-retaining polymers has also been recommended to improve tree establishment by alleviating the effects of drought (see Callaghan et al. 1989), initial field results have not been encouraging (Newton *et al.* 1993; Wilson *et al.* 1991).

Many tropical soils are degraded, contain low concentrations of plant nutrients, and have high phosphorus-fixing capacity (Sanchez & Salinas 1981). Attempts to solve this problem usually involve application of chemical fertilizers or the addition of organic matter. Since chemical fertilizers are unaffordable by most subsistence farmers, except through credit schemes which can plunge the farmer into debt, this review examines the role of soil microflora in tree establishment.

The role of VA mycorrhizas

Symbiotic soil micro-organisms possess the potential to assist trees and crops to access greater quantities of nutrients (Torquebiau 1992) and therefore survive better in difficult habitats (Wilson *et al.* 1991; Sprent, pp176–182; Mason & Wilson, pp165–175). Vesicular–arbuscular (VA) mycorrhizal fungi perform a range of functions, including enhancement of mineral nutrient uptake (particularly phosphorus) by the plant root system (Harley & Smith 1983). Under tropical conditions, little is known about the occurrence and distribution of VA mycorrhizal fungi, but they are considered essential for the growth of many grain crops, forage legumes, pasture plants, forest trees and horticultural plants (Janos 1987). In degraded arid areas, there may be a need to enhance the mycorrhizal and rhizobial symbioses if, as is likely, the processes of degradation have had detrimental effects on the soil inoculum.

In Kenya, observations of spore numbers and types were made around naturally occurring *Acacia tortilis* trees at Olorgasailie, in the Rift Valley. Samples were taken in April 1989, at the end of the wet season, from the top 15 cm layer of soil along transects from the boles of *A. tortilis* trees outwards to bare ground. The trees were of variable size and unknown age, and transect lengths were varied according to tree size so as to accommodate variation in the areas of canopy and rooting zone influence.

Following extraction from the collected soil samples, the numbers of live and dead spores were counted and types were distinguished. Twelve types were found, including *Acaulospora scrobiculata*, *Entrophospora* sp., *Scutellospora* sp., *Glomus geosporum*, six other *Glomus* species, and two unknown types (J Wilson, unpublished data). This is a reasonably diverse population. Total numbers of spores were 5–6 times greater close to the trees than at a distance (Table 5). Live spores, which probably represent an important component of the soil inoculum in degraded sites (see Mason & Wilson, pp165–175), outnumbered dead spores in each sample, and the ratio of live/dead spores was 1.6–2.7 close to the trees, while it was lower (1.2–1.3) away from the trees. The presence of higher spore numbers with a greater proportion of viable spores close to trees may be a direct effect of their root systems or an indirect effect of soil temperature, moisture, chemistry or other factors.

Table 5. Distribution of live and dead VA mycorrhizal spores in soil samples taken close to and on bare ground at a distance from naturally occurring *Acacia tortilis* trees at Olorgasailie, Kenya (results are numbers per 50 g fresh mass of soil)

	Tree A			Tree B		
	Live	Dead	Total	Live	Dead	Total
Close	369	231	600	664	242	906
Distant	61	46	107	100	82	182

In Kenya two trials have recently shown the benefits of nursery inoculation on tree survival in semi-arid lands (Wilson *et al.* 1991). Inoculation of four tree species was examined: *Acacia tortilis, Prosopis juliflora, Terminalia brownii* and *Terminalia prunioides* (Wilson *et al.* 1991). Pre-germinated tree seedlings were inoculated with root and adhering soil inoculum of endomycorrhizal fungi cultured on maize and cowpea. The leguminous trees were also inoculated with rhizobia. After growth in a nursery, they were planted in two successive wet seasons at two sites, Marimanti and Olorgasailie, both semi-arid but with annual rainfalls of 847 mm and 476 mm, and soil pH of 6.5 and 8.1, respectively. The percentage of seedlings surviving at each site 30 weeks after planting is shown in Table 6.

Table 6. Percentage survival of inoculated (+S) and uninoculated (-S) plants 30 weeks after outplanting, and improvement in survival (% gain) as a result of inoculation with VA mycorrhizal and with rhizobia for leguminous tree species. Experiment at two semi-arid sites in Kenya (data based on 90 plants per treatment of *Acacia* and *Prosopis* and 45 plants for the *Terminalia* spp. in each experiment)

	Planting date					
	Experiment 1 November 1988			Experiment 2 March 1989		
	+S	–S	% gain	+S	–S	% gain
Marimanti						
*A. tortilis**	94	78	21	98	76	29
*P. juliflora**	92	84	9	76	73	4
T. brownii	89	87	2	61	44	39
T. prunioides	93	68	37	64	31	106
Olorgasailie						
*A. tortilis**	100	81	23	94	87	8
*P. juliflora**	97	91	6	65	80	–18
T. brownii	89	76	18	94	90	4
T. prunioides	84	47	79	87	70	24

* Leguminous tree

Inoculation generally improved plant survival, although effects varied with both season and species. Substantial effects of inoculation on tree growth were also observed in the nursery prior to outplanting. Observations on these experiments and others indicate that benefit from mycorrhizal inoculation is most marked when roots are more than 70% mycorrhizal at planting (Wilson *et al.* 1991) and when environmental conditions are most stressful.

Irrespective of the cause, the presence of a greater quantity of inoculum in the soil close to trees may lead to higher rates of mycorrhizal infection in crops grown among trees than in those grown on their own, provided that the types of inoculum are compatible. The dynamics of VA mycorrhizal populations in agroforestry systems are unknown, although the cycle of soil and vegetation disturbance is likely to have adverse effects. Agricultural crops can benefit substantially from inoculation with VA mycorrhizal fungi (Howeler, Sieverding & Saif 1987). While inoculation of agricultural crops is restricted by the large quantities of inoculum required, inoculation of nursery-grown trees intended for agroforestry systems may be worthwhile, particularly in stressful environments. Because of the wide host ranges of these fungi, and the diversity of fungal species occurring with trees, the tree roots may sustain inocula which are also of value to the intercrop (Wilson *et al.* 1991). Inoculation of trees, therefore, may have two benefits:

i. improvement of tree survival and growth, and
ii. maintenance of populations of mycorrhizal species suitable for intercrops in the period between harvesting one intercrop and sowing the next.

Past experience would indicate that, if an adequate heterogeneous VA mycorrhizal population is present, crops should have no problem in finding sufficient compatible fungi for growth (Sieverding 1991). However, more extensive observations are needed to confirm this effect of trees and to examine the effects on intercrops.

Rhizobia and nitrogen fixation

A large programme of research is in progress on nitrogen-fixing trees at the Kenya Forestry Research Institute (KEFRI). The work entails isolation, characterisation and screening for the effectiveness of indigenous rhizobial strains, found in association with selected N-fixing trees. This programme is also developing appropriate inoculation techniques for tree seedlings, for enhanced nodulation, nitrogen fixation and tree establishment (D Odee, personal communication). As already mentioned, microsymbiont inoculation (VA mycorrhizas and rhizobia) has improved tree establishment on degraded sites (Table 6). In collaboration with the Department of Biological Sciences, University of Dundee, KEFRI is also engaged in programmes to map and test indigenous tree rhizobial flora across the various ecoclimatic zones of Kenya; and to test inoculants for *Acacia* spp. of East and southern Africa. Further studies are planned to determine the compatibility of Kenyan rhizobial strains with Australian *Acacia* spp., when grown in Kenya (J Sutherland, personal communication).

CONCLUSIONS

The domestication of trees for the production of wood and other products in semi-arid areas of East Africa is at an early stage. A wide range of exotic and indigenous species have been tested for their suitability. In general, indigenous trees have shown better survival but slower growth than exotics, especially the Australian acacias (see Booth & Turnbull, pp189–194). To what extent this better survival of indigenous species may be related to their symbiotic relationships with soil microflora is not known, but it seems clear that inoculating trees with root symbionts can greatly enhance tree establishment. Following on from species selection, a start has been made on provenance selection in the African acacias and the development of vegetative propagation techniques so that the potential of clonal approaches can be evaluated.

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Domestication potential of indigenous fruit trees of the miombo woodlands of southern Africa

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ABSTRACT

This paper presents results of various studies on the identification, propagation and growth of fruit trees indigenous or naturalised to the miombo ecozone of southern Africa. In 1989, ethnobotanical surveys were conducted in eastern Zambia, western Tanzania and Malawi to identify the range, uses and management of undomesticated trees in farmers' fields and around their homesteads. During these surveys, over 50 indigenous tree species were identified by farmers as providing edible fruits. Those mentioned in more than one country included *Adansonia digitata, Annona senegalensis, Azanza garckeana, Flacourtia indica, Strychnos spinosa, Uapaca kirkiana, Sclerocarya caffra, Tamarindus indica, Grewia bicolor, Parinari curatellifolia, Diospyros mespiliformis, Syzygium cordatum, Rothmannia englerana, Ximenia caffra, Vangueria infausta, Ziziphus mauritiana, Trichilia emetica, Parkia filicoidea, Bauhinia petersiana, Canthium crassum* and *Bridelia micrantha.*

Considerable information is available on the nutritional attributes of many of these species but little is known about propagation and field performance following artificial regeneration. A series of studies are in progress in Malawi and Zambia to address this gap in knowledge as a first step towards the conservation and domestication of this valuable resource.

INTRODUCTION

More than 50 indigenous or naturalised tree species of the miombo ecosystem of southern Africa bear edible fruits which are important sources of vital nutrients (Food and Agriculture Organisation 1983; Fanshawe 1972; Saka & Msonthi 1993). A few of these, such as *Adansonia digitata, Bauhinia petersiana, Grewia flavescens* and *Tamarindus indica,* serve as food reserves during seasonal food shortages and in times of famine (see also Campbell 1987). Studies on the nutritional value of indigenous fruits show many to be rich in sugars, essential vitamins, minerals, vegetable oils and proteins (Saka, Msonthi & Sambo 1989; Wehmeyer 1966; Hans, Parker & Kumar 1978; see also Table 1). Thus, *Annona senegalensis* and *Trichilia emetica* fruits are important protein supplements, while *Strychnos spinosa, Azanza garckeana* and *Parinari curatellifolia* have on average high crude fat (31%), crude fibre (45%) and total carbohydrates (88%) (Saka & Msonthi 1993).

In spite of their importance, however, indigenous fruit trees of the miombo ecozone have not been subject to agricultural or forest policies (Campbell 1987). There has been limited interest in their conservation, propagation and improvement. Farmers are interested in indigenous fruit trees only to the extent that they can extract edible fruits and medicines. Beyond that, the only other effort made is to select the more valuable fruit trees before clearfelling the miombo forest prior to cultivation.

Domestication, or even the planting of wild fruit tree seedlings, is not common. For example, in the Condo area of Zimbabwe, only nine out of 102 households had planted a wild fruit tree (Campbell 1987). In Zambia, most indigenous fruit-bearing tree species are left standing during land clearing, with a view to continue providing a food supplement to the diet in the form of fruit. Wild fruit tree cultivation is not practised traditionally. In eastern Zambia, none of the 112 farmers interviewed had ever planted an indigenous fruit tree (Kwesiga & Chisumpa 1992).

It is clear, therefore, that there is need for a concerted effort towards understanding why farmers do not domesticate indigenous fruit trees, and to encourage this process by developing strategies for domestication of this valuable resource through tree improvement programmes. Failure to do so may lead to loss of genetic diversity of the indigenous fruit trees in the miombo ecozone. This paper presents results of ethnobotanical surveys, nursery and field performance in parts of the miombo ecozone.

Table 1. Nutritional value of some indigenous fruits (source: Hans *et al.* 1978)

Species	Protein (g 100 g^{-1})	Fat (g 100 g^{-1})	Carbohydrate (g 100 g^{-1})	Thiamine (mg g^{-1})	Riboflavine (mg g^{-1})	Niacin (mg g^{-1})	Ascorbic acid (mg g^{-1})
Adansonia digitata							
Pulp	–	–	–	–	–	–	High
Seed	–	14.5	–	–	–	–	–
Parinari capensis							
Seed	29.3	65.1	–	–	–	–	–
P. curatellifolia							
Pulp	1.6	0.5	28.9	0.02	0.07	1.06	124
Parkia filicoidea							
Pulp	Low	Low	High	–	–	–	–
Seed	High	17	–	–	–	–	–
Ricinodendron rautanenii							
Dry pulp	9.4	1.2	72.9	0.49	0.21	4.79	15
Kernel	26.0	57.3	5.9	0.31	0.21	0.31	–
Sclerocarya caffra							
Pulp	–	–	–	–	–	–	68
Seed	23–31	56–61	–	–	–	–	–
Tamarindus indica							
Pulp	2.8	0.6	62.5	0.34	0.14	1.20	2.0
Seed	–	High	–	–	–	–	–
Uapaca kirkiana							
Pulp	0.9	0.3	27.0	0.01	0.12	0.49	12.1
Ximenia americana							
Pulp	–	66.0	–	–	–	–	–

DETAILS OF RESEARCH PROGRAMMES

The International Centre for Research in Agroforestry (ICRAF), through the southern Africa AFRENA (Agroforestry Research Networks for Africa) and the collaborating national institutions in Malawi, Tanzania and Zambia, undertook ethnobotanical studies in 1989 with the following objectives:

- to explore what uses the farmers actually make of indigenous trees;
- to incorporate indigenous knowledge of the management and conservation of the miombo woodland through new or improved agroforestry systems;
- to provide a basis for research on identification, selection, propagation and tree improvement strategies of the most commonly preferred indigenous trees.

In addition, propagation studies and field planting of selected indigenous fruit trees were initiated by both the Forestry Research Institute of Malawi (FRIM) and the Southern Africa Development Coordination Conference (SADCC)/International Centre for Research in Agroforestry (ICRAF) programme on the improvement of multipurpose trees (MPTs) at Makoka, Zomba, in Malawi. The objectives of these studies were to:

- develop or simplify propagation techniques for native fruit trees;
- raise suitable planting stock of native fruit trees;
- evaluate growth and fruit yield from these fruit trees after artificial regeneration in the field.

In Zambia, the Department of Forestry started research on the domestication of wild trees as far back as the 1930s, but the emphasis then was on timber-producing species. It is only recently that fruit trees have been included in the research programme. Since 1976, research work has been conducted on the domestication of various indigenous timber and fruit tree species at Chati Forest Research Station, 40 km west of Kitwe. The results so far show that fruit trees in general are growing faster than most timber species (Figure 1).

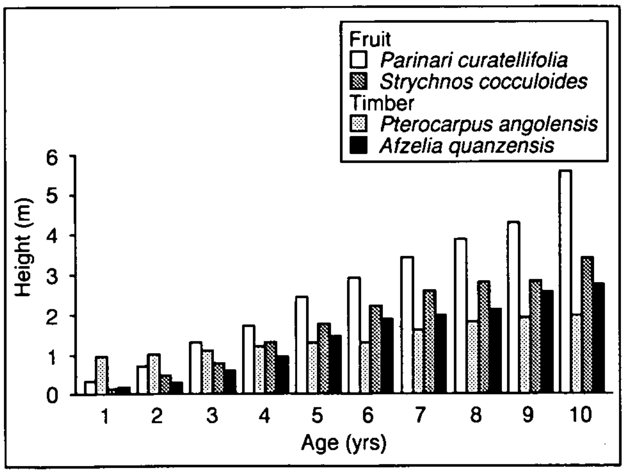

Figure 1. Comparison between growth of indigenous fruit trees and timber trees in a field trial at Chati Forest Research Station, Zambia. Tree species were allocated randomly to plots of approximately 28 m x 28 m, and were direct sown at the onset of the rainy season

Table 2. Common indigenous fruit trees of the miombo ecozone of southern Africa (source: Kwesiga & Chisumpa 1992; Maghembe & Seyani 1991; Karachi *et al.* 1991; Campbell 1987)

Species	Eastern Zambia	Whole of Malawi	Western Tanzania	Communal areas of Zimbabwe
Adansonia digitata	X	X	–	X
Adenia senensis	X	X	–	–
Annona cherimolia	X	–	–	–
Annona senegalensis	X	X	X	X
Azanza garckeana	X	X	X	X
Bauhinia petersiana	X	X	–	–
Berchemia discolor	X	–	–	X
Borassus aethiopum	X	X	–	–
Bridelia cathartica	X	X	X	–
Bridelia micrantha	X	–	X	–
Canthium crassum	X	–	–	–
Canthium burtii	–	X	–	–
Canthium huillense	–	X	–	–
Diospyros mespiliformis	X	–	–	X
Ficus vallis–choudae	X	X	–	–
Ficus sycomorus	X	X	X	–
Flacourtia indica	X	X	X	X
Friesodielsia obovata	X	X	X	–
Garcinia smeathmanni	X	–	–	–
Grewia biscolor	X	–	–	–
Hexalobus englerane	–	–	X	–
Hexalobus monopetalus	X	–	–	X
Lannea discolor	X	–	–	–
Lannea edulis	–	–	–	X
Manilkara mochisia	–	X	–	–
Parinari curatellifolia	X	X	–	X
Parkia filicoidea	X	X	X	–
Piliostigma thonningii	X	X	–	–
Ricinodendron rautanenii	X	X	–	–
Rothmannia englerana	–	X	X	–
Rothmannia fischeri	–	–	X	–
Sclerocarya caffra	X	X	–	–
Sclerocarya birrea	–	–	X	–
Strychnos cocculoides	X	X	–	X
S. pungens	X	X	–	–
S. innocua	X	–	X	–
S. madagascariensis	–	–	–	–
S. spinosa	X	X	–	–
Syzygium cordatum/guineense	X	X	–	X
Syzygium guineense ssp. *afromontanum*	X	X	–	X
Tamarindus indica	X	X	X	–
Uapaca kirkiana	X	X	–	X
Uapaca nitida	X	X	–	X
Vangueriopsis lanciflora	X	X	–	X
Vangueria infausta	X	X	–	X
Vitex doniana	X	X	–	–
Vitex iringensis	X	–	–	–
Vitex mombassae/payos	X	X	X	X
Ximenia americana	X	X	X	X
Ximenia caffra	X	X	X	X

ETHNOBOTANICAL SURVEYS

The results of ethnobotanical surveys in Malawi (Maghembe & Seyani 1991), the Tabora region in Tanzania (Karachi *et al.* 1991), the eastern province in Zambia (Kwesiga & Chisumpa 1992) and in the Condo area of Zimbabwe (Campbell 1987) have shown that there are over 50 known indigenous trees with edible fruit in the miombo ecozone (Table 2). However, these fruit trees are still largely in the wild because no systematic efforts have been made to domesticate them through selection and planting, and very limited scientific effort (Mwamba 1989) has been channelled towards understanding their reproductive biology, growth rates and genetic variation. This neglect has resulted in the lack of a genetic conservation strategy for these species.

As a result of burning and clearfelling for agricultural expansion to meet the needs of the fast-growing population of southern Africa, genetic erosion of native fruit trees has probably occurred in the miombo region. A narrow range of exotic fruit trees (mangoes, guavas, pawpaws, avocado, etc) has been promoted by extension agencies, resulting in further neglect of domestication, utilisation and marketing of miombo tree species.

GERMINATION OF FRESHLY COLLECTED SEED

Germination studies were initiated with freshly collected seed (Maghembe & Prins 1993) at the SADCC/ICRAF nursery at Makoka in Zomba, Malawi, using 17 indigenous fruit tree species (Table 3). Seeds were subjected to eight treatments under conditions that can be repeated at village level (see Table 4) involving no soil sterilisation and no chemical treatments. Seeds of most species were collected in August and December 1989 from an area between Namadzi (15°34′S latitude, and 36°13′E longitude) and Mangochi (14°34′S latitude, 35°16′E longitude) in Malawi. The seeds were stored at ambient temperature and sown within three weeks of collection. For each treatment, 30 seeds were used in a randomised complete design, replicated three times. Although the Institute for Seed Testing Association (ISTA) recommends 100 seeds per replicate, it was not possible in this case.

Germination tests were carried out in transparent plastic containers (20 cm x 10 cm x 7.5 cm) filled with sieved river sand and kept moist with a sprinkler. During experimentation, temperatures ranged from 15.5°C to a maximum of 37°C. Germination was recorded daily and germinants were removed and transplanted into polythene tubes. Observations continued for 45 days. After germination studies, seedlings were grown at both sites (FRIM and SADCC/ICRAF) in a soil mixture of forest soil and river sand in a 50:50 ratio, thereby ensuring that local microflora and root symbionts were present. The seedlings were watered twice a day and root-pruned weekly.

At least one of the simplest treatments, such as direct sowing (T1), soaking (T2) and cleaning and soaking (T3), resulted in over 80% germination in all species, except *Azanza garckeana, Canthium foetidum, Flacourtia indica, Parinari curatellifolia* and *Vangueria infausta* (Table 4). For *Azanza garckeana* and *Canthium foetidum,* high germination rates (100% and 93%, respectively) were achieved by chipping (T7). *Flacourtia indica* and *Parinari curatellifolia* germinated poorly in all treatments.

It must be emphasised that conclusions drawn from these studies are based on the use of seeds stored for not longer than three weeks at ambient temperature. With *Uapaca kirkiana,* completely different results can be experienced when using older seeds. In nature, the fruits of *Uapaca kirkiana* ripen at the beginning of the rainy season, facilitating germination of the young seedlings. Seeds stored for long periods in cold room conditions show poor germination, and studies in Malawi (Ngulube & Kananji 1989) found that viability of carefully stored seeds of *Uapaca kirkiana* was lost within a month of collection.

Table 3. Some information on occurrence, distribution, tree form and fruits of the tree species tested at Makoka, Malawi

Species	Family	Characteristics
Azanza garckeana	Malvaceae	In all types of woodland, sea level to 1700 m. Bushy shrub to medium-sized tree, 3–10 m height. Fruits Feb–Sep, spherical, 2–4 cm. Sweet mucilage comes out when chewed
Bridelia carthartica	Euphorbiaceae	Stream banks, riverine fringe thicket and littoral scrub. Multistemmed shrub or tree, 4–6 m. Fruits Apr–Sep, 1 cm
Bridelia micrantha	Euphorbiaceae	Riverine forest, relic forest and open woodland. Small- to medium-sized tree, 7–15 m. Fruits Jan–Mar, ellipsoidal, 0.5–1 cm. Taste like blackcurrants
Canthium foetidum	Rubiaceae	Medium altitudes. Open woodland. Small tree, 3–5 m. Fruits Jul–Oct, 1 cm. Edible but slightly astringent
Diospyros mespiliformis	Ebenaceae	Low to medium altitudes. Woodlands, along rivers, rarely on rocky hill slopes. Medium-sized tree, 10–15 m, with dense, rounded crown giving excellent shade. Fruits Apr–Sep, ovoid, fleshy, 2.5 cm. Eaten fresh and preserved
Flacourtia indica	Flacourtiaceae	Woodland, from sea level to 1600 m. Thorny shrub or small tree, 3–5 m. Fruits Apr–Sep, berry-like, fleshy, up to 2.5 cm. Sweet/acid
Parinari curatellifolia	Chrysobalanaceae	Open deciduous woodlands on sandy soils, 500–1200 m. Large tree, up to 21 m, with a heavy, rounded crown. Evergreen. Fruits Oct–Jan, oval, 5 cm, with astringent pulp and three edible seeds
Parkia filicoidea	Leguminosae	Riparian forests, 500–1200 m. Large tree, up to 25 m, with spreading, umbrella-shaped crown. Fruits Nov–Feb; pods (15–30 cm) contain sweet, orange floury pulp
Piliostigma thonningii	Leguminosae	Woodland and wooded grassland, medium to low altitude, 300–1200 m. Small- to medium-sized tree, 3–5 m height. Fruits Jun–Sep; dry pods (pulp) and seeds as famine food (10–25 cm)
Strychnos spinosa	Loganiaeae	From sea level to 1500 m. Open woodland and riverine fringes. Shrub or medium-sized tree, 1–9 m height. Fruits Mar–Aug, spherical, with woody shell, edible pulp, 8–15 cm
Syzygium cordatum	Myrtaceae	Medium to high altitude. Riverine thickets and forests; always near water or along watercourses. Medium-sized tree, 8–15 m in height. Fruits Nov–Mar, ovoid, 1.5 cm long, fleshy, slightly sweet/acid
Tamarindus indica	Leguminosae	Low-altitude woodland, wooded grassland and bush along rivers. Medium to large evergreen tree (20–24 m) with a dense crown. Fruits Jun–Jul; pods with sticky, edible pulp, acid
Terminalia catappa	Combretaceae	Introduced from Middle East and now naturalised. Low altitudes. Medium to large evergreen tree (8–15 m). Fruits Jul–Sep; stringy, edible pulp with edible nut, 10–15 cm long
Uapaca kirkiana	Euphorbiaceae	Medium altitude, 500–1300 m. Open woodland, dominant on gravelly soil. Medium to small tree (5–10 m), with open rounded crown. Fruits Oct–Dec, spherical, 2–3.5 cm
Vangueria infausta	Rubiaceae	Medium altitude. Wooded grasslands, among rocks and sand dunes. Small deciduous tree (3–7 m) with open crown. Fruits Feb–Apr (Aug), spherical, 2–3.5 cm, sweet, edible pulp
Ziziphus abyssinica	Rhamnaceae	Medium to low altitudes. Open woodland, wooded grassland and along river banks. Shrub or small tree, up to 7 m. Fruits Jun–Sep, spherical, 1–3 cm, edible, slightly acid
Ziziphus mauritiana	Rhamnaceae	Medium to low altitudes. Small tree, 7–12 m. Open woodland, wooded grassland. Fruits Jun–Sep, edible, slightly acid, also used for distilling spirit, 1–3 cm

Table 4. Mean cumulative germination (%) of freshly collected seed studies at SADCC/ICRAF nursery, Zomba, Malawi

	Treatments[1]									
Species	T1	T2	T3	T4	T5	T6	T7	T8	F probability	Least significant difference (P<0.05)
Azanza garckeana	17	40	43	23	0	0	100	63	0.001	17
Bridelia cathartica	93	75	–	73	0	0	90	–	0.001	25
Bridelia micrantha	0	93	–	60	–	0	–	73	0.001	20
Canthium foetidum	10	47	43	13	0	0	93	87	0.001	39
Diospyros mespiliformis	80	60	–	60	0	3	87	–	0.001	22
Flacourtia indica	20	0	7	–	–	3	13	3	0.026	19
Parinari curatellifolia	0	–	–	–	–	–	17	13	0.290	NS*
Parkia filicoidea	100	77	3	–	–	–	13	97	0.001	42
Piliostigma thonningii	50	90	–	77	10	–	–	–	0.001	31
Strychnos spinosa	–	–	80	–	–	0	0	0	0.001	13
Syzygium cordatum	0	–	93	27	–	–	–	27	0.007	44
Tamarindus indica	100	93	–	–	–	–	87	–	0.444	NS
Terminalia catappa	70	97	–	17	–	–	–	–	0.008	37
Uapaca kirkiana	–	43	93	–	–	–	87	100	0.021	34
Vangueria infausta	–	–	–	–	–	–	40	–	–	–
Ziziphus abyssinica	100	80	–	87	20	0	–	–	0.001	36
Ziziphus mauritiana	100	87	–	100	0	0	–	–	0.001	16

*NS, not significant

[1] T1, Direct sowing of seed after removing the fruit pulp; T2, Soaking seeds in cold water for 24 hours after removing the fruit pulp; T3, Cleaning seeds thoroughly, ie removal of all mesocarp carefully, and soaking at room temperature for 24 hours; T4, Cleaing seeds and placing in warm water at 65°C, and left to cool for 24 hours; T5, Cleaning seeds and placing in hot water at 100°C and leaving to cool for 24 hours; T6, Cleaning seeds and placing in hot water at 100°C, allowing to boil for one minute then leaving to cool for 24 hours; T7, Scarification, ie making a hole in the seed coat, through abrading or nicking; T8, Complete removal of the seed coat

Strychnos spinosa is a species known to be difficult to germinate (Ngulube & Kananji 1989). Its seed coat may contain a germination inhibitor which is only deactivated by proper washing. Such a strategy would allow germination only after heavy rains when enough moisture is available to secure suitable growing conditions.

GERMINATION OF SEED SUBJECT TO COLD STORAGE

Seeds of 13 indigenous fruit tree species were collected locally in 1988 by the FRIM (Table 5). The seeds were kept under cold storage (4–10°C) for six months before they were tested for germination. Six pre-treatments, including a control, were applied to the seeds, including mechanical hand scarification, soaking in cold water and soaking in boiling water (see Table 6). After pre-treatment, the seeds were nursery sown into black polythene tubes (10 cm x 15 cm) filled with woodland soil. Treatments were arranged in blocks each containing 100 seeds. The plants were watered twice a day (morning and evening) for 30 days during which germination counts were made daily.

Untreated seed of *Adansonia digitata, Tamarindus indica* and *Ximenia caffra* germinated successfully during the 30-day experimental period. The

Table 5. Seed sources of the indigenous fruit trees tested at Naungu, Machinga

Species	Locality	Latitude	Longitude	Elevation (m)
Adansonia digitata	Shire valley, Nsanje	16°43′	35°00′	200
Azanza garckeana	Liwonde, Machinga	15°05′	35°25′	700
Strychnos spinosa	Liwonde, Machinga	15°05′	35°25′	700
Tamarindus indica	Shire valley, Nsanje	16°43′	35°00′	200
Ziziphus mauritiana	Liwonde, Machinga	15°05′	35°25′	700
Uapaca kirkiana	Malosa, Machinga	15°10′	35°25′	900
Uapaca nitida	Chongoni, Dedza	14°15′	30°15′	1300

results also indicate that mechanical scarification is effective with *Adansonia digitata, Uapaca kirkiana, Ximenia caffra* and *Ziziphus mauritiana* (Table 6). Cold and hot water treatments were only effective with *Adansonia digitata* and *Ximenia caffra*, but only *A. digitata* responded to hot water. Germination with the rest of the species was very poor: *Flacourtia indica, Parinari curatellifolia, Parkia filicoidea, Strychnos spinosa* and *S. innocua* did not germinate at all, regardless of pre-treatment. Boiling water did not enhance germination in any species, and prevented it in most instances. Observations on the development of *Uapaca kirkiana* seed revealed that the mature seed contains primordial leaves rather than fully developed cotyledons. It is possible that the cotyledons are killed when the seed is exposed to heat. Seed quality assessments indicated that around 90% and 12% of the seeds of *Flacourtia indica* and *Uapaca kirkiana*, respectively, were empty, which obviously affected the overall germination success, regardless of pre-treatment procedures.

The study has shown that, although it is possible to collect, germinate and store some indigenous fruit trees, there are difficulties with most species. These germination problems are possibly due to wrong timing of seed collection periods, poor processing and storage procedures, and lack of proper pre-treatment methods. It is apparent that information on the reproductive biology of most Malawian and indeed southern African indigenous fruit trees is lacking. Such information is very important for the development of suitable propagation techniques for successful domestication programmes. It is, therefore, recommended that detailed biological studies (including vegetative propagation) be undertaken to address the above aspects on selected species commonly found in traditional farming systems.

FIELD PLANTINGS AT MAKOKA AND NAUNGU, MACHINGA

The fruit trees at Makoka were assessed in June 1992 (ie after 27 months' growth), whereas those at Machinga (FRIM) were assessed after 18 months. Survival, height, root collar diameter, crown diameter and fresh mass of fruits (Makoka) were assessed. Data were based on all surviving trees at Makoka; at Machinga, 25 trees per plot were assessed. All data were subjected to analysis of variance using GENSTAT 5 (Payne *et al.* 1987).

At the SADCC/ICRAF site at Makoka, seedlings were planted out in February 1990, except for *Vangueria infausta* which was planted in January 1989. The experiment was arranged in a randomised complete block design (RCBD) with 19 accessions replicated three times. Each tree accession constituted a line plot of 2.25 m x 14 m, with seven trees planted on the ridge 2 m apart. The plots were kept free of weeds, and no fertilizers or herbicides were applied.

All fruit tree species reported survival above 90%, except *Cordyla africana* at 85% (Table 7). Differences in height were quite prominent. The fastest-growing species was *Ziziphus mauritiana*, which achieved a mean height of more than 4 m, followed by *Cordyla africana* (3.62 m), *Bridelia micrantha* (3.43 m), *B. cathartica* (3.31 m) and *Parkia filicoidea* (3.23 m). Both *Ziziphus* species showed good growth and heavy

Table 6. Germination response (%) of indigenous fruit tree seeds following pre-treatment at FRIM, Zomba

Species	Control	Scarification	Cold	Hot	Boiling[1]	Boiling[2]
Adansonia digitata	82	90	92	96	23	35
Annona senegalensis	8	12	10	2	0	0
Flacourtia indica	0	0	0	0	0	0
Strychnos spinosa	16	0	1	0	0	0
Syzygium cordatum	0	0	0	0	0	0
Strychnos innocua	0	0	0	0	0	0
Parkia filicoidea	0	0	0	0	0	0
Parinari curatellifolia	0	0	0	0	0	0
Uapaca kirkiana	10	17	12	0	0	0
Tamarindus indica	92	100	10	100	92	0
Ziziphus mauritiana	10	70	5	4	5	3
Vangueria infausta	5	20	4	6	3	5
Vitex doniana	4	3	0	0	1	0
Ximenia caffra	60	84	65	0	0	0

[1] Immersed for 30 s then sown

[2] Immersed in boiling water and allowed to cool for 12 h

Table 7. Performance of indigenous fruit trees at 27 months after planting at Makoka, Malawi

Species	Survival (%)	Height (m)	Crown diameter (m)	No. stems	Root diameter (cm)[1]	Fruit mass (g)2	Observations
Annona senegalensis	81	1.48	1.08	1	4.3	–	–
Azanza garckeana	100	1.6	1.48	2	4.4	455	–
Bridelia cathartica	90	3.31	2.9	2	7.4	97	–
Bridelia micrantha	95	3.43	2.59	2	8.5	–	–
Cordyla africana	57	3.62	4.02	2	9.3	–	–
Diospyros usambarensis	91	1.06	0.83	2	2.3	–	–
Ficus vallis-choudae	100	2.51	3.69	11	18.2	3101	Dense crown
Flacourtia indica	91	0.42	0.21	1	0.6	–	–
Parinari curatellifolia	95	1.2	1.06	11	3.4	–	–
Parkia filicoidea	100	3.23	1.19	1	6.1	–	–
Sclerocarya caffra	81	1.85	1.19	2	4.9	–	–
Strychnos spinosa	91	0.89	0.68	1	1.4	–	–
Syzygium cordatum	95	2.74	1.87	1	6.1	–	–
Tamarindus indica	100	1.78	1.74	2	4.9	–	–
Terminalia catappa	86	2.32	2.37	2	6.5	–	–
Uapaca kirkiana	100	1.74	1.43	2	5.8	–	–
Vangueria infausta	83	2.57	2.03	5	8.1	2615	–
Vitex doniana	100	0.4	0.4	1	1.2	–	–
Ziziphus abyssinica	100	2.77	3.5	1	9.1	3622	Thorny
Ziziphus mauritiana	100	4.04	2.74	3	15.5	240	Thorny

[1] Measured at the root collar

[2] Calculated as the fresh mass of fruits per tree

branching with thorns, suggesting their potential for live fencing. In addition, the species provide fodder from their leaves, and their flowers are rich in pollen and nectar and are relished by bees.

Azanza garckeana, Bridelia cathartica, Ziziphus abyssinica, Z. mauritiana, Ficus vallis-choudae and *Vangueria infausta* all produced fruits within two years after planting. For *Azanza garckeana,* this result was rather unexpected: this tree grows to over 10 m in height at maturity, yet the young trees produced fruits at 1.6 m tall. This early fruiting provides an opportunity for farmers to grow the tree and harvest fruits continuously as the tree matures. *Terminalia catappa* flowered but produced no fruits, perhaps a result of the severe drought gripping southern Africa at the time.

Seedlings of seven indigenous fruit tree species (Table 7) were tested at Naungu forestry research experimental site in Machinga (15°24′S latitude and 35°21′E longitude, 650 m asl). The site receives a mean annual rainfall between 500 mm and 800 mm. Seedlings were planted in an RCBD at 2 m x 2 m in January 1991. However, because of variation in numbers of seedlings available, the size of blocks varied for the seven species.

Tamarindus indica and *Ziziphus mauritiana* showed excellent survival (>90%), followed by *Adansonia digitata* and *Azanza garckeana* (>70%) (Table 8). The survival of *Strychnos spinosa, Uapaca kirkiana* and *U. nitida* was generally poor (Table 8). Seedlings of the three species were relatively small at planting time, which could explain the poor survival. Alternatively, they may have required mycorrhizal inoculation (see Lapeyrie & Högberg, pp158–164).

In terms of height, the fastest-growing species was *Ziziphus mauritiana*, which achieved more than 2 m (Table 9), followed by *Azanza garckeana* (1.4 m), but the rest were relatively slow-growing (<1.0 m). Similar growth rates of <1.0 m yr^{-1} were recorded for *Strychnos cocculoides* and *Parinari curatellifolia* in a field trial at the Chati Forest Research Station in Zambia. Branching height was generally less than 20 cm above-ground in all the species (Table 8), the highest being *Azanza garckeana* and *Uapaca nitida* (19 cm), and the lowest being *Uapaca kirkiana* and *Ziziphus mauritiana* (6 cm and 5 cm respectively). *Z. mauritiana* had the highest number of branches (25), followed by *Adansonia digitata* and *Tamarindus indica* (11); the other species had fewer than ten branches.

Flowering and fruiting was observed in *Azanza garckeana* and *Ziziphus mauritiana* 18 months after planting. It was, however, observed that less than 40% of the trees planted produced fruits.

Table 8. Species and source of the indigenous fruit trees seed studied at the Forestry Research Institute of Malawi

Species	Locality	Latitude	Longitude	Elevation (m)
Adansonia digitata	Shire valley, Nsanje	16°43′	35°00′	200
Annona senegalensis	Malosa, Machinga	15°10′	35°25′	90
Flacourtia indica	Malosa, Machinga	15°10′	35°25′	900
Parinari curatellifolia	Sadzi, Zomba	15°25′	35°28′	1500
Parkia filicoidea	Naisi, Zomba	15°25′	35°28′	1950
Syzygium cordatum	Naisi, Zomba	15°25′	35°25′	1950
Strychnos spinosa	Liwonde, Machinga	15°05′	35°25′	700
Tamarindus indica	Shire valley, Nsanje	16°43′	35°00′	200
Uapaca kirkiana	Malosa, Machinga	15°10′	35°25′	900
Vangueria infausta	Malosa, Machinga	15°10′	35°25′	900
Vitex doniana	Nauko, Machinga	15°05′	35°25′	1070
Ziziphus mauritiana	Liwonde, Machinga	15°05′	35°25′	700
Ximenia caffra	Chongoni, Dedza	14°15′	30°15′	1300

Table 9. Survival and growth of 18 months old indigenous fruit trees at Naungu site, Machinga

Species	Survival (%)	Height (m)	Collar diameter (cm)	Branching height (m)	No. of branches
Adansonia digitata	75	0.7	5.5	0.11	11
Azanza garckeana	78	1.4	3.1	0.19	8
Strychnos spinosa	21	0.3	1.4	0.11	5
Tamarindus indica	96	0.9	1.8	0.09	11
Ziziphus mauritiana	94	2.4	5.7	0.05	25
Uapaca kirkiana	28	0.5	3.3	0.06	6
Uapaca nitida	36	0.6	1.5	0.19	8
Least significant difference (at P<0.05)	NA	0.22	0.38	0.04	2.40
Coefficient of variation	NA	76.3	56.6	49.4	63.9

Furthermore, fruit size and taste varied between trees. Early fruiting is an important characteristic as it may encourage farmers to plant indigenous fruit trees in anticipation of early benefits. The fruiting results of *Ziziphus mauritiana* in the present study also provide an opportunity of selecting individual trees for early fruit production, as well as quality. Early fruiting was also recorded in *Strychnos cocculoides* (wild orange) and *Carissa edulis*, which fruited within five years of growth at the Chati Forest Research Station in Zambia, thus comparing favourably with exotic *Citrus* species.

PROSPECTS FOR DOMESTICATION OF FRUIT TREES OF THE MIOMBO REGION

Even though the indigenous fruit trees are a cheap source of food, medicine and fodder, there are some problems which discourage their domestication. They are perceived to grow slower and to take longer to produce fruits compared with exotic species, and often have a low ratio between edible and non-edible parts, as in the case of *Vangueria infausta* and *Uapaca kirkiana*. These problems could be overcome through selection and improvement programmes. Indigenous fruits often have little market value. For example, out of 30 indigenous fruit tree species in Malawi, only five were sold on roadside markets (Maghembe & Seyani 1991), while in eastern Zambia only 20% of the farmers have ever sold indigenous fruits (Kwesiga & Chisumpa 1992). Even if they sold some fruits on the roadside, farmers complained of low prices. Indigenous fruits with a market potential in the region include *Adansonia digitata, Uapaca kirkiana, Annona senegalensis, Vangueria infausta, Ziziphus mauritiana, Azanza garckeana* and *Strychnos spinosa*, depending on location within the miombo. Marketing will remain the single most important constraint on the domestication and genetic improvement of indigenous fruit trees in the miombo ecozone.

In addition, there is lack of appropriate technologies for preservation and processing of the fruit. Preparation of some indigenous fruits before consumption is very labour-intensive. For example, in order to consume *Tamarindus indica*, some form of processing is required to improve its taste and palatability. In the Luangwa valley of Zambia, farmers soak *T. indica* fruits in water and add ash from *Colophospermum mopane* for two days before mixing with sorghum flour to make porridge. Others which require processing are *Trichilia emetica* and *Parinari curatellifolia*. In the case of *Ricinodendron rautenenii*, the seeds have to be crushed to remove kernels which in turn have to be pounded before the oil is extracted.

Farmers in northern Malawi and most parts of Zambia do not perceive deforestation as a big problem. The majority of these farmers have not found ways of propagating the indigenous fruit trees. On the other hand, nearly every household in the miombo ecozone has several exotic fruit trees, the most widespread being *Mangifera indica*. Most adults have ignored indigenous fruit trees as they consider them only of interest to children. However, during drought and famine, these trees assume significance for the whole family. Other constraints, such as the insecurity of land tenure, technical knowledge in handling propagules, and termite and livestock damage to seedlings, are all common concerns of farmers. Irregular fruiting times and the short period when preferred fruits are available add to the discouragement of domestication. Even if the nutritional value of indigenous fruit trees is well known, very little knowledge is available to farmers about propagating this germplasm; there is no institutional framework for the promotion of planting materials, and therefore they are not available through the traditional channels of research and extension. Without overcoming most of these constraints, it will take some time before the domestication process is initiated.

The upsurge of interest in commercialisation of indigenous fruit tree products in the region is very recent. In Zambia, several years of experimentation with *Uapaca kirkiana* by the National Council for Scientific Research (NSCR) has resulted in a new brand of wine, 'MASUKU'. Following such successful ventures, further research has been initiated on natural variation in fruits of *U. kirkiana* with a view to grading fruits according to size at harvest and to provide advice in selecting orchard sites and planting stock (Mwamba 1989). Research at NSCR in Zambia is underway and aimed at selection, tree improvement and domestication of several indigenous fruit trees, including *Anisophyllea pomifera, Parinari curatellifolia, Uapaca kirkiana* and *Ricinodendron rautenenii*, which have potential for beverages, conserves, wine and oil, respectively.

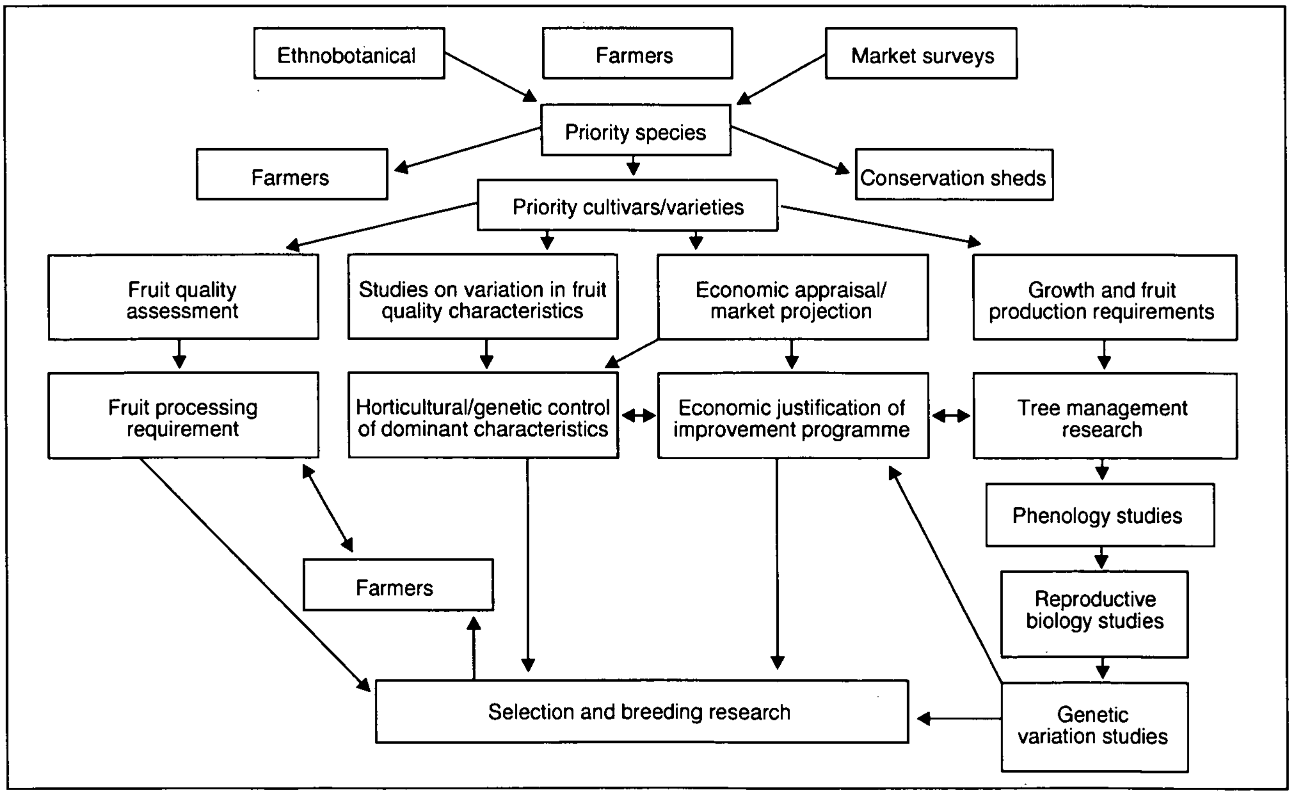

Figure 2. Diagramatic representation of the strategy developed by ICRAF for domestication of indigenous fruit trees

In Malawi, *Ziziphus mauritiana* is traditionally used in the brewing of a potent liquor, 'KACHASU'; more recently, *Z. mauritiana* fruits have been integrated with fruits of *Uapaca kirkiana* in the brewing of a new popular brand of 'MULUNGUZI' wine. In Tanzania, *Trichilia emetica* is already domesticated for the production of vegetable oil and soap.

These examples further indicate that commercialisation is the key incentive for the selection, improvement and eventual domestication of indigenous fruit trees. For example, in southern Malawi, there is a very high demand for planting material of *Uapaca kirkiana,* as well as for conserving miombo woodlands with *U. kirkiana* trees: indigenous fruit trees are known to have a market value, because the Mulunguzi winery in Blantyre is willing to purchase good-quality *U. kirkiana* fruits. Consequently, sources of the fruit are being brought under individual farmers' ownership, stretching claims to those areas where these local fruit trees are encountered. This development has implications for land tenure and the allocation of land resources between agriculture and forest conservation.

Indigenous fruit trees are a key component of agroforestry systems of the miombo ecozone, given their potential to contribute to the nutrition and cash economy of small-scale farmers (Aiyelaagbe 1992). Individual species of fruit tree cut across national boundaries and are widespread throughout the region (Table 2). Therefore, international agricultural research centres, and ICRAF in particular, should take the lead with the national institutions to develop research into domestication of this valuable resource.

ICRAF is now in the process of developing a strategy for the improvement of indigenous fruit trees (Figure 2) through the multipurpose tree improvement and management programme. Initial work in the miombo ecozone is to prioritise those indigenous fruit trees that the national institutes and farmers wish to see improved. The criterion being followed is marketability. Already, studies are underway to determine the market potential of indigenous fruit trees of the miombo.

Deforestation has almost certainly eroded much of the genetic resource of indigenous fruit trees. It is important that clear policies are adopted for conservation, and that selection, multiplication and improvement of this germplasm are initiated soon. The different interested agencies, such as universities in the region, ICRAF, forestry and agricultural research institutes and non-governmental organisations, should create a forum to discuss and co-operate on conservation and domestication strategies for indigenous fruit trees, if their genetic potential is to be fully developed in the future.

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Amazonian fruits and nuts: potential for domestication in various agroecosystems

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ABSTRACT

New crops and new agroecosystems are required to move tropical agricultural development towards sustainability, while conserving sufficient tropical forest to avoid serious erosion of tropical biodiversity and to slow global climate change. In Amazonia, numerous fruit and nut species have been identified as having sufficient potential to merit research attention; some of these are already being planted commercially. It is useful to classify these species by their degree of domestication and by their population biology because these factors can suggest the most suitable agroecosystem for a species' continued development. At least 12 fruit species were semi- or fully domesticated by native Americans before European contact, one of which was probably a staple. Several dozen were managed in swidden agroforestry or in the indigenous forest management practices that follow swiddens. A hundred or more were collected from the wild without apparent management. The population biology of most of these species requires scarcity as a strategy to limit pest and disease damage, but a few commonly occur at moderate to high densities. One domesticate, two managed species and several wild species can occur as monospecific populations, covering tens, hundreds or thousands of hectares. Because of extreme biotic pressures, conventional agroecosystems (ie monocultures) are only suitable where sufficient capital and infrastructure are available to sustain them, unless the species is pre-adapted to monoculture or research can identify production techniques that allow monoculture at low capital levels. Numerous agroforestry practices, from simple to highly heterogeneous systems, are currently the subject of intensive research and many development projects, but require new tree components. The transformation of 'natural' forests into multipurpose forest management systems, based upon the harvest of sustainably extracted fruits, nuts, and other forest products, is starting to be evaluated. The latter option offers the potential for sustainable economic yields, while maintaining forest biomass and considerable biodiversity. To develop sustainably, Amazonia must evolve into a mosaic of human settlements, conventional agroecosystems, agroforests, managed forests for multiple products (only one of which will be timber) and preservation areas. International assistance to support and expand this research and development effort is essential, and will benefit not only Amazonians but all humanity.

INTRODUCTION

During this century, agricultural development inspired by the rich societies of the northern hemisphere has reduced the number of crops planted, their genetic diversity and the complexity of the agroecosystems used to produce them. Concurrently, yields of many crops have increased dramatically, owing to improved agrotechnology and increased capital inputs. Nonetheless, the current preoccupation with sustainability suggests that, with these technologies, temperate agriculture has become more unstable, rather than less so. This is also true for tropical agriculture because the biophysical and economic factors that make temperate agriculture unstable are more intense in the tropics. Students of modern tropical agriculture now recognize that: (i) diversity can and should contribute to stability and sustainability, although this is not always true; and (ii) there is a need for the conservation of sufficient tropical forest to avoid serious erosion of tropical biodiversity (Smith *et al.* 1992). Nevertheless, the erosion of crop genetic diversity is reducing our ability to develop new crop varieties in response to current and future agricultural crises. In parallel with the increasing awareness of the need for genetic diversity, recognition is dawning of the need to conserve cultural diversity as well, as the techniques of diversified agriculture are still used by many non-Western cultures and these cultures are the *de facto* curators of the majority of the world's crop genetic diversity.

In short, it is recognised that agricultural sustainability in the tropics requires 'new' crops and 'new' agroecosystems, to run in parallel with increased conservation. 'New' crops are necessary because markets for the currently recommended tropical cash crops are at or near saturation. 'New' agroecosystems are necessary because of the poor adaptation of the northern hemisphere conventional agricultural model in many parts of the humid tropics. This approach may help to slow global climate change, because many of the 'new' agroecosystems will be based upon tree crops, and may also help to reduce the instabilities of agricultural production in many areas. This combination of new crops and new agroecosystems, with conservation, is a tall order for the research community and the development agencies. Recognition of the challenge is increasing, however, and positive steps are being taken in many countries.

In Amazonia, research on 'new' crops has been under way for the past 50 years, although continuity and comprehensiveness have been problems in all countries of the region. During the past two decades, agroforestry has also received considerable attention. Additionally, ethnobiological research has found that many native American practices extend agroforestry into multipurpose forest management systems (eg Posey 1985). Recent research suggests that at least 12% of the Amazonian forest originated from these systems (Balée 1989). Some researchers even suggest that a primeval Amazonian forest does not exist and that all the forest was modified by human intervention (Clay & Clement 1993)[1].

Among the potential 'new' crops, many fruit and nut species have sufficient merit to warrant research attention. Some of these are already planted commercially, both in monoculture and in agroforestry. It is useful to classify 'new' crops by their degree of domestication and by their population biology, because these classifications can suggest the most suitable agroecosystem for a species' continued development. This paper will focus upon a few species, their potential, the current research efforts to utilise them, and how they fit into different types of agroecosystems suitable for use in Amazonia.

Some definitions

Domestication is human-induced change in the genetics of a plant population to conform to human desires and agroecosystems, culminating in the plant's loss of its ability to survive in natural ecosystems (Harlan 1975). A full domesticate, therefore, requires human intervention to survive. A semi-domesticate is significantly modified from the wild state, but can survive if abandoned. A managed species is one that receives some degree of care but is not cultivated in Harlan's sense, ie no agroecosystem is prepared for it. A managed species may be protected during clearance of the forest for swiddens, or its volunteer seedlings may be encouraged along paths and around dwellings, or selected seed may be sown outside of cultivated areas. As Rindos (1984) points out, even managed species are subject to genetic changes and thus start to become domesticated. Cultivation is the preparation of an agroecosystem for the growth of either wild or domesticated plants (Harlan 1975).

THE DOMESTICATION CONTINUUM IN AMAZONIA

In Amazonia, it is possible to find indigenous fruit crops and potential crops in all stages of the domestication process, from wild to fully domesticated.

Wild and oligarchic species

As indicated by Prance (pp7–15), extractivism has been practised in Amazonia for millennia and may initiate the domestication of the extracted species. A hundred or more Amazonian fruits and nuts are currently collected from the wild without apparent management, although they may have been managed in the past. The population biology of most of these species apparently requires scarcity (ie a low population density) as a strategy to limit pest and disease damage in nature, but a few commonly occur at moderate to high densities in oligarchic forests.

Caryodendron orinocensis (inchi) is distributed throughout north-western Amazonia, both in the lowlands and in the Andean foothills. A closely related species, *C. amazonicum*, which may actually be an ecotype of *C. orinocensis*, occurs in north-western Brazil. The dove egg-sized nut of *C. orinocensis* is reputed to taste like the nut of *Corylus avellana* (hazel) (Recklin 1982), although one of its common names is 'tree peanut'. There are several small plantations in Colombia and Ecuador, where some research has been initiated. Some small germplasm collections exist and are partially evaluated (J B Martinez, University of Nario, personal communication, 1985). In addition, in the transitional ecotone between the Colombian Llanos and the humid tropic forest, the Corporación Araracuara systematically collected germplasm and established this in several small germplasm collections in San José de Guaviare, Colombia (E Duran, Corp. Araracuara, personal communication, 1990). However, caterpillars have become an extremely serious pest, causing complete defoliation several times a year, reducing growth and eliminating yield. This pest has not been reported in other areas (eg see Recklin 1982), but highlights the susceptibility of some wild species in low-input monoculture agroecosystems in Amazonia.

One domesticate, two managed species and several wild species can occur in Amazonia as natural or anthropogenic monospecific populations, covering tens, hundreds or thousands of hectares. Peters *et al.* (1989a) have used the term 'oligarchic' to describe this group of species (see Prance, pp7–15) and discuss four palms, *Jessenia bataua* (managed), *Euterpe oleracea, Mauritia flexuosa* and *Orbignya phalerata* (all wild), and two dicots, *Grias peruviana* (Lecythidaceae) and *Myrciaria dubia* (Myrtaceae) (both wild). Some castanhais (small areas of high abundance of managed or formerly managed trees) in Amazonia have a high enough density to be classified as oligarchic, as is the case with the domesticated *Poraqueiba sericea* (Icacinaceae), planted in low-input near-monocultures in Tamshiyacu, Peru (Padoch *et al.* 1987).

In both Brazil and Peru, research has been undertaken on the shrub *M. dubia* (caçari or camu-camu). This species is indigenous to the floodplains, where it can spend three to four months partly submerged. Its red/purple-skinned fruits contain a translucent white pulp and one or two seeds. Both the pulp and the skin contain high concentrations of vitamin C, up to 4 g in 100 g fresh pulp with skin, with higher concentrations in the skin than in the pulp (J Andrade, National Research Institute for Amazonia (INPA), personal communication, 1990). In natural stands, Peters (1990) estimated yields of 9–12 Mt ha^{-1} yr^{-1}. These yields require no agronomic or capital input, being fertilized and having pests controlled by the yearly floods (Peters *et al.* 1989a).

The Peruvian Agricultural and Agro-Industrial Research Institute (INIAA) has a small germplasm collection of the shrub-type *M. dubia* located at Iquitos with 40+ accessions (Mendoza, Picon & Gonzales 1989), while the Brazilian National Research Institute for Amazonia (INPA) maintains a much smaller one (4 accessions) at Manaus (W B Chàvez F, INPA, personal communication, 1990). INIAA researchers recently collected a tree-type *Myrciaria*, very similar in most respects to *M. dubia*, but with lower fruit acidity. It has not yet been described taxonomically.

Managed species

Several dozen Amazonian fruit and nut species were managed in swidden agroforestry or in the indigenous forest management practices that follow swiddens. *Bertholletia excelsa* (Lecythidaceae) (Brazil nut) is probably indigenous in south-eastern Amazonia, but was distributed by native Americans to most corners of the basin (Mori & Prance 1990). Until recently, this forest emergent was managed sustainably in most areas where it occurs, but some of the prime *B. excelsa* areas in south-eastern Amazonia are now being subjected to severe deforestation for pasture, charcoal production, and other land uses (Kitamura & Müller 1984).

Recently, Posey and collaborators at the Museu Paraense Emilio Goeldi, in Belém, Brazil, have shown that Amazonia's famous castanhais are mostly due to native American agroforestry and forest management practices (eg Posey 1985). *B. excelsa* seedlings were transplanted into new swiddens and then managed during the succeeding swidden fallow, thus creating the castanhais. In south-eastern Amazonia and southern Peru, these castanhais contain 50–200 trees each, at densities of 5–20 trees ha^{-1}, and occur scattered over areas of hundreds to thousands of hectares. At one time, Brazil nuts were second only to rubber (*Hevea brasiliensis*, Euphorbiaceae) as an export product from Amazonia (Mori & Prance 1990) and retain their importance in some areas, eg Madre de Dios, Peru (Sánchez 1973) and Acre, Brazil (Mori & Prance 1990).

Since the mid-1970s, the Agricultural Research Center of the Humid Tropics (CPATU-EMBRAPA), in Belém, has researched *B. excelsa* (Müller 1981; Mori & Prance 1990). CPATU has a small clonal germplasm collection. A small seedling progeny and clonal germplasm collection also exists in Acre state, at the local EMBRAPA station. A few grafted clones are being planted commercially on 3000 ha about 200 km east of Manaus (C H Müller & A Kato, CPATU, personal communication, 1990). INIAA is evaluating (1988–92) individual tree yield in castanhais near Puerto Maldonado and Iquitos to identify high-yielding trees with non-alternating harvests to form a clonal germplasm collection at Iquitos.

Theobroma grandiflorum (Sterculiaceae) (cupuassu) is a *T. cacao* relative that is enormously popular for juices, ice-creams and other confectionery products in eastern and central Amazonia (Clement & Venturieri 1990). Like *B. excelsa*, *T. grandiflorum* is indigenous to eastern Amazonia and was either collected from the wild or managed in agroforestry systems. Today it is cultivated around Belém and Manaus, where hundreds of hectares are planted annually to supply the strongly increasing demand for its pulp.

Unlike *T. cacao*, *T. grandiflorum* is exploited principally for its aril, the pulp around the seed. This has a strong flavour and aroma, which most consumers prefer diluted (eg in juice or ice-cream). The pulp (35–45% of fresh fruit mass) is frozen for export to other parts of Brazil, the United States and Europe. The seed (15–20% of fresh fruit mass) is rich (50% dry mass) in unsaturated fats (45–50% unsaturation), but has a different fatty acid profile from *T. cacao* and so makes only low-quality chocolate (Clement & Venturieri 1990). The fat is being tested for use in skin creams and other beauty products in Manaus.

There is a seedling germplasm collection of 100+ progenies of *T. grandiflorum* at INPA, Manaus, a clonal collection of more than 30 genotypes at the Amazonian Agroforestry Research Center (CPAA-EMBRAPA), Manaus, and a further collection at CPATU, Belém (20+ clones). Most of the current planting, however, uses unselected or mass-selected germplasm from established plantations (Venturieri, Alves & Nogueira 1985). CPAA and CPATU currently have active tree improvement programmes.

Domesticated species

At least a dozen Amazonian fruit species were semi- or fully domesticated by native Americans before European contact. One of these, *Bactris gasipaes* (pejibaye or peach palm), was probably a staple (Clement 1988, 1992) and is native to south-western Amazonia. It is a thorny, multistemmed palm that produces bunches of starchy fruit that are popular throughout the lowland humid tropics, from Costa Rica to Brazil. While it may have entered the domestication process in several places (Mora Urpí 1984), the most derived landraces occur in north-western Amazonia (Mora Urpí & Clement 1988). Clement and Mora Urpí (1987) have discussed its potential, and Clement and Arkcoll (1989) review the current state of knowledge.

Although *B. gasipaes* was domesticated as a staple starch crop, it is now widely planted for its heart of palm. There are about 5000 ha planted to high-density monocultures, mostly in Costa Rica, although Brazil, Colombia, Ecuador and Peru are rapidly planting large areas. Current world trade in palm hearts exceeds US$50 million, mostly extracted from wild populations of *Euterpe oleracea* in the Amazon River estuary (Mora Urpí *et al.* 1991). Several tropical American countries have active germplasm banks of *B. gasipaes* (Clement 1991), the largest being located in Costa Rica. In 1983–84, the US Agency for International Development (AID) financed a pan-Amazonian germplasm collection (Clement & Coradin 1988). Although this germplasm is conserved in all active banks, it is most actively used for improvement in Costa Rica, and to a lesser degree in Brazil and Peru.

The Costa Rican programme is concentrating on improving *B. gasipaes* for palm heart, fruit for human consumption and fruit for animal feed, with the first by far the most important. Many controlled hybridisations were made and several progeny trials installed in Costa Rica (J Mora Urpí, University of Costa Rica, personal communication, 1991). INIAA is using mass selection for fruit yield and quality and taking the resultant progeny to field trials; initial selections for palm heart have also been made. In addition to the Costa Rican priorities, the Brazilian programme, located at INPA, includes fruit for vegetable oil (Clement & Arkcoll 1991). The state of São Paulo, Brazil, has recently started a programme for palm heart (Bovi, Godoy & Saes 1988).

Another domesticate is *Eugenia stipitata* (Myrtaceae) (araza). This small shrub yields a large (50–800 g) berry with a canary-yellow, highly perfumed rind, and a canary-yellow, acid, pleasantly flavoured mesocarp. The fruit's flavour is ideal for juices and flavourings that require little or no cooking (ice-creams, creams, etc), but its flavour is lost on cooking (Clement 1990a). The perfumed rind requires investigation as a source of essential oils. Pinedo, Ramirez and Blasco (1981) suggest that the domesticated form originated in Peru, between Iquitos and the lower Ucayali River basin. Chávez Flores and Clement (1984) note that the domesticate is the subspecies *sororia* and that the wild form is subspecies *stipitata*, possibly native to Acre state, Brazil. Recent germplasm collections made by INIAA found both subspecies in Peru, adjacent to Acre state (Bello 1991).

INIAA maintains an active germplasm bank of *E. stipitata* at Iquitos with 20+ accessions (Bello 1991) and INPA maintains a much smaller one (5 accessions) at Manaus (Clement 1990a). INIAA has established field trials near Iquitos to evaluate mass-selected progenies from plants yielding the equivalent of 11–15 Mt ha^{-1}. INIAA and INPA have used phenotypic selections in experimentation and for distribution to farmers in the Iquitos and Manaus areas, respectively.

AGROECOSYSTEMS

Given our definitions of domesticated, managed and wild, it is logical to expect that each category is best adapted to the agroecosystem in which it is found or in one with a higher level of inputs. Thus, domesticates grow best in monocultures and in specific locations in agroforestry systems, although pest and disease incidence may increase as crop diversity decreases. Managed species grow best in their traditional agroecosystem but are easily introduced into monocultures, again with increased risk of pest and disease attack. While it is relatively easy to take a species from any part of the domestication continuum into a higher-input system, eg monoculture, the reverse is not true. A domesticate, adapted to high-input systems, cannot be grown successfully in systems with significantly lower inputs, eg a multipurpose forest management system. For example, *Bactris gasipaes* does not yield in closed second-growth forest (Clement 1990b). Hence, continued domestication of these crops should be designed with the appropriate agroecosystem in mind. Agronomic research in various agroecosystems on the six species discussed above is reviewed here.

Monoculture

Because of extreme biophysical pressures in Amazonia, monocultures are only suitable where sufficient capital and infrastructure are available to sustain them (Villachica *et al.* 1990), unless the species is pre-adapted to monoculture, eg oligarchic species such as *M. dubia.* Nonetheless, considerable research has been undertaken with monocultures, both as a final objective and to compare with agroforestry systems.

Table 1. Export-quality palm heart yields (kg ha^{-1}) of *Bactris gasipaes* from the first harvest at several densities and nutrient availabilities on Amazonian oxisols (nutrient availabilities given as g $plant^{-1}$ of N, P_2O_5 and K_2O) (source: Gomes *et al.* 1988; Gomes & Arkcoll 1988)

Densities (plants ha^{-1})	(0 g)	Rondônia (50 g)	(100 g)	Manaus (200 g)
1600	–	–	–	580
2500	–	–	–	1100
4444	240	640	690	1290
6666	240	1030	1290	–
10 000	290	1260	1630	–

Table 2. Yields (Mt ha^{-1}) of the first three harvests (year 3–5) of *Eugenia stipitata* at 3 m x 4 m, with and without fertilization, on a yellow oxisol (Manaus) and on a sandy entisol (Iquitos) (nutrient availabilities given as g $plant^{-1}$ of N, P_2O_5 and K_2O) (source: Villachica 1993; Alfaia *et al.* 1987)

Years	Iquitos		Manaus	
	0	0	60–120–180	60–180–120
3	2.8	4.2	4.2	4.4
4	5.5	5.9	6.8	8.8
5	12.6	9.6	15.1	17.5

Monoculture yields of *B. gasipaes* for palm heart of up to 1.6 Mt ha^{-1} have been estimated with unselected germplasm at several densities on low-fertility oxisols near Manaus (Gomes & Arkcoll 1988) and in Rondônia state (Gomes, Menezes & Viana Filho 1988), the latter at three nutrient availabilities (Table 1). These yields compare favourably with those obtained in Costa Rica on more fertile soils and with a more favourable rainfall distribution. Similar work exists in Peru, but data have not yet been published.

Monoculture yields of *B. gasipaes* for fruit from plants of different ages have been reported to vary between 3 and 30 Mt ha^{-1} yr^{-1} (Clement & Arkcoll 1989), although most of these are based upon estimates rather than measurements. Szott, Palm and Sanchez (1991) suggest yields of up to 20 Mt ha^{-1} when the plantation reaches full development on an ultisol at Yurimaguas, Peru. Picon and Ramirez (1991) report yields of 2.3 Mt ha^{-1} for the first harvest, obtained at three to four years after transplanting on to a sandy inceptisol at Iquitos. Both experiments used annual crop interplantings to simulate farmer establishment practices.

B. gasipaes is susceptible to many pests and diseases, although none have proved to be economically severe except locally. Fruitfall is a serious problem in fertilized monocultures. It is probably a nutritional (micro-nutrient) problem in which fruits from fertilized plants are susceptible to Heteroptera damage and fruitfall (Couturier, Clement & Viana Filho 1993). Fruitfall has not been reported from unfertilized plots or from agroforestry systems. A coleopteran has recently become a significant pest in the Chocó region of Colombia, causing severe losses (A Velasco F, Palmito del Pacifico, personal communication, 1991).

E. stipitata monocultures have proven to be very productive, both in Brazil and in Peru (Table 2). In Manaus, maximum yields were obtained in the fourth harvest (sixth year), estimated at 35 Mt ha^{-1} with the maximum fertilization at a density of 1667 plants ha^{-1} (2 m x 3 m). Yields in Peru are similar and still increasing; it is expected that maximum yields will be attained at nine or ten years. Fruitflies limit yields, however, although they can be controlled at economic levels with baited traps and good plantation sanitation.

A moderately fertilized, high-density (1667 plants ha^{-1}), ten-year-old monoculture of *M. dubia* at INIAA in Pucallpa has yielded 7–8 Mt ha^{-1}. Growth was slow for the first six years, which stimulated research to use grafted plantings. Grafted plants often flower and produce fruits earlier than seedlings (2–3 *versus* 4–5 years). At INPA, 300 plants were established on the dry uplands (oxisols) where the species does not normally occur. Only five plants (2%) presented good yields, extrapolated to 7 Mt ha^{-1} yr^{-1} (W B Cháves F, INPA, personal communication, 1990). INIAA has started to encourage small commercial plantings in the floodplain near Iquitos and on poorly drained soils near Pucallpa, on the lower Ucayali River.

Experimental yields of *B. excelsa*, *T. grandiflorum* and *C. orinocensis* have not been reported to date. The fertilization and spacing requirements of *T. grandiflorum* are being studied in Brazil, but the two nut species are not receiving the same attention. *C. orinocensis* is limited by a defoliator in monocultures. *T. grandiflorum* is limited by *Crinipellis perniciosa* (witch's broom) in Amazonia, which is more severe in monoculture than in agroforestry systems (Clement & Venturieri 1990). Neither *B. excelsa* nor *M. dubia* have had severe pest problems reported to date.

Agroforestry

Many agroforestry practices, from simple to highly heterogeneous systems, are now the subject of intensive research and many development projects in Amazonia. Many of the fruit and nut crops listed here have great potential for agroforestry systems and are now being incorporated in both experimental and developmental plots.

Clement (1986, 1989) has reviewed the early, more empirical studies and discussed the agroforestry potential of *B. gasipaes*. More recently, Szott *et al.* (1991) discussed results obtained at Yurimaguas, while Picon and Ramirez (1991) presented results of a *B. gasipaes* x *E. stipitata* trial near Iquitos. In the latter trial, *Manihot esculenta* yielded close to the regional mean in the first two years, but yielded poorly in year three because of competition from *B. gasipaes* and declining soil fertility (Table 3). It is, however, too early to determine whether the polycrop systems yield better than the monocultures.

Table 3. Establishment phase yields (Mt ha^{-1}) of *Bactris gasipaes* and *Eugenia stipitata* in monoculture (625 plants ha^{-1}) and polyculture (312 plants ha^{-1} of each species) at Iquitos, with *Manihot esculenta* used as an intercrop (source: Picon & Ramirez 1991)

Cropping system	Crop	Years 1987	 1988	 1989	 1990	Total
Monoculture	*B. gasipaes*	–	–	–	2.3	2.3
	M. esculenta	7.2	8.5	3.5	–	19.2
Monoculture	*E. stipitata*	–	–	0.4	3.7	4.1
	M. esculenta	6.9	8.5	6.8	–	22.2
Polyculture	*B. gasipaes*	–	–	–	1.3	1.3
	E. stipitata	–	–	0.2	0.3	0.5
	M. esculenta	7.7	8.5	3.1	–	19.3

Promising results were obtained from *B. gasipaes interplanted with Artocarpus altilis* (Moraceae) and *A. integrifolia* at INPA (Arkcoll 1982). *B. gasipaes* as a shade for *T. cacao* gave such promising results that the Brazilian Cacao Commission (CEPLAC) recommends its use as productive shade in Amazonia (P T Alvim, CEPLAC, personal communication, 1989). *B. gasipaes* is intercropped with *T. grandiflorum* and many other species in Brazil, Peru and elsewhere in tropical America, as well as being a common component of most Amazonian swiddens (Clement 1986, 1989).

The managed species, *B. excelsa* and *T. grandiflorum*, are traditionally planted in swiddens, although monocultures have recently become fashionable. The CPATU station, in Belém, has several experiments with *B. excelsa* as shade for *T. cacao* and other small-statured perennials. Because *T. grandiflorum* has a growth habit similar to that of *T. cacao*, current recommendations are that it should also be planted in partial shade (G A Venturieri, University Federal do Pará, personal communication, 1990).

C. orinocensis is occasionally planted in swiddens or private gardens (Recklin 1982). Given its susceptibility to pests, however, its further development should be encouraged in agroforestry systems or multipurpose forest management areas. *M. dubia* is an ecological weed in its natural environment, which is why it can occur at monoculture densities and has adapted so well to agroecosystems. Peters (1992) has recommended sustained yield management of natural populations of *M. dubia* in Peru, and this species is now being researched by INIAA.

Multipurpose forest management

The transformation of 'natural' forests into traditional multipurpose forest management systems, based upon the harvest of sustainably extracted fruits, nuts, and other forest products, is starting to be evaluated (Lamb 1991; Nepstad & Schwartzman 1992). This practice offers the potential for sustainable economic yields, while maintaining forest biomass and considerable biodiversity (Myers 1984).

Peters, Gentry and Mendelsohn (1989b) suggest that this type of management in a Peruvian forest near Iquitos could sustainably yield sufficient income to be attractive to farmer-foresters, but transportation and marketing are limiting factors there. Anderson (1990) states that this type of management of an oligarchic forest of *Euterpe oleracea* is sustainable near Belém. Anderson, May and Balick (1991) suggest that oligarchic forests of *Orbygnia phalerata* can be sustainably managed in south-eastern Amazonia, although these forests are being degraded rapidly today.

To make multipurpose forest management viable in Amazonia or elsewhere, new markets must be found for traditional products and developed for new ones (Clay & Clement 1993). Often, economic densities of species with markets must be created in the forest to facilitate harvesting (Clement 1993). Of the species discussed in this paper, only the managed species, *B. excelsa* and *T. grandiflorum,* and *C. orinocensis* (wild nut) are suitable for inclusion in forest management plots, because they are still adapted to forest conditions, and especially to competition for light.

SUSTAINABLE DEVELOPMENT BASED UPON TREES

To develop sustainably, Amazonia must evolve into a mosaic of human settlements, conventional agroecosystems, agroforests, managed forests for multiple products (only one of which will be timber) and preservation areas. Sustainability can be attained technologically, as shown by Sanchez *et al.* (1982) at Yurimaguas and by many Brazilian and Peruvian researchers (Villachica *et al.* 1990), but this alternative is only viable if the technology is available to farmers and they have the capital to pay for it.

Unfortunately, the vast majority of Amazonian farmers do not have either the capital or the access to the technology that would allow them to farm sustainably in conventional high-input, low-diversity agroecosystems. For these farmers, agroforestry holds great promise because it is a practice with which they are already familiar. Furthermore, it husbands scarce resources, both biologically and in terms of family labour and capital. The establishment phase of agroforestry systems requires special attention, so that farmers can generate income while their tree crops are maturing (Villachica *et al.* 1990). However, the number of crops that currently have extensive markets and that can be grown in agroforestry systems is small. Thus, to enhance the viability of expanded agroforestry production in Amazonia, it will be essential to search for new crops and to develop new markets for them (Clay & Clement 1993).

Multipurpose forest management systems are already practised by many small farmers/extractivists in Amazonia and elsewhere in the wet tropics (eg Gómez-Pompa & Kaus 1990; Groube 1989) and potentially offer the most sustainable form of land use. Research in this area has barely started, however, so that almost everything remains to be done to develop this desirable blend of production and conservation. International assistance to support and expand research and development into this area is essential, and will benefit not only Amazonians but all humanity.

NOTE

[1] Although this suggestion has not yet been proved, it is based upon a synthesis of the following sources: large human populations in pre-history (Denevan 1992); occupation of all major natural ecosystems in Amazonia, both in pre-history (Denevan 1992) and currently; the existence of sophisticated resource management systems to support these populations in pre-history and in the present (Posey & Balée 1989); agroecosystems that extend our western ideas of such systems and include all of the environment manipulated by human groups (Alcorn 1989), including both indigenous (Alcorn 1989; Balée 1989; Moran 1989) and folk groups (Moran 1989; Parker 1989). Balée's (1989) estimate of 12% of Amazonia being anthropogenic forests includes only those with the most obvious changes caused by human intervention. Less obvious changes are more likely in most of the region but more difficult to detect.

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Genetic improvement of West African tree species: past and present

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ABSTRACT

Internal and external demand for indigenous tropical hardwoods is increasing in many West African countries, while natural forests have become depleted as a result of over-exploitation. Selective logging has probably eroded the gene pools of some traditionally well-known species. Owing to a lack of information and various biological problems, insufficient seed is available for the reforestation programmes which are required to reduce the deforestation pressures on the surviving areas of natural forest.

The identification of these biological problems, and the realisation of their imminent environmental and commercial consequences, resulted in enhanced research efforts in various West African countries in the late 1960s. Studies on seed management, provenance evaluation, vegetative propagation and genetic selection for improved yield and quality are some of the areas of research initiated for the domestication of a few important indigenous hardwood species. These developments by the individual countries of West and Central Africa have been supported by the UK Overseas Development Administration, the International Tropical Timber Organisation, the Danish International Development Agency and the World Bank.

Provenance trials and gene banks have been established in Ghana, Cameroon, Nigeria and in Côte d'Ivoire, representing much of the geographical range of certain species, with clonal testing also initiated in Nigeria, Côte d'Ivoire, and currently Cameroon. Clonal evaluations have resulted in better understanding of genetic variability, and for *Triplochiton scleroxylon* (obeche) an overall gain in stem volume of over 30% has been achieved. Studies on the early growth of obeche clones have included the relationship between branching frequency and apical dominance, as well as measurements of photosynthesis, as aids to early selection of desirable genotypes. Developments from these research efforts have enhanced reforestation, particularly in Côte d'Ivoire and Nigeria.

At least in the short term, substantial benefits could be achieved in West Africa by the establishment of clonal plantations of indigenous trees, exploiting variation present in wild populations. Renewed efforts in this area could help to ensure a continuing timber supply in the future.

INTRODUCTION

In most West African countries, the demand for indigenous tropical hardwoods for export and domestic consumption is increasing, while the natural forest is being depleted as a result of over-exploitation (Table 1). Population pressure on the forests and demand for land for other uses are major issues affecting the forest industry (Table 2). In addition to these problems, selective exploitation of the remaining forest resources has

Table 1. Balance of supply and demand for major wood products in Nigeria (millions of m^3 roundwood equivalent) (source: Agricultural Development in Nigeria, 1983–2000, Forestry Sector Review)

		1975			1985			1995	
Product	Demand	Supply	Deficit	Demand	Supply	Deficit	Demand	Supply	Deficit
Sawnwood	2.0	2.0	–	4.8	2.2	2.6	11.6	2.4	9.2
Plywood	0.1	0.1	–	0.4	0.1	0.3	1.4	0.1	1.0
Paper products	0.6	–	0.6	1.9	0.5	1.4	5.2	1.0	4.2
Poles	1.6	0.8	0.8	2.0	0.8	1.2	2.3	1.0	1.3
Firewood	42.0	42.0	–	48.0	49.0	(+1.0)	54.0	54.0	–
Total	46.3	44.9	1.4	57.1	52.6	4.5	74.5	58.5	16.0

Table 2. Area of tropical moist forests in some West African countries (source: FAO/UNEP 1981)

	Area (km^2)		Estimate of population	
	Total	Tropical moist forest	Total (10^6)	Persons km^{-2}
Cameroon	475 442	179 200	7.1	15
Côte d'Ivoire	322 463	44 580	8.0	25
Gabon	267 670	205 000	0.5	2
Ghana	238 538	17 180	11.4	48
Liberia	96 320	20 000	2.0	21
Nigeria	923 768	59 500	85.0	92
Sierra Leone	73 326	7 400	3.4	46

probably reduced the diversity of the available gene pool of most of the important timber species, such as *Milicia* (syn. *Chlorophora*) *excelsa, Entandrophragma angolense, Terminalia* species and *Triplochiton scleroxylon*, among others. However, the information on this aspect is scant.

Hardwood timber supplies have traditionally depended on natural forest management techniques for regeneration (Kio 1983), until this method was found to be insufficiently productive (Food and Agriculture Organisation 1989). The dependence on natural regeneration, coupled with poor control of logging in the Forest Reserves, has led to over-exploitation of the forest in humid W Africa, except where the terrain does not allow easy access, or where the areas are traditionally protected (fetish groves). Such areas are a valuable resource of germplasm, but they are being threatened by deforestation, which is continuing to have serious environmental and economic consequences. Reviewing the forest situation in Côte d'Ivoire, Caulfield (1982) reported that this country had lost more than 70% of its rainforests since the turn of the century. A continuing annual rate of deforestation of around 10% was expected to make Côte d'Ivoire a net importer of timber in the 1990s (Bourke 1987). Similarly, Nigeria and Ghana are expected to be unable to meet the internal demand for timber in a very short time. Because of this, Nigeria and Ghana banned further exports of certain timbers in 1976 and 1978, respectively, in order to help meet domestic wood requirements (Kio 1983). Partly as a result of its lower population and poor access to the eastern part of the country, Cameroon still has a significant timber resource, but at the International Tropical Timber Organization (ITTO) meeting at Yaoundé in May 1992, it was revealed that Cameroon loses 200 000 hectares of its moist forests annually.

With the high rates of deforestation, it became clear in the late 1960s that action was needed to restock the moist forests and to initiate intensive plantation forestry. At this time, most re-afforestation schemes in West African countries depended on exotic fast-growing hardwoods such as *Tectona grandis* and *Gmelina arborea* to meet the future hardwood needs of the population. *Eucalyptus* and *Pinus* species were grown for pulp. Seeds of these exotic species were available from trials located at various sites in these countries, so allowing the implementation of large-scale reforestation programmes for the production of lumber, industrial cellulose and poles. Attempts to plant indigenous species were also made, whenever seeds were available. However, the tendency was to plant exotics rather than indigenous species, as the silviculture of the former was better known. In the case of *Triplochiton scleroxylon*, the lack of planting was due to the poor and irregular seeding habit and the susceptibility of the seeds to insect attack (Britwum 1973b; Jones 1974; Howland & Bowen 1977). In others (iroko and mahogany), there were severe pest problems. In general, however, exotics were preferred because of their faster growth and the expectation of greater economic returns.

Despite early interest in indigenous hardwoods going back to colonial times (eg 1930–50s), it was not until the late 1960s and 1970s that it was realised that research on regeneration methods was needed, and that tree improvement could generate improved economic returns. Tree improvement programmes were, therefore, initiated at this time in Ghana, Côte d'Ivoire and Nigeria. The present paper presents what has been accomplished over the past 25 years under these and other more recent programmes with indigenous species.

COLLABORATIVE SCHEMES FOR RESEARCH AND DEVELOPMENT

The history of tree improvement in West Africa cannot be complete without mention of various overseas governments, institutes and agencies. The example of *T. scleroxylon* will be emphasised as this was recognised as the species for which there were major problems and great commercial interest. The first action was in Ghana, at the Forest Products Research Institute at Kumasi, where clonal seed orchards of *T. scleroxylon* and *Terminalia ivorensis* were established in 1972 and 1973 and techniques of rooting juvenile cuttings were pioneered (Britwum 1970b), with external funding by the UK Overseas Development Administration (ODA). Subsequently, in 1971, the West African hardwoods improvement project (WAHIP) was initiated for the most promising indigenous hardwood tree species of West Africa at the Federal Department of Forest Research (later the Forest Research Institute of Nigeria [FRIN]) at Ibadan. WAHIP continues to the present day, but overseas funding ceased in 1977. This project was based on the use of vegetative propagation and clonal selection, again with external funding from ODA (Howland & Bowen 1977). In 1974, WAHIP was supplemented by a project to study the physiology of rooting in *T. scleroxylon* at the UK Institute of Tree Biology (later the Institute of Terrestrial Ecology [ITE]) in Edinburgh. Research on this and other West African hardwoods at ITE has continued up to the present. Together, these projects have developed techniques in *T. scleroxylon* to store seeds, root stem cuttings, select superior clones, induce flowering and establish breeding programmes, as part of an overall package to domesticate this commercially important timber tree (Longman & Leakey 1993).

As a result of this research, commercial planting of clonal *T. scleroxylon* was initiated by 'Safa Splints' in the 1980s, using a mixture of selected clones provided by FRIN. A somewhat similar programme of vegetative propagation and clonal selection started in Côte d'Ivoire in the 1970s at Centre Technique Forestier Tropical (CTFT), with funds from the French Government (Verhaegen 1992). The practical application of these techniques, particularly with *Terminalia ivorensis*, was initiated as part of a World Bank/ Commonwealth Development Corporation project based in the Société de Dévéloppement des Forêts (SODEFOR), in collaboration with CTFT. Later in 1987 with funds from French Aid and Cooperation Fund, a similar industrial-scale project was initiated by SODEFOR at Téné (Verhaegen *et al.* 1992). Currently work continues at the Institut de Dévéloppement des Forêts (IDEFOR, previously CTFT) with clonal selection of *Triplochiton scleroxylon.*

In the early 1980s, an attempt was made to initiate a 'regional programme for improvement of tropical hardwoods for West and Central Africa'. Detailed proposals were prepared with funding from the European Commission (Leakey & Grison 1985) but the programme, which spanned Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Nigeria, Cameroon and Congo, never materialised.

In the late 1960s and early 1970s, CTFT in the Congo was also developing a clonal approach to indigenous hardwoods (in parallel with their well-known programme on *Eucalyptus* species at Pointe Noire [Delwaulle, Laplace & Quillet 1983]), but with *Terminalia superba* instead of *Triplochiton scleroxylon* (Martin & Quillet 1974; Koyo 1983, 1985). Similarly, early studies in Gabon by CTFT concerned another hardwood, *Aucoumea klaineana* (Grison & Hamel 1978).

In addition to timber tree species, genetic improvement studies were in progress in Nigeria in the 1970s and 1980s with indigenous fruit trees (see Okafor & Lamb, pp34–41). Further work to domesticate fruit trees is currently in progress in:

- Cameroon with *Ricinodendron heudelottii* and *Irvingia gabonensis* at the Forest Research Station of Agronomic Research Institute at Kumba (P Shiembo, unpublished) and with *Dacryodes edulis* (J Kengue, unpublished) at the Agronomic Research Institute at Nkolbisson; and
- Côte d'Ivoire with *Coula edulis* (L Bonnélin, unpublished) in Tai National Park, in collaboration with Wageningen University.

Currently, much of the research done with *T. scleroxylon* over the past 20 years is being applied in Cameroon by the Office National de Dévéloppement des Forêts (ONADEF, formerly the Office National de Regénération des Forêts (ONAREF)) in collaboration with ITE and with external funding from ODA (see Lawson, pp112–123). This project is part of the Cameroon and UK governments' response to the Tropical Forest Action Plan. This project has built on the earlier activities of the ONAREF Parc de Bouturage (Leakey 1985), which was part of the Cameroon/World Bank forestry project.

Current studies are also in progress in Ghana, with ITTO funds, to select and propagate vegetatively clones of *Milicia* (syn. *Chlorophora*) spp. resistant to the gall-forming psyllid *Phytolyma lata* (Cobbinah 1990). Further work on the vegetative propagation of *M. excelsa* is in progress at FORIG, Kumasi (D Ofori, unpublished).

Studies have also been made with clones of *Gmelina arborea* in Cameroon (Bibani 1983) and in Côte d'Ivoire (Kadio 1990), while other approaches to tree improvement are in progress with exotic hardwoods in Ghana, eg *Tectona grandis* provenance trials in collaboration with Danish International Development Agency; *Cordia alliodora* and *Cedrela odorata* provenance trials in collaboration with Oxford Forestry Institute; and *Gliricidia sepium* with the International Centre for Livestock in Africa.

DEVELOPMENTS FROM RESEARCH ACTIVITIES, ESPECIALLY WITH *TRIPLOCHITON SCLEROXYLON*

Substantial information has been acquired over the past 20–25 years of research on various aspects of tree improvement in West Africa. To establish plantations, and to make better use of available land, there is a need to domesticate commercially important species. Genetic variation within a tree species offers the opportunity for selection of superior high-yielding populations and individuals. However, very few tropical trees have been improved genetically because of the difficulties of making improvements by breeding in tree species which have such a long life cycle, which do not flower regularly and do not become sexually mature for many years, and which are not self-fertile (Burley 1985).

Seed storage

It is now known that seed of *T. scleroxylon* is available each year in small quantities and that mast years occur every four to seven years. Further, with adequate seed harvesting, processing and storage as developed by Howland and Bowen (1977), viability can be maintained for six years (Ladipo 1984). Regular power failures, however, result in considerable losses of stored germplasm. Seed of a number of other species (eg *Mansonia altissima* and *Entandrophragma angolense*) have also been stored successfully (Gyimah 1984; Damptey 1968).

Provenance trials

Provenance trials provide information on geographical variation within species, which enables the best seed sources to be identified and selected. This was the first strategy employed in tree improvement in West Africa (Britwum 1973a, 1978).

Triplochiton scleroxylon

A major provenance trial established in Nigeria under WAHIP included investigation based on seed collected from the following six countries: Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Nigeria and Cameroon, forming the West African moist forest region and spanning most of the natural range of this species. Results revealed substantial variation in growth, with the Nigerian and Côte d'Ivoire provenances showing the greatest promise (Howland & Bowen 1977).

Working on some Nigerian provenances, Adedire (1986) also reported substantial early variation between the seedlots evaluated. The Oturkpo provenance performed better in height and diameter than the Obubra and Ubiaja provenances.

Terminalia superba

In 1969, CTFT, Côte d'Ivoire, started provenance trials of *T. superba* using 16 provenances from Sierra Leone (1), Côte d'Ivoire (3), Ghana (3), Cameroon (3), Gabon (3), Congo (1) and Central African Republic (2). Results of assessment three years after establishment showed significant differences between provenances in height growth and stem form (Delaunay 1978a). The best provenance was from Ghana (Abofour) with a mean height of 9.4 m, almost double that of Dahomey (Quedo) provenance with a height of 5.3 m. The Ghana-Abofour provenance was followed by two provenances from Côte d'Ivoire and two from Cameroon. The provenances from Congo and Gabon were poor and that of Dahomey was the worst. Studies using electrophoresis have examined the polymorphism of enzymatic systems differentiating 'fraké' in Côte d'Ivoire from 'limba' in Congo (Vigneron 1984). The former were more polymorphous.

Terminalia ivorensis

This species has been planted extensively in many countries in West Africa, especially under the taungya system in high forest areas. Provenance trials exist in Ghana, Côte d'Ivoire and Cameroon.

In 1973, Ghana and Côte d'Ivoire exchanged *T. ivorensis* seeds for provenance studies. The provenances tested in Ghana included five from Ghana, three from Côte d'Ivoire and one from Cameroon. Results of assessment for height growth in Ghana showed a highly significant difference between the Cameroon provenance and the provenances from Ghana and Côte d'Ivoire (Britwum 1978; Delaunay 1978b). The Cameroon seed source was the poorest on all the three sites tested. There were no significant differences between the Ghana and the Côte d'Ivoire provenances. Some of the trees in this study started to flower in 1976. There was no observed provenance variation in flowering.

Tree breeding

Plus-tree selection and seed orchards

To aid genetic improvement, it is important that superior genotypes are identified and centralised. In Nigeria (FRIN), budwood from 105 plus-trees of *Triplochiton scleroxylon* were collected and propagated by grafting before 1976 (Howland & Bowen 1977). These were preserved in field plantings at three sites and in the nursery. Many of the identified and labelled plus-trees in farmland were subsequently felled. Thus, the grafted material provides an important germplasm resource, although relatively few of these grafts have subsequently provided seeds. These nursery plants at least are not subjected to the risks of fire or logging.

A similar programme of selecting provisional plus-trees of T. scleroxylon and T. ivorensis in Ghana, in the natural high forest, was started in 1968 (Jones 1968, 1970; Britwum 1970a). The phenotypic characteristics on which selection was based, as in Nigeria, included height growth and tree form. Most of these plus-trees, other than those in clonal seed orchards, have subsequently been lost through logging.

Clonal seed orchards

Apart from the nursery stock described above, all other propagules derived from 30 mature plus-trees were in established experiments and have now been converted into clonal seed orchards (Howland & Bowen 1977) at field sites in southern Nigeria.

Clonal seed orchards of *T. scleroxylon* and *Terminalia ivorensis* were established in Ghana in 1972 and 1973, using scion material collected from provisional plus-trees and budded on to seedling root stock. Twenty clones of each species were used to establish the two orchards in South Formangsu Forest Reserve (Britwum 1973a).

Flowering and fruiting in both the Ghanaian and Nigerian *Triplochiton scleroxylon* seed orchards have generally been poor. Some of the clones have never fruited, but clone 4 in Ghana has flowered almost every year since 1974. In Nigeria, two trees of S93 in Sapoba have flowered consistently and much more frequently than the other clones.

Vegetative propagation

Cuttings of *T. scleroxylon* were rooted originally to circumvent seed problems. Subsequently, the extent of clonal variation indicated the potential of selecting clones for their superiority in growth and form. Research on the rooting of single-node leafy cuttings has reflected these changes in the reason for clonal propagation.

In the early 1970s, the objective was to achieve a practical and reliable method of bulking up planting stock (Britwum 1970b; Okoro 1974; Howland 1975) using mist and non-mist propagators. Ladipo (1985) further demonstrated that rooted cuttings could be as good as seedlings for commercial field use and that no problems of plagiotropism occurred. From 1974, greater emphasis was placed on understanding the sources of variation in rooting ability and the achievement of physiological understanding, such that stockplant management could ensure cost-effective and sustainable methods of rooting to retain juvenility during mass propagation (Leakey 1983; Leakey, Dick & Newton 1992). This work to acquire physiological understanding of the rooting process continues and is presented in greater detail by Leakey, Newton and Dick (pp72–83).

More recently, since 1986, progress has been towards scaling up the operation and applying the existing knowledge in a forest regeneration project in Cameroon (Lawson, pp112–123) and Côte d'Ivoire (Verhaegen *et al.* 1992). Currently, in Cameroon, propagation in the ONADEF/ODA forest management and regeneration project's Parc de Bouturage is producing about 20 000 rooted cuttings for planting about 30 ha each year (Leakey, Njoya & Bockett 1992; Lawson, pp112–123). This project is utilising low-technology non-mist propagators (Figure 1), which have been adapted from an earlier design used in Nigeria. These propagators are cheap and simple and so are suitable for rural development projects in the tropics (Leakey *et al.* 1990).

In Côte d'Ivoire, cuttings are rooted under mist propagators with a capacity of 250 000 cuttings per year. For research purposes, these propagators are enclosed with shade cloth (40% shade) and misted twice a day (Verhaegen *et al.* 1992). On average, the rooting success is 68%. In the period December 1990 to March 1991, 40 000 cuttings had been set in these propagators, and mean rooting success had increased to 80%.

The developments with *T. scleroxylon* have now been transferred to other species (Table 3), with intensive projects on *Khaya ivorensis* and *Lovoa trichilioides* (Tchoundjeu 1989; see also Newton *et al.*, pp256–266). In addition, detailed studies on *in vitro* micropropagation have been completed with *Khaya ivorensis* and *Nauclea diderrichii* (Mathias 1988).

Clonal selection

Selection for improvement is one element of the domestication process currently employed for *Triplochiton scleroxylon* and some other native hardwood species in West Africa. It has been used at FRIN and by ITE in Nigeria (Howland & Bowen 1977; Leakey & Ladipo 1986), at CTFT/IDEFOR in Côte d'Ivoire (Verhaegen *et al.* 1992), and has recently started at ONADEF in Cameroon (Leakey, Njoya & Bockett 1992). Many species have problems of seed availability, and vegetative propagation is capable of

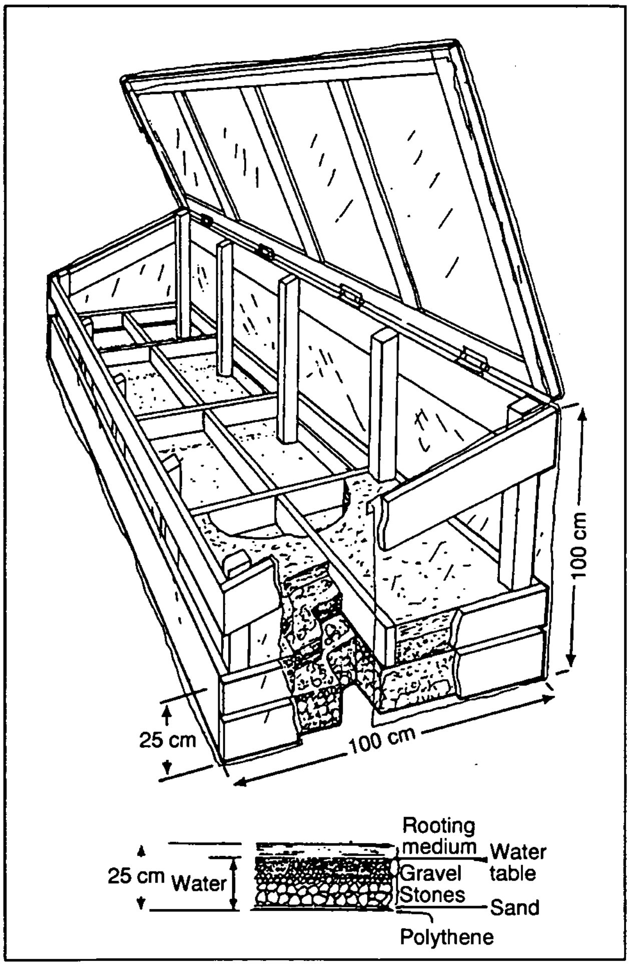

Figure 1. Diagram of the construction of an ITE non-mist propagator (source: Leakey *et al.* 1990)

Table 3. Indigenous timber tree species of moist forests of W Africa vegetatively propagated using intermittent mist and simple low-technology propagators

Species	Family	Other uses	Country where propagated
Entandrophragma angolense	Meliaceae		UK
Entandrophragma cylindricum	Meliaceae	Carving	Nigeria, Cameroon, Ghana
Entandrophragma utilis	Meliaceae	Medicine	Ghana, Nigeria
Khaya ivorensis	Meliaceae	Carving	Cameroon, Nigeria, UK
Lovoa trichilioides	Meliaceae	Carving	Cameroon, Côte d'Ivoire, UK
Mansonia altissima	Sterculiaceae	Fuelwood/food	Ghana, Nigeria
Mitragyna stipulosa	Rubiaceae	Carving	Ghana, Nigeria, Cameroon, UK
Milicia excelsa	Moraceae	Medicine	Ghana, Cameroon
Nauclea diderrichii	Rubiaceae	Carving	Nigeria, Ghana, Cameroon, UK
Pericopsis elata	Leguminosae	Carving	Ghana
Terminalia ivorensis	Combretaceae	Fuelwood	Nigeria, Côte d'Ivoire, Cameroon, UK
Terminalia superba	Combretaceae	Fuelwood	Nigeria, Cameroon, Côte d'Ivoire, UK
Triplochiton scleroxylon	Sterculiaceae	Canoe building	Ghana, Nigeria, Cameroon, Côte d'Ivoire, UK

circumventing them. With propagation methods already well developed, it is then possible to increase the productivity of the plantations or agroforestry systems by selecting elite clones and propagating them vegetatively to provide large quantities of genetically superior planting stock.

In Nigeria, clonal trials representing the full geographical range of *T. scleroxylon* have been established at five sites. The first phase of the study examined the variation in a wide range of growth characteristics among large numbers of clones of different seed origins in an attempt to identify criteria for clonal selection (Ladipo *et al.* 1983). Selection of the ten tallest clones at 18 months old from this randomly chosen clonal population of 98 clones originating from 15 seedlots showed a potential height gain of 16.5% over the mean of all plants. At nearly five years, a selection of 33% of the clones with both above-average mean stem volume and mean stem scores resulted in potential overall gains in volume of 30.5%. These gains could be substantially improved, however, by the selection of the best ten clones, resulting in about 80% improvement in yield (Leakey & Ladipo 1986). For a large-scale clonal reforestation programme, it is necessary to have a strategy of clonal selection and deployment that will maximise productivity while minimising the risk of utilising a narrow genetic base and also minimising the risks of ecological problems. Consequently, an approach has been developed for *T. scleroxylon* to introduce a large number of unrelated clones (Leakey 1991; see also Foster & Bertolucci, pp103–111), and to ensure the conservation and wise use of germplasm.

To achieve this objective by testing large numbers of clones in field trials is not practicable, so efforts have been made to identify desirable characteristics at an early age. This approach is geared towards screening for 'superior' seedlings in the nursery, as a preliminary procedure to reduce the numbers of clones to be tested in the field. Having examined the possibilities of identifying selection criteria, it became apparent that branching frequency was important to both yield and form, with low branching frequency being preferred. Consequently, after standardising environmental and morphological variables, Ladipo (1981) examined clonal variation in apical dominance (the process of determining branching frequency). He identified conditions under which a nursery study of sprouting following decapitation could be used as a 'predictive test' to select potentially superior clones (Ladipo, Leakey & Grace 1991a, b). Using this test, a strong relationship (r=0.76; P=0.001) was found between the bud activity at weeks 3–4 in young decapitated plants of *T. scleroxylon* and the branchiness of four-year-old trees of the same clones in plantations (Ladipo *et al.* 1991c). It, therefore, seems that, at least for trees conforming to Rauh's model of branching architecture (Hallé, Oldeman & Tomlinson 1978), there is potential for screening seedlings in the nursery for those worthy of inclusion in clonal field trials.

The predictive test described above is currently being utilised in the Parc de Bouturage of the ONADEF/ODA forest management and regeneration project at Mbalmayo in Cameroon. Recently, 14 000 seedlings of *T. scleroxylon* of ten seed origins have been subjected to the test to identify those for subsequent cloning and field plantings (see Lawson, pp112–123).

In Côte d'Ivoire, a different approach has been taken to clonal selection in *T. scleroxylon*. In this instance, a four-year-old plantation of 191 ha on good soil at Mopri was used to select plus-trees (Verhaegen *et al.* 1992). The seeds for this plantation were of local origin. It was felt that at four years of age these trees, which had a mean height of 11 m and basal area of 10 m^2 ha^{-1}, had expressed their potential and yet were young enough to be multiplied vegetatively. As the first stage, the best 35 trees ha^{-1} were selected (5% selection intensity) on the basis of visual appearance. In the second stage, these 35 trees were assessed for their form and vigour relative to their neighbours (Boutin 1983, 1991). Relative vigour (E) was assessed as stem circumference at 1.5 m of the selected tree (C_S) and the mean circumference of its eight nearest neighbours (MC_V):

$$E = \frac{(C_S^2 - MC_V^2)}{\delta\ cv}$$

where cv is the coefficient of variation. On the basis of this analysis, 308 trees were selected, of which 154 were selected by a second visual inspection as plus-trees. This represents an 0.3% selection intensity.

The plus-trees were then coppiced at 0.4–0.5 m in 1984 and cuttings collected one month later; 116 clones were established. Stockplants of these clones have subsequently been planted at Téné, and clonal trials covering 23.8 ha established in 1987–90 at Mopri, Téné and Sangoué. These clones have performed better at Mopri than at Téné (Kadio, Legaré & Bohousson 1991). After two to five years, the mean performance of the clones was 14% better than a control plot of unselected seedlings (Verhaegen *et al.* 1992).

Ladipo *et al.* (1984) reported considerable clonal variation between clones of *T. scleroxylon* in net photosynthesis, stomatal resistance and mesophyll resistance. A good relationship was found (r=0.81; P=0.05) between gas exchange parameters and yield. To date, this relationship has not been used in selection programmes, and further work is needed to take advantage of such physiological selection criteria.

RESEARCH ON WILD FRUIT OR FOOD TREES

The basic principles of vegetative propagation and clonal selection of indigenous hardwoods are equally applicable to the domestication of wild fruit tree species (see Okafor & Lamb, pp34–41) (see Table 4).

In addition to Okafor's (1975, 1981) extensive studies with *Irvingia gabonensis*, *Treculia africana*, and other species, there are currently other studies in Nigeria by the International Centre for Research in Agroforestry (ICRAF) (multipurpose tree species project), in Cameroon by the Agronomic Research Institute, and in Côte d'Ivoire by Wageningen University. Further objectives of these projects are to determine the ecological, biological and physiological factors influencing the domestication process, to select superior trees for mass production and to test these cultivars under agroforestry situations. Techniques of marcotting have been developed in Nigeria (ICRAF/International Institute of Tropical Agriculture/Oregon State University) for *Treculia africana*, *Irvingia gabonensis* and *Dacryodes edulis*, while the rooting of stem cuttings has been used in Cameroon for *Ricinodendron heudelotii* and *Irvingia gabonensis*. This approach is particularly aimed at improving the compound farm system of agroforestry.

Currently, there are proposals to add studies on the vegetative propagation and clonal selection of fruit trees to the ODA/ONADEF project in Cameroon, perhaps including the domestication of *Cola nitida*, *Cola lepidota*, *Xylopia* spp., *Cola pachycarpa*, *Tetrapleura tetraptera*, etc, and their genetic improvement by selection at ICRAF (Nigeria/Cameroon). This aspect of the project is important as the demand for some local fruit products in the urban areas of West Africa is expanding, while some products like the cola nut have considerable importance in regional trade.

GENETIC RESISTANCE TO PESTS

Not surprisingly, there are pest and disease problems associated with cultivating indigenous tree species. Recently, however, attempts have been made to search for pest-resistant genotypes (Ladipo 1986; Cobbinah 1990). In Nigeria, work on *Terminalia ivorensis* leaf gall commenced in 1986, while at the Forestry Research Institute of Ghana (FORIG) work is in progress with ITTO funds to screen Iroko half-sib progenies of *Milicia*

Table 4. Some indigenous fruit tree species vegetatively propagated using simple horticultural methods in West Africa

Species	Family	Method of propagation	Country
Garcinia kola	Guttiferae	Marcotting and stem cuttings	Nigeria, Cameroon, Côte d'Ivoire
Irvingia gabonensis	Irvingiaceae	Grafting/marcotting and stem cuttings	Nigeria, Cameroon, Côte d'Ivoire
Pentaclethra macrophylla	Leguminosae	Marcotting	Nigeria, Côte d'Ivoire
Dialium guineensis	Leguminosae	Stem cutting	Nigeria
Dacryodes edulis	Burseraceae	Marcotting	Nigeria, Cameroon, Côte d'Ivoire
Maesobotrya barterii	Rubiaceae	Marcotting	Nigeria
Treculia africana	Moraceae	Grafting	Nigeria, Côte d'Ivoire
Masularia acuminata	Rubiaceae	Stem cuttings and marcotting	Nigeria

excelsa for resistance to *Phytolyma lata* galls. Evidence has been obtained that some *M. excelsa* trees are probably resistant to attack by this psyllid (Cobbinah 1990). This ITTO project aims to quantify possible sources of resistance and to test them using two bioassay techniques (insect bioassay and the standard choice bioassay). For these tests, both susceptible and resistant trees will be cloned using stem cuttings. Initial results have shown that some individuals are less frequently attacked and that insects in the galls formed do not develop to maturity. Similar studies on genetic resistance to *Hypsipyla* shoot-borers in Central American mahogany (Newton *et al.*, pp256–266) could be applied to the W African members of the Meliaceae, such as *Khaya* spp.

REPRODUCTIVE BIOLOGY AND BREEDING

There have been limited studies on the breeding systems of tropical hardwoods of West Africa. Howland and Bowen (1977) reported that *Triplochiton scleroxylon* is self-sterile and is pollinated by many insect species from several families. Pollen management and storage of *T. scleroxylon* have been investigated (Leakey, Ferguson & Longman 1981; Oni, Fasehun & Ladipo 1988) and deep-frozen pollen has been successfully used for cross-pollination. Attempts to induce precocious flowering in *T. scleroxylon*, while not successful in all clones, did demonstrate that flowering can be initiated in young plants (18 months old) by inducing root dormancy in plants with active shoots (Leakey *et al.* 1981). Subsequently, cross-pollinations resulted in the development of normal seedlings and, in one instance, a second-generation progeny was also created as a result of precocious flower induction. It thus appears that there is potential to add early breeding techniques to the domestication procedures of this species and so obtain full-sib progeny on a short generation cycle (1.5–2 years). Studies by Grison (1978) on *Aucoumea klaineana* described the flowers and their pollination mechanisms, and reported some successful controlled pollinations.

Recent studies on *Terminalia ivorensis* have shown that the species is andromonoecious. The flowers are either male or bisexual, with both hermaphrodite and male flowers occurring on the same spike. The distribution of male and hermaphrodite spikes on flowering twigs of *T. ivorensis* differed significantly between sites at 1% probability. The ratio of male/hermaphrodite spikes (MF:HF) is 1.9:1 (Oni 1989). The flowers are mostly insect-pollinated. Results of controlled pollination carried out on the species indicated self-compatibility. The reproductive efficiency of the species is 21%. Pollen grains of *T. ivorensis* are amenable to storage at –17°C or –30°C and can be grown successfully on a medium containing 0.1% boric acid + 20% sucrose (Oni 1989). In Ghana, seeds have been obtained from a clonal seed orchard. The size of the fruits varied among the different clones.

Flowering and flower morphology of *T. superba* have also been studied in Ghana (see *FORIG Technical Note*, no. 29). Flowering occurs at not earlier than ten years of age, and takes place between mid-October and early January. The flowers appear in a whorl of spikes, and last for one month. The whorl contains 19 flower spikes, of which nine are entirely composed of hermaphroditic flowers, two of only male flowers, and the remaining eight contain hermaphroditic flowers at the base with staminate flowers arranged above them in an average ratio of 29:47. The ovary is inferior and unilocular. The hermaphroditic flowers are self-compatible, and pollination by the staminate flowers is restricted if not inhibited.

GERMPLASM CONSERVATION

Deforestation poses a major threat to the genetic resources of indigenous tree species in West Africa. In Nigeria, 12 strict Natural Reserves have been established in various ecological zones to provide *in situ* conservation of these and many other species. Similar action has been or is being taken in several other countries in the region. With more efficient control and management, Forest Reserves can play a major role in germplasm conservation. However, as already mentioned, *ex situ* conservation by seed, pollen and live plants also has an important contribution to play, especially when linked to tree improvement programmes.

CONCLUSIONS

In conclusion, much progress has been made in West Africa by local research organisations with and without international collaboration. What is needed is greater regional collaboration, particularly in germplasm collection and exchange, and the widespread application of this research, together with ongoing studies to deepen understanding and broaden the spectrum of species domesticated for the production of timber and non-timber products. This development would have significant implications for the timber and wood supply, economy and environment of West Africa.

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Genetic improvement of trees in Central America, with particular reference to Costa Rica

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ABSTRACT

Central America has little or no forestry tradition other than widespread clearance and exploitation of its natural forests. Planting of trees to provide for a shortfall of timber and other products is a recent event, and has only reached a significant scale in the past decade. Tree improvement activities in Central America, starting in 1977 at the Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE) in Costa Rica and the National School of Forest Sciences, Honduras, therefore developed initially in a vacuum, without the usual demand for improved seed. The Honduran project was curtailed in 1982 owing to the lack of finance. Work started again in 1987 with the conservation and genetic improvement of Honduras forest resources project (CONSEFORH), working with a greater number of species, a wider remit, and greater emphasis on the conservation of native tree genetic resources. In Costa Rica, the tree improvement project (TIP) has worked continually since 1977. Central to the approach of the TIP has been the establishment of trials on farmers' land to ensure the performance of selected provenances/genotypes on the type of land to be reforested. More recently, a bilateral project funded by the Danish International Development Agency started in Nicaragua, focusing on the improvement and conservation of various native species. No formal tree improvement programmes exist in the other Central American countries, although seed stands have been established for a number of species.

Given population densities and the land tenure situation in Central America, the majority of reforestation is and will continue to be by farmers with small and medium-sized holdings, using both timber and multipurpose trees. The great diversity of climatic and edaphic conditions encountered in Central America, and the varied demands of farmers for trees, result in the need for work on a greater number of species than is normal in tree improvement programmes. These include both native species, such as *Albizia guachapele, Alnus acuminata, Bombacopsis quinata, Cedrela odorata, Cordia alliodora, Gliricidia sepium, Pinus* spp., *Swietenia macrophylla* and *Vochysia guatemalensis,* and exotics, mainly *Acacia mangium, Gmelina arborea* and various *Eucalyptus* species. With particular reference to activities in Costa Rica, this paper reviews past, present and planned tree improvement activities in the region and the effect of some of the peculiarities of the region in developing strategies for tree improvement and domestication.

INTRODUCTION

Few areas of the tropics of a similar size to Central America show such wide variations of topography, climate, soil and vegetation. According to Holdridge's life zone classification, there are 17 major zones in Central America (Holdridge 1967). Vegetation ranges from very dry forest to rainforest, depending on the amount of rainfall, and with altitude from basal to paramo. Vavilov (1935, 1951) and Zohary (1970) identified Central America as one of the principal areas of the world for genetic diversity of plant life. This botanical wealth is shown as much in tree species as in shrubs and herbs. With a total number of more than 4000 tree species, the region's tree genetic resources are enormous.

Various tree species now planted on a large scale in many tropical countries of the world are indigenous to Central America, eg *Calliandra calothyrsus, Cupressus lusitanica, Gliricidia sepium, Leucaena* spp., *Pinus caribaea, P. oocarpa* and *P. tecunumanii.* Others have been planted on a smaller scale but have great potential for use and development, eg *Alnus acuminata, Bombacopsis quinata, Cedrela odorata, Cordia alliodora, Juglans olanchana, Parkinsonia aculeata.* Furthermore, there are numerous species in the region which may have potential for use in the future. The increasing levels of deforestation endanger the genetic resources of many of the region's species. Particularly in the dry Pacific zone where deforestation has been extensive, species have suffered serious genetic erosion and in some cases are in danger of localised and even regional extinction (Janzen 1986).

Central America has little or no forestry tradition other than widespread clearance and exploitation of its natural forests. The high population growth rate in the region has resulted in a continuing demand for land for agriculture, ranching and forest products, leading in turn to an indiscriminate destruction of the forest. Hartshorn (1982) estimated that 60–70 kha of forest are cut each year in Costa Rica; for every hectare of plantation established, 80 ha of mature forests are cut. There is little indication of a change in this pattern, and the majority of the natural forests outside protected areas will be exhausted by the end of the century.

The necessity for reforestation on a large scale as part of the solution to this critical situation has been evident for some time. Flores (1985) estimated that, for the period 1985–95, 900 kha needed to be planted in the Central American region to supply the internal demand for wood and wood-based products. The demand for seed has, therefore, grown in recent years and will continue to increase, even if only a part of the area needed is planted. As the number of reforestation projects in the region increases, experience shows that inappropriate source of seed, or propagative material, is a major technical cause of observed failures or low yields. Much of the seed collection in the region is carried out by farmers or other unqualified people, without adequate knowledge of the best collection techniques, or of the characteristics that the trees or stands should possess. As a result, the collections are often made from badly formed trees and stands. For this reason, established plantations often show poor growth and a lack of uniformity that makes management difficult and gives reforestation a poor image. These problems have been accentuated by the lack of knowledge about the importance of using appropriate sources of seed and a lack of information of the best sources among the region's scientific personnel and farmers.

In the past ten years, reforestation has increased dramatically in Costa Rica. This increase was due initially to the motivation of a number of small-scale farmers and extension agents and their perceived need to meet the shortfall of timber for local communities, within an affordable price. Within this context, it was important to achieve visible results early on, and species were chosen which were easy to establish, such as *Bombacopsis quinata, Gmelina arborea* and *Tectona grandis.*

Capitalising on this initial success, planting has increased under new fiscal incentives and soft loans, directed more towards small-scale farmers (typically 2–3 ha) organised into groups. The success has 'snowballed', with much larger numbers now being involved, and the resultant plantations have been of a much higher quality than previously. As a result, with respect to forestry, the situation in the region as a whole is now very different from what it was 10–15 years ago. Even though the species chosen have been traditionally regarded as 'industrial species', they are planted by farmers on a small scale for their own use in a non-industrial context. Seed stands of *Gmelina arborea* were later set up using small plots, and sale of seed has become an important source of extra income for farmers.

The availability of propagative material of superior quality could have an important impact on tree planting in the region. Production increases in plantation forestry achieved in the past 30 years in tropical and subtropical countries, through genetic improvement techniques, have been well documented. However, the majority of these programmes, with the exception of *Leucaena leucocephala* (see Brewbaker & Sorensson, pp195–204), have been developed by large businesses at a purely industrial level, and the potential gains from tree improvement have not been made available to medium- or small-scale farmers. Given population densities in Central America, the majority of reforestation will continue to be by small- and medium-scale landowners using both timber and multipurpose trees. It is evident that the farmers of the region plant trees for a variety of products: timber, wood for rural use (construction, carpentry, work tools, posts), protection (live fences, windbreaks), shade (for livestock, crops and the home), firewood production, recuperation of soils, and more recently to produce forage and feed livestock during the dry season, from a variety of species. For this reason and the high degree of environmental variation, tree improvement programmes are obliged to work with a greater number of species than is normal and consequently accept a slower rate of advance with any one species (see Table 1).

Past, present and future plans for tree improvement within the region have therefore developed within these constraints, taking into account the above factors. The present paper, with particular reference to activities in Costa Rica, and without any pretensions to cover all work in the region comprehensively, considers three ongoing projects, with reference to:

- strategies for improvement and conservation;
- the state of progress;
- implementation; and
- future plans.

The three projects are:

i. CATIE tree improvement project;
ii. CATIE tree crop production and management project (Madeleña); and
iii. conservation and genetic improvement of Honduras forest resources (CONSEFORH) project.

ONGOING PROJECTS FOR GENETIC IMPROVEMENT OF TREES

CATIE tree improvement project

Planting trees in Costa Rica to provide for a shortfall of timber and other products is a recent event and has only reached a significant scale in

Table 1. Tree improvement activities by species in the Central American region

Species	Provenance trials	No. plus-trees	Progeny tests	Seed stands	Seed orchard	Cloning
Acacia mangium	10			2		x*
Albizia guachapele	2	54	2		1	x
Alnus acuminata	1	52	1		1	x
Araucaria hunsteinii	2					x
Bombacopsis quinata	6	117	3	1	3	x
Calliandra calothyrsus	4					
Casuarina cunninghamiana	2					
C. equisetifolia	5					
Cedrela odorata	1	31	1			x
Cordia alliodora	8	163	5		5	x
Cupressus lusitanica	6	45	2	2	1	
Eucalyptus camaldulensis	13		4	4	2	
E. deglupta	3	55	4	1	5	x
E. grandis	3		2	2	2	
E. saligna	5		1			
E. tereticornis	2					
E. urophylla	3			1		
Gliricidia sepium	12	177	2	1		x
Gmelina arborea	9	65	8	14	8	x
Guazuma ulmifolia	2					
Inga spp.	4					x
Leucaena leucocephala	11	24	2	4		
Pinus caribaea	20	1218	6			
P. oocarpa	8		2			
P. tecunumanii	4	801	5		2	
Swietenia macrophylla	2	36	2			x
Tectona grandis	3			11		
Vochysia guatemalensis	4	61	3		3	x

*x, species propagated vegetatively, either by leafy cuttings or stakes

the past decade. Up until the beginning of 1983, the total area reforested in Costa Rica was estimated at 4 kha (Hartshorn 1982). Reforestation has increased during the past decade because of a series of incentives given by the government, to reach rates of 12–15 kha per year. However, plantation failures are high, mainly owing to poor quality of nursery stock, inadequate maintenance after planting, and poor seed quality.

The CATIE tree improvement project (TIP), financed by the UK Overseas Development Administration (ODA), the Department for Development Cooperation (DDC/Norway), the Swiss Office of Development Cooperation (COSUDE) and the US Agency for International Development (USAID), has been active in the genetic improvement of traditional agroforestry and timber species since 1977. The TIP began, from 1977 onwards, with the establishment of provenance trials, mainly of *Pinus caribaea, P. oocarpa, Cordia alliodora, Gmelina arborea, Eucalyptus grandis, E. urophylla* and *Acacia mangium*. They were established as a part of international trials co-ordinated by organisations such as the International Union of Forestry Research Organizations (IUFRO), the Food and Agriculture Organisation (FAO) of the United Nations, the Oxford Forestry Institute (OFI), the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Tree Seed Centre in Denmark, funded by the Danish International Development Agency. Species were selected on the results from species trials and plots that were established in many parts of the country (Combe & Gewald 1979; Camacho 1981; Martinez 1981). The strategy was based on the fact that the most economical and rapid means of obtaining gains in the productivity of trees is through the use of the most appropriate species and provenances (Zobel & Talbert 1984). The trials were planted on a variety of sites throughout the country, covering the major ecological zones considered suitable for reforestation with the particular species. The project aimed also to identify any patterns of genotype/environment interaction for each species and their effect on any recommendations for the establishment of particular provenances.

At the time the project started, there was little awareness of, or demand for, the information or material that the project could provide. The project, therefore, aimed to establish trials that would provide appropriate information, genetic material and demonstration units for the medium term when the need became apparent.

The TIP's trials and seed orchard programme relies heavily on the active participation of smallholder farmers, both individually and in organised groups. Virtually all trials are established on small farms under written agreements with the landowners. After final thinning, the trials and seed orchards are used by the individuals or groups in question for timber and/or improved seed sources. The establishment of trials on farmers' land ensures the performance of selected provenance/genotypes on the type of land to be reforested, and permits the combination of the process of genetic testing, seed production and technology transfer.

An important part of the project is the strengthening of capabilities for tree improvement work throughout the region. Short courses and courses at postgraduate level are given to enhance capability within the region for tree genetic improvement.

The need to increase the work of the project to ensure the uptake of its research results by the end users (ie tree planters of all types) has become evident. One example came from the superior growth of *Pinus tecunumanii* to both *P. caribaea* and *P. oocarpa* observed in TIP trials. The results were reported by the project as long ago as 1986 (Boshier & Mesén 1986), but the species was not officially accepted by the Costa Rican General Forestry Directorate as suitable for reforestation until 1991. This acceptance came only as a result of the TIP establishing a number of small demonstration plantations (1–2 ha) on farmers' land. Firm recommendations on seed sources can now be made for *Gmelina arborea, Acacia mangium, Pinus caribaea, P. tecunumanii* and *Eucalyptus urophylla* (Mesén 1991).

While provenance research provides a sound basis for avoiding catastrophic losses in forestry plantations, the TIP's goal is higher than simply to avoid plantation failures. Even within the best provenances, trees show a great variability in traits of economic value. Therefore, a further stage in the TIP was the selection of individual superior trees within provenances, both for the establishment of progeny tests and seed orchards in a traditional breeding programme, and for inclusion in a vegetative propagation and clonal selection programme. An additional component within the TIP's activities is the screening of *Cedrela odorata* and *Swietenia* spp. families for genetic resistance to the shoot-borer (*Hypsipyla grandella*), and the eventual cloning of pest-resistant genotypes (see Newton *et al.*, pp256–266).

Progeny tests

The natural ranges of all the native species included in the TIP progeny test programme are not restricted to Costa Rica, but extend to many other Central and South American countries. In this regard, international co-operation for exploration, tree selection and exchange of seed becomes a critical matter. A particularly fruitful link was initiated in 1989 between the Central America and Mexico Coniferous Resource Cooperative (CAMCORE) and CATIE, through a USAID-funded project which focused on the exploration and collection of seed from superior trees of six threatened broadleaved species in Guatemala, Honduras, Colombia and Costa Rica. The species selected – *Albizia guachapele, Alnus acuminata, Bombacopsis quinata, Cordia alliodora, Sterculia apetala* and *Vochysia guatemalensis* – were chosen because all have populations in danger of extinction or genetic impoverishment and, at the same time, have exhibited commercial potential in CATIE or CAMCORE tests (Mesén & Dvorak 1992). In addition, the TIP has carried out selections within Costa Rica for a number of promising non-native species, particularly *Cupressus lusitanica, Eucalyptus deglupta* and *Gmelina arborea.* In total, 597 phenotypically superior trees have been selected and their seed established in provenance/progeny tests in a variety of suitable sites in Costa Rica.

As for the provenance trials, the provenance/progeny tests are established under co-operative agreements with farmers involved in reforestation under the Costa Rican Forestry Directorate incentive scheme. Most trials are designed in such a way that they can be converted into seedling seed orchards after the evaluation period. Thus, in addition to the basic objectives of genetic testing and providing material for advanced selections, the trials are also used for demonstration purposes and the production of improved seed, tested directly in the area where reforestation is to be carried out.

Vegetative propagation and clonal selection

It is now recognised that vegetative propagation and clonal selection offer a means to enhance greatly the yield and quality of forest products (Leakey 1987; Libby & Rauter 1984). The tremendous improvements in productivity and form of clonal *Eucalyptus* in Brazil, for example, are well known by foresters. Most advances in clonal silviculture, however, have been developed by large companies and the techniques are not available to farmers in developing countries. Since 1989, the TIP has concentrated on the development of low-cost, appropriate technology cloning techniques, through a co-operation link with the Institute of Terrestrial Ecology (ITE), Scotland. The main obstacle for the use of cloning in small-scale programmes, that of the sophisticated and expensive equipment needed, has been overcome by the use of ITE's low-technology, non-mist propagators, as described by Leakey *et al.* (1990), Leakey and Mesén (1991) and Mesén, Leakey and Newton (1992) (see also Leakey, Newton & Dick, pp72–83). Through the ITE/CATIE link, the TIP has developed considerable expertise in the use of these techniques and in understanding the basic physiological principles, both pre- and post-severance, affecting the rooting ability of leafy cuttings. All priority species included in the programme, some of which were formerly considered to be difficult to root, are now being cloned routinely. They include *Albizia guachapele, Bombacopsis quinata, Cordia alliodora, Cedrela odorata, Gmelina arborea, Swietenia macrophylla* and *Vochysia guatemalensis.* The use of low-cost and easily transferred cloning methods offers excellent prospects for both the conservation and the commercial use of genetically high-quality germplasm of valuable species.

Seed stands and the Madeleña project

The focus of the Madeleña project is towards the development of techniques for the planting of multipurpose trees in different systems, including agroforestry, in small or relatively small farms in Central America. The main aim was to develop and strengthen the capabilities of CATIE and public and private organisations in the Central American region to allow them access, to promote and to disseminate on-farm, market-oriented tree crop technologies for the use and benefit of small- and medium-scale farmers and rural industries. This project developed from an initial attempt to address fuelwood shortages on a regional basis, begun in 1980, under the fuelwood and alternative energy sources project based at CATIE. The project screened more than 100 species to determine their feasibility for fuelwood and latterly multipurpose uses. Fourteen priority species were identified and a variety of promotional, extension and training activities carried out. The exclusive focus on fuelwood was broadened under the project extension (USAID/Regional Office for Central America and Panama tree crop and management project) to include a mix of species and management systems which can be utilised to provide a variety of products and economic benefits.

Traditional guides to the establishment of seed stands argue that areas of 2–5 ha are recommended for seed stands (Matthews 1964). Generally, in the Central American region, there are few large plantations and the problems of contamination from surrounding stands of trees are reduced. Genetic constraints can, however, be avoided by the use of much smaller areas, and economies of scale may be very significant if a farmer can receive income from both the timber and the seed from his trees. This approach has worked in all the countries of the region in conjunction with each country's national institutions, and national seed banks. The project aims to establish a network of seed stands for the multipurpose species it has identified as promising and of high priority for the region.

CONSEFORH project

The genetic improvement programme in Honduras started in 1977 at the National School of Forest Sciences, but was curtailed in 1982 because of a lack of finance, leaving only a few established trials (Gibson & Romero 1988). Work recommenced in 1987 with the CONSEFORH project, through an agreement between the Honduran Corporation for Forestry Development and ODA. CONSEFORH is working with a large number of species, both native and exotic, with particular emphasis on the conservation, evaluation and genetic improvement of native species. This work involves explorations to determine the current distribution and conservation status of the species, seed collections for the establishment of genetic trials, gene conservation banks and seed orchards, establishment of silvicultural trials, and research on the properties and potential uses of the timber. Work with exotics involves the establishment of seed orchards and provenance trials.

CONSEFORH is active in the four major forest types found in Honduras, namely dry forest, cloud forest, humid forest and coniferous forest. The number of forest species in these areas is enormous, some of which (eg *Pinus caribaea* var. *hondurensis*) are planted on a large scale in many tropical countries of the world, or may have great potential for future use and development. Up until the present, the efforts of the project have been concentrated in the dry forest, being the most severely disturbed forest association in Honduras and where there are more than 300 tree species. Large-scale ecological restoration of the type currently being implemented in the dry forest of Costa Rica is not an option in Honduras, because of the land tenure pattern and consequent pressure from subsistence farmers (Gibson 1993). The project has thus taken a varied approach, depending on the importance and usage of the individual species. It involves collection and management of germplasm in both *in situ* and *ex situ* conservation units, while for some species the possibilities of conservation through use by local communities are also being explored (Gibson 1993).

Work began with priority species selected as endangered, commercially valuable and with characteristics making them acceptable to farmers and others interested in tree planting (Gibson 1993). Extensive exploration was carried out to define the distribution and status of populations and to assess options for conservation of these species. Seed collections were then made, followed by the establishment of breeding seedling orchards (BSOs) as a basis for their conservation and improvement. The species in this programme included *Albizia guachepele, A. niopoides, A. saman, Bombacopsis quinata, Cordia alliodora, Enterolobium cyclocarpum, Gliricidia sepium, Hymanaea coubaril, Leucaena salvadorensis, Simarouba glauca* and *Swietenia humilis* (Gibson 1993). Work with *Pinus* has also involved the establishment of BSOs to ensure the conservation of endangered provenances of *P. caribaea*.

Most trials have been planted in one of the experimental stations that the project maintains in Honduras, which range from 100 m to 1100 m above sea level. The concentration of activities in the experimental stations allows for better maintenance and protection of trials and conservation of the local flora and fauna, and at the same time facilitates education and demonstration activities. Many valuable species grow naturally in these stations: for example, *Albizia guachapele, Bursera simarouba, Enterolobium cyclocarpum, Guazuma ulmifolia, Pithecellobium dulce* and *Swietenia humilis* are common in the dry forest station. Therefore, the stations themselves offer opportunities for detailed growth and phenological studies and for the development of appropriate techniques for *in situ* conservation. At present, a large proportion of the project's resources are concentrated in this area.

CONCLUSION

In Central America, the justification for tree improvement has never been the straightforward economic one appropriate to countries and companies with large reforestation programmes; the lack of adequate levels of reforestation is precisely one of the problems which the region faces. At CATIE, at least, workers in tree improvement have long been conscious that tree improvement in Central America must lead, rather than follow, reforestation, through the provision of excellent-quality material whose field performance will in itself stimulate tree planting by farmers.

This concept must be reflected in the tree improvement strategies adopted in the region. For this reason, at CATIE, the TIP is pursuing and advocating ambitious strategies of individual tree selection based, at the highest intensity, on clonal selection and vegetative propagation. Obviously, lower-intensity activities such as provenance selection will remain crucially important. However, the best provenance contains bad as well as good genotypes, and in itself even the use of the best provenance is unlikely to achieve the sort of 'quantum leap' in the quality of plantations that is necessary to change completely perceptions of and attitudes towards plantation forestry, and to stimulate reforestation on a large scale. Clonal methods have the potential to transform smallholder forestry as effectively as they have transformed industrial forestry, although different strategies of clonal deployment may need to be developed (cf Foster & Bertolucci, pp103–111), and a complementary programme of sexual improvement should be maintained.

Domestication by vegetative propagation and clonal selection is just one example of an improved production system made possible by, but not solely dependent on, genetic improvement. Workers in tree improvement in the region should be looking for other possibilities offered by genetic improvement to develop improved production systems which meet specific problems or which offer new opportunities. An obvious example is the work on selection for pest resistance in mahoganies mentioned above; other possibilities abound.

At a wider level, there is a need for an overall strategy of management of Central American forest genetic resources, of which the development of genetically improved forestry and agroforestry production systems would constitute only a part. The genetic base of many species is being rapidly eroded by deforestation, often before we know anything about their genetic structure or even have complete knowledge of their natural distribution. For this reason, there is now some initial work in progress in the region on genetic conservation and baseline exploration, taxonomic and population genetic studies. However, there is little co-ordination between these activities on a regional or even national basis. An integrated forest genetics resource management strategy might be founded upon a regional network of resource management units, each consisting of a specific type of population. They might range from national parks or reserves, with the objective of *in situ* genetic conservation, through to clonal multiplication gardens, dedicated exclusively to the production of improved germplasm for particular production systems. Between these two extremes there could be a variety of other options, such as seed stands, natural relict stands, seed orchards, etc, each with its own clearly defined role in relation to the overall genetic management of the species. Through such a network, priorities for funding and action would be made clearer, and national and regional co-operation on tree improvement and related activities could be greatly improved.

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Domestication of mahoganies

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ABSTRACT

Despite the economic importance of mahoganies, few attempts have been made at genetic improvement, partly because of the high incidence of pest attack when mahoganies are grown in areas where they are native. A suggested domestication strategy for mahoganies is outlined, centred on the selection for pest resistance as part of a genetic improvement programme, the capture of selected genotypes using vegetative propagation techniques, and the deployment of selected material in appropriate silvicultural systems which optimise pest control. Current progress in developing such a strategy is described, including the assessment of genetic variation using field tests and molecular methods, and the development of vegetative propagation techniques with *in vitro* approaches. The importance of conserving genetic resources of mahogany species is highlighted, and the prospects for the future development of a domestication strategy are discussed. It is suggested that the development and implementation of such a strategy should be given high priority, if a sustainable resource of mahogany is to be guaranteed in the future.

INTRODUCTION

Mahoganies are among the most economically important tropical timber species, accounting for a significant proportion of world trade in tropical hardwood. Despite this fact, the mahoganies remain largely undomesticated: very little is known about the extent of genetic variation in wild populations, and very few attempts have been made at genetic improvement (see Palmer, pp16–24).

In the strict sense, the term 'mahogany' applies to members of the genus *Swietenia* (Meliaceae), which comprises three species, all native to the neotropics (see Styles 1981, for a detailed review). The natural distribution of *S. humilis* is the Pacific coast region of Central America, whereas *S. mahagoni* is found on a number of Caribbean islands and mainland USA (southern Florida). *S. macrophylla*, now the principal mahogany of commerce, occurs over a large geographical area, from Mexico to the southern Amazon in Bolivia and Brazil (see Styles 1981).

In this paper, mahogany is also taken to include the closely related genus *Khaya* (African mahogany), which bears a number of morphological and ecological similarities to *Swietenia*. A number of points are illustrated by reference to other economically important genera in the same family, such as *Cedrela* and *Lovoa*. About seven species of *Khaya* are recognised by Styles (1981), including *K. anthotheca*, *K. grandifoliola*, *K. ivorensis*, *K. madagascariensis*, *K. nyasica* and *K. senegalensis*. Most of the species are native to tropical Africa; *K. ivorensis* is native to coastal rainforests of West Africa, whereas *K. senegalensis* occurs in the drier northern parts of the same region.

The most important product obtained from mahogany is timber, which is principally used for furniture and veneers; it is easily worked and strong for its weight (Lamb 1966). Often, mahogany species are also favoured for use in agroforestry systems (eg in Central America and parts of Indonesia), where they may provide shade for crops and fuelwood. Other products derived from Meliaceae include oil (derived from the seed of *Carapa* spp.; see Prance, pp7–15) and biological insecticides (such as neem, obtained from *Azadirachta indica*). Medicinal products, such as treatments for whooping cough, rheumatism and lumbago, are derived from *Khaya* spp. (Abbiw 1990). Products such as these could potentially be derived from other meliaceous species by appropriate selection programmes.

The main factor which has limited the cultivation of mahoganies is attack by shoot-boring moths (*Hypsipyla* spp.), which are widespread throughout the tropics. The moth larvae destroy the terminal bud of the young tree, which then frequently branches or forks, reducing the economic value of the timber considerably. This pest has resulted in the failure of many attempts at reforestation with mahoganies in countries where they are native, including Puerto Rico, Guatemala, Peru and Cuba in the case of neotropical species (see Newton *et al.* 1993 for details). Similarly, planting of *Khaya* spp. has been almost completely abandoned in both Ghana and Nigeria because of shoot-borer attacks (Wagner, Atuahene & Cobbinah 1991). For this reason, selection for pest-resistant genotypes may form a critical part of the domestication strategy for mahoganies.

As few successful examples exist of mahogany cultivation in plantations, most timber continues to be derived from the exploitation of natural forests. This work is largely undertaken in a non-sustainable way. Domestication of mahogany is crucial for the development of an alternative resource, to guarantee the supply of high-quality timber into the future. In this paper, we consider three stages in the domestication process:

i. the assessment and selection of genetic variation;

ii. the capture of selected genotypes by the use of propagation techniques; and

iii. the deployment of genetically improved material in silvicultural or agroforestry systems to realise the full genetic potential.

THE ASSESSMENT AND SELECTION OF GENETIC VARIATION

Assessments of genetic variation have traditionally been made by comparing the growth of material from different geographical origins in provenance and progeny tests. However, recently developed molecular techniques enable the extent of genetic differentiation between genera, species and populations to be quantified directly. Preliminary results from both these approaches are described below, together with a consideration of selection for pest resistance and genetic conservation.

Provenance and progeny tests

Very few genetic tests have been established with either New or Old World mahoganies (see Palmer, pp16–24). For example, the National Research Council (1991) reported that there are no active tree improvement activities with *Swietenia* species. The most extensive provenance tests of *Swietenia* which have been established to date are those of the Institute of Tropical Forestry in Puerto Rico (Geary, Barres & Ybarra-Coronado 1973; see also Boone & Chudnoff 1970), although no data have apparently been published describing the variation observed (but see Glogiewicz 1986). However, the broad ecological and geographical ranges of *Swietenia* species, coupled with their ability to hybridise, suggest that a high degree of genetic diversity may exist within the genus (Newton, Leakey & Mesén 1993; see also Liu 1970).

Even less is known about the extent of genetic variation in *Khaya* spp. than in their neotropical relatives. A number of workers have outlined the early stages of genetic improvement programmes with *Khaya* spp. Betancourt, Marquetti and Garcia (1972) described the possibility of hybridisation between *K. nyasica* and *K. senegalensis*, and noted that a programme for selection of resistance to stem cankers was initiated in Cuba. A preliminary programme of plus-tree selection was undertaken in Ghana, including six trees of *K. anthotheca* and four of *K. ivorensis* (Britwum 1970). However, there are apparently no published data describing results from progeny or provenance tests of *Khaya* spp. in any area, although Chapuis (1990) gave brief details of the breeding programme with both *Khaya* and *Swietenia* spp. in Cuba.

The only species of the Meliaceae which has been investigated in any detail with respect to genetic variation is *Cedrela odorata* (Spanish cedar). A series of international provenance trials were co-ordinated by the Oxford Forestry Institute, UK, in the 1960s and 1970s (Chaplin 1980; see also Burley & Lamb 1971). In 1967, seedlots of 14 provenances were distributed to 21 collaborating countries throughout the tropics, for use in trials. Provenance differences in mean height growth by up to a factor of six were subsequently recorded (see papers in Burley & Nikles 1973; Nikles, Burley & Barnes 1978). In general, the most promising provenances in terms of height growth were those from Costa Rica and Belize (Chaplin 1980). These results indicate the extent of genetic variation which could potentially be recorded in other species of Meliaceae, were they to be investigated (Newton, Leakey & Mesén 1993). The pattern of genetic variation within the genus *Cedrela* is obscured, however, because some of the species (such as *C. angustifolia*) are poorly defined taxonomically (see Styles 1981) and susceptible to hybridisation.

A number of small-scale provenance/progeny trials of neotropical mahogany species have recently been established in Central America and the Caribbean, in an attempt to initiate a programme of genetic selection and conservation. For example, two progeny tests and a provenance test of *Swietenia macrophylla* have been established in Costa Rica and Trinidad as part of a collaborative link between the Institute of Terrestrial Ecology (ITE), the Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE) and the International Institute of Biological Control (Newton 1990; Newton, Mesén & Leakey 1992; Newton, Leakey & Mesén 1993). In addition, the conservation and genetic improvement of Honduras forest resources (CONSEFORH) project (see Mesén, Boshier & Cornelius, pp249–255) has established two progeny tests of *S. humilis*, which are probably the first for this species. No results of these trials have been published so far.

Preliminary results from the *S. macrophylla* trials in Costa Rica and Trinidad indicate a significant degree of genetic variation in rate of height growth. In a progeny test at CATIE, Costa Rica, half-sib progenies differed by a factor of two in mean height after 15 months' growth (Figure 1i). A similar degree of variation (by a factor of 1.5) was recorded in a progeny test in Trinidad after 17 months (Figure 1ii), but five provenances tested at CATIE were less markedly different (Figure 1iii).

Molecular techniques

Traditionally, genetic resources have been characterised on the basis of morphological and agronomic traits. The effectiveness of this approach for estimating genetic diversity, however, has been questioned by several authors (Gottlieb 1977; Brown 1979). The subsequent development of isozyme and other biochemical markers represented a significant improvement. However, the effectiveness of such biochemical markers is limited by the number of polymorphic loci detected.

With the advent of molecular techniques, DNA-based procedures for detecting genetic variation have been proposed. They include restriction fragment length polymorphisms (RFLPs) which have the potential to detect almost unlimited amounts of variation. Although chloroplast DNA (Palmer *et al.* 1988) and nuclear RFLPs (Debener, Salamini & Gebhardt 1990) have been used for taxonomic studies, the

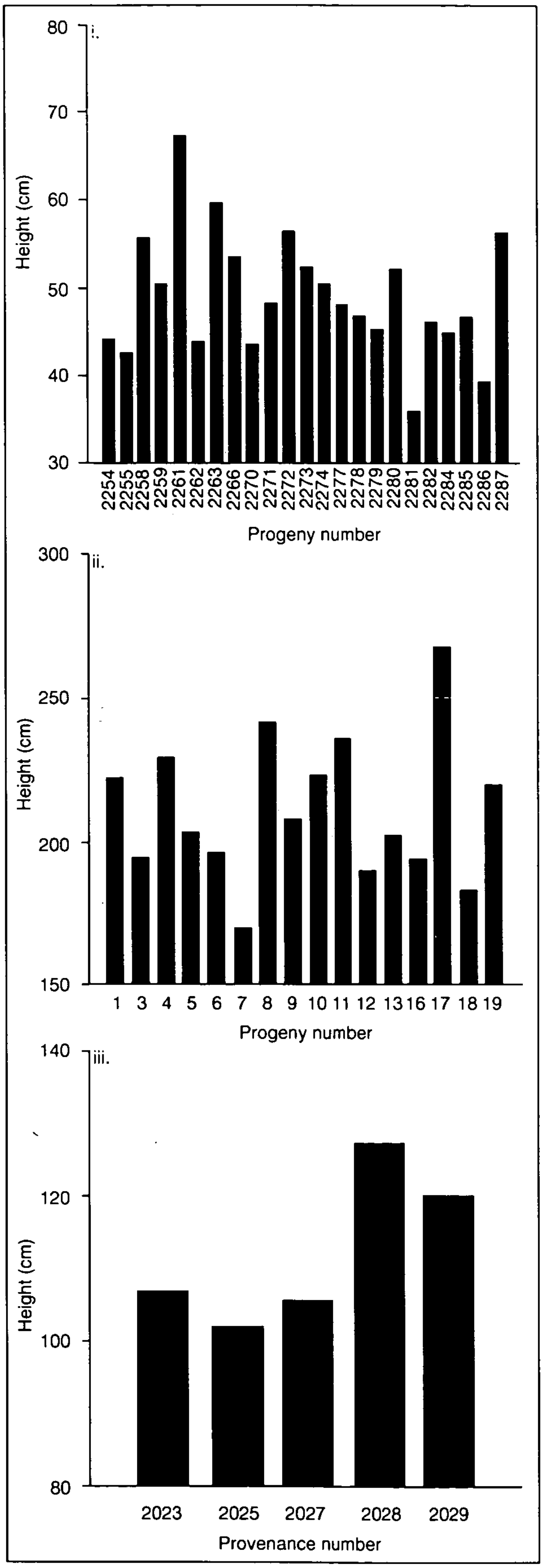

Figure 1. Preliminary results from field trials of *Swietenia macrophylla*, illustrating the extent of genetic variation in height growth

i. progeny test, including 23 half-sib progenies from a range of sites in Costa Rica, Honduras and Trinidad, after 15 months' growth at Bajo Chino, CATIE, Costa Rica
ii. progeny test, including 16 half-sib progenies from a range of sites in Trinidad, after 17 months' growth at Moruga, Trinidad
iii. provenance test, including five provenances from the Central American/Caribbean region, after 14 months' growth at Florencia Sur, CATIE, Costa Rica

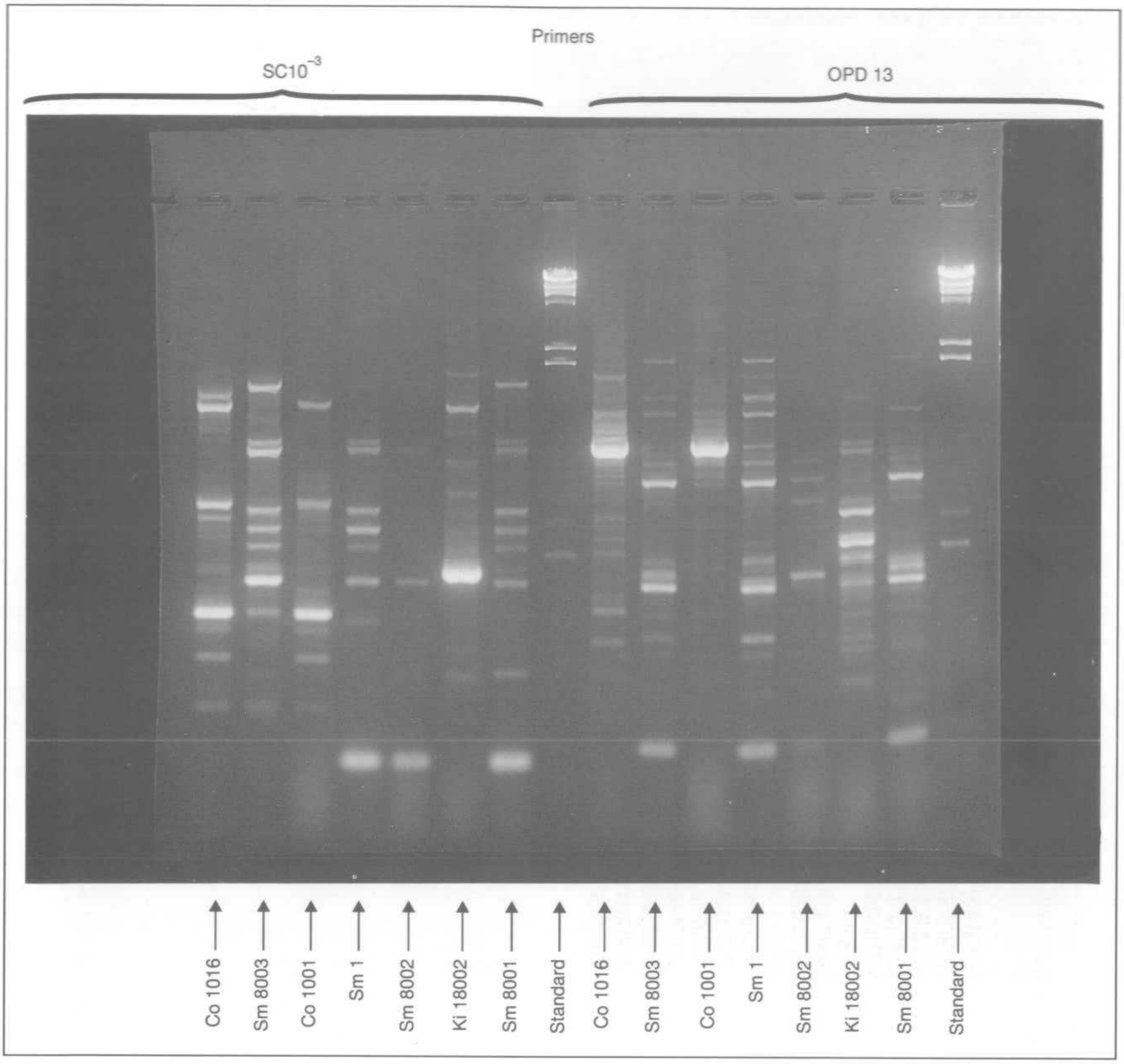

Figure 2. Genetic variation in mahogany species, detected using RAPDs (for details of methods, see text). The Figure presents amplification products of *Swietenia macrophylla* (Sm), *Cedrela odorata* (Co) and *Khaya ivorensis* (Ki) on an ethidium bromide-stained gel, using two primers, SC10^{-3} and OPD 13

usefulness of these markers is limited by the fact that they are costly, time-consuming and technically demanding.

Recently, a new procedure based on the polymerase chain reaction, termed randomly amplified polymorphic DNA (RAPDs), has been developed for detecting polymorphisms in plants (Williams *et al.* 1990; Welsh & McClelland 1990; Waugh & Powell 1992). This technique is based on the polymerase chain reaction (PCR) amplification of unknown DNA sequences using short (10-mer) synthetic oligonucleotide primers. Polymorphisms can simply be identified as the presence or absence of an amplification product on an ethidium bromide-stained gel. The RAPD method overcomes many of the limitations of RFLP and has been used for clone identification in cocoa and banana (Wilde, Waugh & Powell 1992), population differentiation in *Gliricidia* spp. (Chalmers *et al.* 1992), and genetic mapping (Carlson *et al.* 1991; Roy *et al.* 1992).

Recently, RAPDs were applied for the first time to mahoganies in a preliminary investigation to test the applicability of the techniques to these species. A number of different genera were compared, including *Khaya*, *Swietenia* and *Cedrela* spp., and pronounced polymorphisms were detected at the genus level (Figure 2). These encouraging results suggest that DNA extraction of these species is not difficult, and that a more detailed investigation using RAPDs may be profitable to assess the extent of genetic variation within and between mahogany populations, and to resolve some of the taxonomic difficulties with mahogany species and hybrids (W Powell *et al.*, unpublished).

Selection for pest resistance

As attack by shoot-borers (*Hypsipyla* spp.) is the main factor restricting the cultivation of mahoganies in plantations, selection for pest resistance could be considered to be a key aim of a domestication strategy. Pest resistance may arise through three main mechanisms (Grijpma 1976):

i. *non-preference*, when the insect is not attracted to or is actively repelled from ovipositing or feeding on the tree;

ii. *antibiosis*, in which the insect is killed, injured or prevented from completing its life cycle after feeding on the tree; and

iii. *tolerance*, in which the tree recovers from attack to an acceptable level.

There is evidence for all three mechanisms within the Meliaceae family as a whole. With respect to non-preference, some mahogany species are clearly less susceptible to attack than others, such as *S. mahagoni* compared with *S. macrophylla* (Whitmore & Hinojosa 1977). Such differences in susceptibility may reflect variation in the production of chemical attractants, although differences in growth rate may also be influential (Grijpma 1976). Antibiosis is demonstrated by species such as *Toona ciliata*, a native of SE Asia and Australasia, which produces water-soluble compounds toxic to *Hypsipyla grandella*, the native shoot-borer of the Americas (Grijpma & Roberts 1975). Some mahoganies produce resins, which may also hinder shoot-borer attack (Wilkins 1972; Lamb 1968; Whitmore 1978). The ability of individual trees to tolerate attack by strong apical growth has also been observed in both *Cedrela* spp. (Chaplin 1980; Grijpma 1976; Vega 1976) and *Swietenia* spp. (A C Newton, personal observation).

However, little information is available on the intraspecific variation in these mechanisms of pest resistance. To investigate this aspect, the genetic tests established by the ITE/CATIE link and CONSEFORH project (see above) have been intensively assessed for the incidence of pest attack. Preliminary results, from combined provenance/progeny tests of C. *odorata* in Costa Rica, have indicated intraspecific variation in different forms of resistance. Apart from pronounced differences in growth rate, different families displayed three-fold variation in susceptibility to attack (Newton, Leakey & Mesén 1993). In addition, some individuals were able to tolerate attack by vigorous growth of a new dominant lateral shoot, although the genetic basis of this characteristic has not yet been examined in detail. These preliminary results suggest that selection for pest resistance may be an achievable objective in mahoganies, although further research on this aspect is clearly required.

Genetic conservation

Concern has recently been voiced about the conservation status of neotropical mahoganies (Newton, Leakey & Mesén 1993; Rodan, Newton & Verissimo 1992), as reflected in the listing of two species (*S. humilis* and *S. mahagoni*) on Appendix II of the Convention on International Trade in Endangered Species (CITES). A proposal to include *S. macrophylla* on this listing was made in 1992 by the governments of the USA and Costa Rica, but was eventually withdrawn prior to consideration by the committee (Rodan *et al.* 1992). It is possible that this proposal will be renewed in the future. *S. macrophylla* is considered by some to be endangered or vulnerable in a number of countries (US CITES proposal 1992), although others have suggested that large stocks still exist (Anon 1992). In fact, little detailed information exists on the extent of remaining populations.

Many of the Old World mahogany species are perhaps in an even more precarious state, and are considered to be vulnerable or endangered in many parts of their range (World Conservation Monitoring Centre, Cambridge, UK, unpublished information). Germplasm collection and exploration of *Khaya* spp. have been accorded high priority by the Food and Agriculture Organisation (1989), and there have been suggestions that this genus should also be listed on Appendix II of CITES (Flora and Fauna Preservation Society, UK, personal communication).

The concerns about genetic conservation arise from the fact that the vast majority of mahogany timber is harvested from natural stands. Selective logging, involving removal of the most economically desirable phenotypes, may result in the genetic depletion of the forest stand and a reduction in its future economic value. *Swietenia mahagoni*, which has been logged intensively over the past 400 years, is perhaps the most striking example of genetic erosion in tropical forestry: most individuals which remain are highly branched or forked (Styles 1981). The same processes are undoubtedly acting on *S. macrophylla* and other mahogany species currently being harvested, although the extent of any genetic erosion which may be occurring is difficult to assess quantitatively.

CAPTURE OF GENETIC VARIATION

Selected genotypes may be captured for use in cultivation by seed and vegetative propagation techniques. The requirements for the storage of mahogany seed are described elsewhere (Tompsett, pp61–71) and are therefore not discussed further in this paper. Instead, the progress made in developing practical protocols for the vegetative propagation of mahoganies is described, including both propagation by leafy cuttings and *in vitro* techniques.

Vegetative propagation by rooting of leafy cuttings

A number of Meliaceae species, including most mahoganies, have now been successfully propagated by rooting leafy cuttings (Leakey, Last & Longman 1982; Newton, Leakey & Mesén 1993). Successful results have been obtained with a number of different propagation systems, including traditional mist propagators (Howard, Verkade & DeFilippis 1988; Tchoundjeu 1989), and also low-technology non-mist propagators (Leakey *et al.* 1990; see also Leakey, Newton & Dick, pp72–83; Mesén *et al.*, pp249–255). However, if mahoganies are to be propagated on a commercial scale, detailed information is required on the appropriate treatments which should be applied to both the stockplants and the cuttings to obtain consistently high rooting success. Such information is gained primarily through specific experimental programmes with individual species.

The most extensive propagation studies to date have been with *Khaya ivorensis* under mist (Tchoundjeu 1989) and with *Lovoa trichilioides* (African walnut) in non-mist propagators (Tchoundjeu 1989). These examples are consequently described here in some detail. Initial experiments were designed to determine the optimal conditions for rooting single-node, leafy cuttings from hedged juvenile stockplants. It was hypothesised that, for a species for which little is known about the conditions for rooting, the most important factors to test and optimise were auxin concentration, leaf area, cutting length and node position (Tchoundjeu & Leakey 1993). The basic methods and mist propagation system used were as previously described by Leakey *et al.* (1982) for the West African hardwood *Triplochiton scleroxylon*.

By comparison with *T. scleroxylon*, the highest rooting percentages of *K. ivorensis* were obtained with a considerably higher applied auxin concentration (200 µg IBA per cutting) but a smaller leaf area (10 cm^2). Subsequently, Asanga (1989) determined that the optimal leaf area under the conditions tested was about 30 cm^2. As with many other species, long cuttings (39 mm) rooted better than short ones (19 mm), especially if associated with a supra-optimal leaf area. Unlike *T. scleroxylon* and some other light-demanding species, the cuttings from basal nodes rooted better than those from apical nodes. These basal node cuttings had higher N, P, K, soluble carbohydrate and starch contents than those from apical nodes. One other observation from this study was that cuttings developed a one-sided root system if the cutting base was made by an oblique cut as opposed to a square cut (Tchoundjeu 1989).

Like many other members of the Meliaceae, plants of *K. ivorensis* grow by recurrent flushing; there are, therefore, alternating periods of terminal bud activity and dormancy. Higher rooting percentages were obtained when cuttings were taken from dormant shoots than from flushing shoots, although the latter had higher concentrations of soluble carbohydrates throughout the period of propagation.

In a more detailed study of the rooting of *K. ivorensis* cuttings, an attempt was made to investigate the relationships between rooting and the carbohydrate dynamics of the cuttings (Tchoundjeu 1989). This study included an examination of the effects of stockplant irradiance and nutrient applications on the dynamics of reducing sugar and starch contents of both the leaf and stem portions of cuttings in the propagator. Results showed that rooting never seemed to be limited by the stored carbohydrate reserves of the cuttings. Leakey *et al.* (pp72–83) present evidence derived mostly from light-demanding, pioneer species that rooting generally tends to be carbohydrate-driven. It, therefore, appears that, for *K. ivorensis*, and perhaps other relatively shade-tolerant species, rooting ability may not be limited by either carbohydrate reserves or the production of current assimilates. This conclusion was clearly demonstrated in a further study of the effects of stockplant nutrition on rooting. In this case, there was no effect of nutrient application on stockplant growth or rooting, although there were very considerable effects on the conversion of stored starch to sugars. Cutting mortalities were, however, greatest in cuttings from stockplants receiving the highest rate of nitrogen application (Tchoundjeu 1989).

Additional experiments were undertaken in Cameroon, investigating the factors which influence the rooting of *Lovoa trichilioides*, using a non-mist propagator as described by Leakey *et al.* (1990). In the early experiments, the propagators were not as air-tight as in later experiments, and the rooting percentages were frequently less than 50%. Nevertheless, by comparison with *K. ivorensis*, the auxin requirements of *L. trichilioides* cuttings were relatively low (Tchoundjeu 1989), with an optimal concentration in one experiment of 50 µg per cutting, while, in another, untreated controls rooted as well as treated cuttings. The highest rooting percentages were achieved with leaf lamina areas of 200 cm^2, about ten times that of *K. ivorensis*. These large-leaved cuttings also produced the most roots and had the lowest cutting mortalities. In a number of experiments, it was found that, as in *T. scleroxylon* but in contrast to *K. ivorensis*, a higher proportion of cuttings rooted from apical nodes of the top shoot, while those from basal nodes had the greatest mortality rates (Tchoundjeu 1989). Higher rooting percentages were obtained with cuttings from basal shoots, these having the greatest leaf and stem nitrogen concentrations, and high foliar carbohydrate contents.

In an attempt to examine the effect of cutting size (stem length and diameter), cuttings of three size categories were collected from similar positions within shoots. In this case, higher rooting percentages were obtained with long thin cuttings (38 mm x 4 mm) than long thick cuttings (45 mm x 8 mm); short thin cuttings (15 mm x 4 mm) were intermediate. To examine the effects of cutting origin on rooting, cuttings were collected from hedged stockplants producing one, two, three or four shoots per plant. In this instance, the mean percentage rooting of all cuttings harvested per plant was similar in all four treatments (Tchoundjeu 1989). However, the relative rooting percentage of cuttings from the different shoots was strongly influenced by the number of shoots per plant and their position on the plant.

As in *K. ivorensis*, the effects of stockplant management treatments, such as nutrient application and shading (irradiance and light quality), were not conclusive. It seems that, unlike light-demanding species such as *T. scleroxylon* and *Eucalyptus grandis* (Leakey & Storeton-West 1992; Hoad & Leakey 1992), rooting in relatively shade-tolerant hardwoods is not predetermined by the stockplant's light environment and the interactions of light with nutrients. Further studies are, therefore, required to examine the differences between these two groups of trees and determine the reasons for these differences in rooting physiology. However, despite this lack of conformity with other well-studied tropical hardwoods, it is clear that both these species of the Meliaceae are relatively easy to root as stem cuttings under either mist or non-mist propagation systems.

Few detailed vegetative propagation experiments have been undertaken with the neotropical species of the Meliaceae. In a preliminary investigation using non-mist propagators, the percentage rooting of *Swietenia macrophylla* cuttings was found to be higher when a rooting medium with a high proportion of sand was used; maximum rooting of over 60% was achieved with 75:25 sand/gravel (Mesén, Leakey & Newton 1992; Newton, Leakey & Mesén 1993). The concentration of IBA applied to the base of the cuttings was found to have only a slight effect on rooting. In these experiments, the cuttings were relatively slow to root (11 weeks), indicating that further research is needed if propagation protocols are to be improved. In general, *Cedrela odorata* appears relatively easy to root, displaying higher rooting percentages in sand than gravel, and with relatively low (0.2–0.4%) concentrations of applied IBA (Maldonado, Salazar & Mesén 1992).

In vitro micropropagation

A number of mahogany species have now been successfully micropropagated using *in vitro* techniques, including *Cedrela odorata* and *Swietenia macrophylla* (Lee & Rao 1988; Maruyama *et al.* 1989). One of the few species which has been investigated in any detail, however, is *Khaya ivorensis* (Mathias 1988), and is described here.

By comparison with another W African hardwood species, *Nauclea diderrichii*, explants of *K. ivorensis* were easy to sterilise with commercial sterilant (5%, 10% and 20% for 10, 20 or 30 minutes) (Mathias, Alderson & Leakey 1989). Those explants treated with 5–10% sterilant were free from tissue browning and were viable. The medium used in this study was that of Murashige and Skoog, with a carbon source of 20 g l^{-1} galactose (Mathias 1988). The stockplants were grown under tropical glasshouse conditions in Britain and explants cultured at 25°C at a photon flux of 50–60 μmol m^{-2} s^{-1} for 16 h each day. The experimental programme examined the effects of pre-severance stockplant treatments on culture initiation and the conditions required for shoot proliferation, and is described in full by Mathias (1988).

The environmental factors investigated in order to improve the success of culture initiation were the photon flux of photosynthetically active radiation (PAR), light quality (red/far-red ratio), daylength, day/night temperatures and stockplant nutrition. In addition, because *K. ivorensis* grows by recurrent flushing, experiments tested the effects of collecting explants at different times during the flushing cycles, as well as at different times after removal of the terminal bud.

Explants collected from dormant shoots had the highest bud activity in culture and the lowest mean callus score. When dormant shoots were decapitated prior to collecting explants, greater bud activities were found in explants collected either two to three or eight to nine days after decapitation than in those collected at other times. The application of fertilizers to stockplants had some effects on shoot growth prior to the collection of the explants, but little effect on culture initiation. In contrast, the stockplant light environment did influence bud activity in culture, with the greatest activity occurring in explants from plants grown at 60 μmol m^{-2} s^{-1} at R/FR of 0.3, especially in the absence of applied nutrients (Mathias 1988). Analysis over a number of different treatments, however, showed that the greatest increases in explant activity were achieved by increases in the red light/photosynthetic photon flux ratio (ie the proportion of red light [660 nm] in the whole band of photosynthetically active radiation [400–700 nm]).

Regarding the stimulation of shoot proliferation in *K. ivorensis*, the cytokinins benzylaminopurine (BAP) and zeatin at 2, 5 and 10 mg l^{-1} increased the mean number of axillary shoots formed per explant. Subsequently, a study of the effects of auxin (naphthalene acetic acid [NAA])/cytokinin (BAP) ratio on bud activity showed that the optimal combination was around 1:100–1:200 in the first subculture, but that in the second subculture even greater bud activities occurred, with an optimum NAA/BAP ratio of 1:25 (Mathias 1988). In another experiment, the transfer of cultures which had previously proliferated and had their shoots harvested, to media containing gibberellic acid (GA_3), stimulated further proliferation/elongation of shoots. However, in all these studies there was evidence that growth regulatory substances accumulated in the tissues, and consequently that they could reach inhibitory concentrations, if applied repeatedly through several subcultures.

In conclusion, it is clear that *K. ivorensis* (African mahogany) is amenable to micropropagation, and that practical protocols could be developed with further study. The major problem encountered in micropropagation was the initiation of a proliferating culture, owing to variability in the explants.

DEVELOPMENT OF APPROPRIATE SILVICULTURAL SYSTEMS

In order to realise the full genetic gains obtained through selection, the trees should be established in appropriate silvicultural systems. The choice of an appropriate system is determined partly by the physiological responses of the individual species (see Fasehun & Grace, pp148–157). The photosynthetic responses of *Swietenia macrophylla, Cedrela odorata* and *Khaya ivorensis* have now been analysed in some detail under controlled conditions (Kwesiga & Grace 1986; Kwesiga, Grace & Sandford 1986; Ramos & Grace 1990). In general, *Swietenia* and *Cedrela* spp. are highly light-demanding, and this fact should be taken into account in cultivation. Many of the failures in mahogany cultivation in silvicultural systems, such as line enrichment, can be attributed to inadequate intervention leading to excessive shading (cf Palmer 1988).

A wide range of different silvicultural approaches has been applied to the production of mahoganies with the aim of controlling shoot-borer attack. Most have resulted in failure, but there are examples of trials where shoot-borer damage has been at least partly controlled by cultural methods (Newton *et al.* 1993). For example, in Puerto Rico, line enrichment plantings resulted in as few as 11% of the trees being attacked (Weaver 1987; Weaver & Bauer 1986). Similarly Vega (1976) described a series of trials in Surinam, involving establishment of *Cedrela* spp. in natural regeneration, line enrichment and open plantation systems. After two years, the proportion of plants attacked was higher in plantations established in the open (10–60%) than in enrichment plantings (4–40% attacked). In other enrichment trials, the proportion attacked was less than 10% after 22 months. In trials established in Brazil, Yared and Carpanezzi (1981) reported that shoot-borer damage of *Swietenia macrophylla* was virtually absent in the line enrichment system employed.

The reasons for the success of these examples have not been investigated in detail, but may involve a variety of processes, such as the effects of shading on the growth rate of the trees and the production of terminal shoots (Newton *et al.* 1993). In particular, it has been suggested that the presence of other tree species may hinder location of meliaceous trees by the adult moth (Grijpma 1976; Morgan & Suratmo 1976). Very little precise information is available to indicate whether this process actually occurs, but it is conceivable that low densities of susceptible trees may prevent the build-up of moth populations (Weaver & Bauer 1986). In addition, populations of natural predators of *Hypsipyla* could be maintained in systems such as line enrichment, where much of the original vegetation is left intact (see Gibson & Jones 1977).

It should be noted that the planting of mahoganies in mixtures with crops or non-susceptible tree species does not guarantee successful shoot-borer control. For example, when a number of different silvicultural and agroforestry systems were tested in Colombia, no consistently successful method of shoot-borer control was identified (Vega 1987; Neyra & Martinez 1985). These results emphasise the importance of viewing the silvicultural system as one aspect of an integrated domestication strategy. Such a system might involve incorporation of pest-resistant genotypes into a silvicultural system optimising natural biological control, such as a line enrichment system, thereby providing an integrated system of pest management (Newton *et al.* 1993).

Mahoganies have been established successfully in monocultures in a number of countries where they are not native, such as *Swietenia macrophylla* in Indonesia and the S Pacific (Evans 1982). In such situations, mahoganies are often (but not always) resistant to the native shoot-borers, and can be grown successfully at high density, offering the prospect of rapid genetic gains in improvement programmes. Plantation establishment of exotic mahoganies is likely to increase in the future (Newton 1993), perhaps including the introduction of *Khaya* spp. into the neotropics (Betancourt *et al.* 1972), an approach which has so far not been tested on a large scale despite its obvious potential.

CONCLUSIONS

The development of a domestication strategy for mahoganies offers the prospect of overcoming the problems which have limited mahogany cultivation so far. Such a strategy should involve selection for pest resistance as one component of a genetic improvement programme, and should also involve the deployment of selected genotypes in appropriate silvicultural systems to optimise pest control as well as growth. Techniques for capturing selected genotypes, including *in vitro* techniques and propagation by leafy cuttings, have been successfully developed for a number of mahogany species, although further research is required to refine the precise treatments required for sustained successful rooting. Application of these propagation techniques to genetic improvement should enable rapid progress to be made in generating superior clonal populations for use in reforestation.

Apart from increasing efforts at genetic improvement of mahoganies, attention should also be directed towards genetic conservation, both of populations *in situ* and of selected genotypes *ex situ*. Increased exploration and testing of genetic resources of mahogany species are urgently required, particularly of the African species, which have hardly been investigated in this regard. High rates of deforestation in both palaeotropical and neotropical regions continue to deplete these genetic resources, and could limit the potential for sustainable production of mahogany in the future.

It is to be hoped that the prospects of developing a successful domestication strategy for mahoganies will stimulate interest within the timber industry, and encourage attempts to regenerate a resource. The economic incentives for such an initiative certainly exist: the demand and value of the timber are likely to remain high for the foreseeable future (Palmer, pp16–24).

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Production of dipterocarp planting stock by cuttings in Indonesia

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ABSTRACT

Dipterocarps belong to one of the most important tropical timber tree families in the world, and, as a result, they have been heavily exploited throughout their range, especially over the past 30 years. When exploited too heavily, logging may lead to an excessive degree of canopy opening, or to longer-lasting damage from which the forest needs a very long time to recover. In Indonesia, it is clear that a continued supply of dipterocarp timber is of the highest importance, with a growing local demand and the importance of forest industries in the overall economy. This paper describes some research work currently being directed towards maintaining a supply of dipterocarp timber, and presents results of its application. The work described is that of the TROPENBOS-Kalimantan project, where research is centred on a priority list of 20 dipterocarp species. In these species, shortages of wildlings arise because the number of seedlings in the natural forests decreases sharply in the years after a mast fruiting. Other means of providing planting stock are, therefore, necessary. For this reason, effort was put into developing a system for vegetative propagation of dipterocarps, involving the setting up of hedge orchards in which the stockplants can be induced to produce vertical shoots suitable for propagation. A propagation system using aerated water is described, and the factors important for successful rooting of dipterocarp cuttings are discussed. Various methods for ectomycorrhizal inoculation are also described. The operational application of these techniques, and the scope for future genetic improvement of dipterocarps are assessed. The research results reported suggest that in the future vegetative propagation of dipterocarps may be applied to the production of highly productive clones, providing a completely new economic outlook on the use of dipterocarps in plantation forestry, as well as in the enrichment of natural stands.

INTRODUCTION

Dipterocarps belong to one of the most important tropical timber tree families in the world. In the world markets, their timber makes up a very large part of the total timber trade. Their presence in the forests of south and south-east Asia is often characterised by their domination of the upper canopy: in some forests, dipterocarps may make up more than 80% of the trees in this layer. With their timber available in large volumes of relatively homogeneous quality, and with the fact that most of their timbers float enabling cheap transportation by river, they have become a popular timber for industrial uses.

As a consequence of their economically attractive characteristics and their common occurrence in the forests of SE Asia, as well as the political situation in a number of countries with dipterocarp forests, their exploitation has been taken up with great vigour, especially over the past 30 years. Countries which started timber exploitation earlier, such as the Philippines, now have virtually no natural forest left. In other countries, the area of dipterocarp forest is also decreasing quickly. The reasons for the diminishing areas of dipterocarp forest are numerous and varied. Exploitation is being practised mostly under selective cutting systems and should not necessarily lead to the disappearance of the whole forest. When exploited too heavily, however, such cutting leads to a large degree of opening up of the upper canopy. Unscrupulous exploitation leads to more long-lasting damage, and the forest will need a very long time to recover from the logging operation. Furthermore, when the initial harvest is followed too soon by relogging, irreparable damage can result; again, the forest will need to be left alone for extremely long periods before similar vegetation grows back. The opened up logged-over forest is more easily encroached by shifting cultivators, while at the same time it becomes more prone to the risks of fire. With human encroachment, the fire risk may become very serious. In addition to the unintended squandering of their diminishing resources, many countries also convert natural forest to other uses, such as rubber and oil palm plantations, agriculture and settlements.

The forest industries are of major importance to the Indonesian economy. In 1991, 2.5 million people were directly involved in the forestry sector for their income and another 1.2 million were involved indirectly. Including their families, this makes a total of more than 14 million people earning their livelihood from the Indonesian forests (MPI 1992). Indonesia has invested heavily over the past years in various timber industries such as plywood mills (156 units), sawmills (468), and furniture construction (340), all of which rely mostly upon dipterocarp timber for their functioning. The dipterocarp timber being exported generated US$3.981 million for the country in 1991 (MPI 1992). It is clear that a continued supply of dipterocarp timber is of highest importance for Indonesia, with its growing local demand for timber.

The Ministry of Forestry in Indonesia has in recent years taken many steps to encourage sustainable dipterocarp forest management. Most of the forests are managed under a natural stand management system, called the Indonesian selective felling and planting system (TPTI). This system is based upon the harvesting of a few trees of mature size (>50 cm dbh) and the consequent tending of trees of commercial species in the diameter range of 20–50 cm dbh. The system also involves planting of the skid roads and log yards, and enrichment planting (stocking) of those areas with a low number of seedlings of commercial tree species. Indonesia also promotes forest regeneration through plantations, resulting in complete conversion of the original vegetation, which is normally achieved through clearcutting followed by replanting. In both TPTI and plantation forestry, there is a need for high-quality planting stock of many species, including dipterocarps.

One of the steps taken to overcome the problem of limited planting stock supply was an increased input into research and development. Research on dipterocarp planting stock production is taking place through various institutions at a number of places in Indonesia, including Bogor (Agricultural University, BIOTROP and the Center for Forestry Research), Yogyakarta (Gajah Mada University), Samarinda (Mulawarman University) and Samboja (Wanariset Dipterocarp Research Station of the Forest Research Institute in Samarinda) through the TROPENBOS-Kalimantan co-operative project. In this paper, we will describe some of this work and present some results of its application. The work described is that of the TROPENBOS-Kalimantan project, aimed at solving the problems of planting stock supply. This project is a co-operative effort of the Agency for Forestry Research and Development of the Indonesian Ministry of Forestry, the Indonesian state forestry enterprises PT. INHUTANI I and PT. INHUTANI II, the TROPENBOS foundation and the Institute for Forestry and Nature Conservation 'De Dorschkamp'.

It should be mentioned that older examples of dipterocarp planting do exist, eg the *Shorea javanica* plantations in Krui, Sumatra, the Tengkawang plantations in West Kalimantan, and the *Shorea platyclados* plantations in Purbatonga, north Sumatra, etc. These examples have shown clearly that it is possible to plant dipterocarps successfully.

PROBLEMS IN PLANTING STOCK PRODUCTION

One particular feature of the dipterocarps is their irregular flowering behaviour. Most trees flower in so-called mast flowering years. During such years most individuals of most dipterocarp species in a given region will flower. Some individuals or species may flower in years in between mast flowering years. Seeds of many dipterocarps cannot be stored for extended periods of time. They are classified as recalcitrant (Tompsett 1987; see also Tompsett, pp61–71). Propagation is further hampered by the fact that many of the seeds are commonly attacked by weevils and suffer other forms of premature death. Even in the instances where seed can be collected, the seedlings produced in the nursery may turn yellow and eventually die. In addition, wildlings which appear healthy in the nursery often die after planting in open terrain. In the past, this combination of factors has made it rather difficult to rely upon seed propagation for any planting scheme involving dipterocarps. The research described below was directed at solving these problems.

PRODUCTION TECHNIQUES

Wildlings

The simplest method of planting stock production involves the collection of wildlings from natural forest during or shortly after periods of heavy rainfall. After a short period in the nursery, the plants are ready for planting. Advantages of this system are that it is relatively simple and cheap, and that the plants are genetically varied (when not originating from single apomictic mother trees, which may in certain instances be the case). In addition, they may have been infected by ectomycorrhizal fungi from the roots of their mother trees. A description of this method of dipterocarp planting stock production was published in a simple manual in Indonesian (Smits 1986), which was reprinted by the Association of Forest Concessions in Indonesia and distributed to all Indonesian timber concessions. This system is now the most commonly used in Indonesia. In 1991 more than 30 million dipterocarps were produced by a limited number of concessions (Smits & Leppe 1991). Preliminary estimates indicate that this number has now doubled. Smits *et al.* (1993) indicate that, by agreement between a number of countries in the Association of South-East Asian Nations, it should be possible to guarantee a constant supply of wildlings by exchanging dipterocarp material between different regions with different mast flowering seasons. Technically, such a scheme has been proved possible, but there are a number of practical problems, including the quarantine regulations of the different countries.

Attention is likely to concentrate on the most commercially important dipterocarp species for use in large-scale planting. At the TROPENBOS-Kalimantan project, a priority list of 20 dipterocarp species is used as a reference for most of the research activities (Table 1). Most of these species occur in the project area and were selected on the basis of their high growth rates, as determined by growth and yield research, the use of their timber, and practical experience. However, if attention concentrates on such a limited number of species, a shortage of wildlings will eventually occur. Such shortages also arise because the number of seedlings in the natural forests decreases sharply in the years after a mast fruiting. Moreover, the older and larger the seedlings, the higher their mortality and the more difficult they are to handle (ie they need longer in the nursery, larger containers, more nursery space, etc). Other means of providing planting stock are, therefore, required in such circumstances. For this reason, much effort was put into developing a system for vegetative propagation of dipterocarps which would make the planting stock supply independent of dipterocarp mast flowering seasons. However, the most practical and economical way of producing planting stock often proves to be a combination of the two systems, producing more plants from wildlings when they are available and switching to cuttings when wildling supplies become scarce. Wildlings can also be used for vegetative propagation, the material still being very juvenile and relatively easily rooted.

Table 1. Priority list of dipterocarp species for future practical research (TROPENBOS-Kalimantan propagation and stand establishment project)

1	*Shorea pauciflora*	11	*Shorea macrophylla*
2	*Shorea parvifolia*	12	*Shorea pachyphylla*
3	*Shorea leprosula*	13	*Shorea dasyphylla*
4	*Shorea seminis*	14	*Dryobalanops aromatica*
5	*Shorea johorensis*	15	*Dryobalanops keithii*
6	*Shorea smithiana*	16	*Anisoptera costata*
7	*Shorea ovalis*	17	*Shorea selanica*
8	*Shorea stenoptera*	18	*Shorea platyclados*
9	*Shorea polyandra*	19	*Shorea albida*
10	*Dryobalanops lanceolata*	20	*Anisoptera marginata*

Vegetative propagation: rooted cuttings and hedge orchards

Vegetative propagation of dipterocarps has been tried by various researchers, with varying degrees of success (Srivastava & Manggil 1981; Hallé & Kamil 1981; Smits 1983; Yasman & Smits 1988). One of the first papers to mention rooting of *Shorea leprosula* cuttings was by Ardikoesoema and Noerkamal (1955). Vegetative propagation of dipterocarps offers several advantages, such as the production of genetically more homogeneous planting stock, the possibility of multiplying selected material, and independence from mast flowering seasons in relation to planting stock supply. There are, however, a number of important factors affecting the vegetative propagation of dipterocarps by the rooting of stem cuttings.

Although rooting is feasible in principle, the matter of juvenile shoot production is critical for large-scale application of vegetative propagation techniques in the field. Cuttings of dipterocarps taken from plagiotropic branches do not, or only very seldom, produce vertically growing trees. Almost all dipterocarps grow according to the architectural models of Roux and Massart (cf Oldeman & Sieben-Binnekamp, pp25–33), so that only one vertical axis (the main stem) is normally available, and the branches are all plagiotropic. This growth pattern severely limits the number of vertical shoots available for taking cuttings. Therefore, it is necessary to set up hedge orchards in which the stockplants can be induced to produce many vertical shoots. Previously developed methods (Leppe & Smits 1988) have now been refined by more recent research. The newer method induces vertical growth of axillary sprouts low on the main stem, and is based upon suppressing apical dominance. Vertical shoots are bent sideways under a rope net. This induces orthotropic shoots to sprout, which emerge distributed evenly through the net. After some time, the bent shoots become woody and the rope net can be removed. Cuttings can be harvested from these vertical shoots. Providing that the shoots are regularly cropped for cuttings, new shoots arise from their axils. It is important to harvest the cuttings constantly to prevent one of the vertical shoots from redeveloping strong apical dominance and suppressing the other orthotropic shoots on the same stockplant from further development.

Those stockplants of *Shorea leprosula* which produced the most axillary shoots were normally found to yield cuttings with quicker rooting and higher total rooting percentages. Furthermore, the resulting plants showed better growth (W T M Smits & A Erwinsyah, unpublished data). If the same is true for all dipterocarp species, this method may present an easy way of selecting superior-quality planting stock for mass production by vegetative propagation. Some of the rooted cuttings of dipterocarps planted in the field show growth over the first five years amounting to over 3 cm diameter increment per year and 2 m height growth per year. Some individuals produced from wildlings growing in the Kiani Lestari concession had increments of 4 cm in diameter per year for the first three years. Although these performance data refer to certain individuals only and in no way present a guarantee for future production of these dipterocarps, they show clearly the great potential for genetic improvement in dipterocarps (see later).

Rooting of dipterocarp cuttings is possible in solid media and in water. Currently the water method, developed at Wanariset, is preferred. In this method, use is made of a kind of 'bubble bath', which may be best compared to a Japanese jacuzzi. The cuttings are held between two palm fibre brushes suspended over water containing IBA or some other auxin. The solution is aerated by a pump via porous aquarium stones. The basal ends of the stem cuttings are inserted in the solution. The leafy parts of the cuttings are partly pruned to enable the stocking of more cuttings per pair of brushes and to decrease transpiration, and a cover is placed over them to maintain high air humidity. The water used for rooting is circulated and constantly filtered through a small commercial drinking-water filter and warmed to over 50°C by solar power.

There are a number of advantages to this rooting method. The first is that the rooting conditions are very homogeneous, especially for research purposes. The large body of water buffers temperature changes in the rooting zone. The aerated water also constantly touches the brushes through which much water evaporates, automatically maintaining a high air humidity around the leafy parts of the cuttings. There is almost no maintenance needed apart from a change of water every two weeks, and assessment of the cuttings is easily achieved by lifting the brushes containing the cuttings out of the water. Rooted cuttings can be removed without causing any disturbance. Another advantage is that more roots develop from lenticels, providing a good connection between stem and root system. In solid media, cuttings tend to produce adventitious roots from callus at the stem base. Many of these root systems can be easily severed at planting time. However, cuttings rooted in water have longer and more fragile roots, which may make them more susceptible to damage, and the plants may need more careful maintenance (watering, misting, hardening off) as a result.

A number of factors have proved to be important for successful rooting of dipterocarp cuttings. One of the most important is the juvenility of the source material. Omon and Smits (1989) found that *Shorea lamellata* cuttings taken from plants younger than one year had 100% rooting within two weeks without any application of auxins. In general, older dipterocarp material needs higher doses of auxin application for successful rooting. Avoidance of extreme temperatures (<15°C or >35°C) is also critical for successful rooting. Relative humidity of the air should be kept constantly high around the leafy parts of the cuttings, and aeration of the rooting medium is essential. When the cuttings are pruned so that the basal part of the stem is cut through a node, rooting occurs more quickly. Large rooting differences are also found between different dipterocarp species. *Dipterocarpus* spp. are the most difficult to root because of the resin which flows from the cut surface of the cutting base. Nevertheless, Somkiat (personal communication) reported 95% rooting of *Dipterocarpus alatus* cuttings from very young source plants in Thailand, even without application of auxins. De Fraiture (unpublished data) found that the mass of the cuttings, as well as the trimming of the leaves, had a significant effect upon rooting of *S. leprosula* cuttings. The time of day at which the cuttings are taken also has some influence upon speed and percentage of rooting (Siagan 1991), as has the degree of irradiance during the rooting process (cf Leakey, Newton & Dick, pp72–83). Given the right combination of these factors, it has now proven possible to root many different dipterocarp species, albeit not all with the same degree of success.

Cuttings of 46 dipterocarp species have been successfully rooted at the TROPENBOS-Kalimantan project (Table 2), and a number of others have been propagated by other researchers. This work indicates that many dipterocarp species are amenable to vegetative propagation, when the right combination of rooting factors is applied. The usefulness of vegetative propagation is a matter of economics. If the species has low growth potential after planting, has very low

Table 2. List of successfully rooted dipterocarp species by means of stem cuttings and/or air layering at the Agricultural University, Wageningen, The Netherlands, and in East Kalimantan, Indonesia

Anisoptera costata
A. marginata
Cotylelobium malayana
Dipterocarpus confertus
D. cornutus
D. gracilis
D. grandiflorus
D. hasseltii
D. humeratus
D. imbricatus
D. lowii
D. mundus
D. tempehes
Dryobalanops aromatica
D. lanceolata
D. keithii
Hopea mengerawan
H. odorata
H. pierri
H. rudiformis
Parashorea tomentella
Shorea albida
S. assamica
S. balangeran
S. bracteolata
S. dasyphylla
S. faguetiana
S. johorensis
S. laevis
S. lamellata
S. leprosula
S. macrophylla
S. multiflora
S. ovalis
S. pachyphylla
S. parvifolia
S. pauciflora
S. platyclados
S. polyandra
S. selanica
S. seminis
S. smithiana
S. stenoptera
Vatica chartacea
V. rassak
V. umbonata

rooting percentages, or yields few vertical shoots suitable for the production of stem cuttings, the costs of production will be very high and vegetative propagation will not be an economical option. Fortunately, members of the genus *Shorea* are among the easiest dipterocarps to propagate, as well as being some of the most commercially important species. Experience has shown that for these species vegetative propagation is a viable alternative to production by wildlings.

Before transplanting, rooted cuttings should be inoculated with ectomycorrhizal fungi (Smits 1983). Various methods for inoculation have been tested in East Kalimantan. The simplest and most practical method is the maintenance of a live inoculum collection. This collection consists of seedlings or cuttings inoculated with spores, pieces of sporocarp, or pure cultures of ectomycorrhizal fungi. Once the establishment of suitable ectomycorrhizal infection is confirmed, these mycorrhizal root systems can be used to inoculate the rooted cuttings.

The use of these techniques should be supported by a clear assessment of the expectations based on the results achieved. For this purpose, a computer cost comparison model has been developed at the project which accurately calculates the cost of dipterocarp planting stock for all possible options and situations. This model is now being extended to include models for planting and maintenance. Initial analyses show that the cost of growing dipterocarps from cuttings can be reasonably low. The programme can assist in determining the most critical factors for affecting the end price of a cutting and help a nursery manager to optimise his operations.

APPLICATION OF VEGETATIVE PROPAGATION IN THE FIELD

As mentioned before, planting of dipterocarps has become popular in Indonesia. A start has been made in a small number of places to apply the vegetative propagation techniques for dipterocarps for production purposes. The first company to apply this technique on an operational scale was PT. INHUTANI I in their timber estate in Longnah (Figure 1). Longnah is located in the middle of the extensive area that was burnt during the long drought of 1982–83, resulting in the destruction of more than 3 million ha of forest in the Indonesian part of Borneo, and about 1 million ha in Sabah. In the neighbourhood of Longnah, very few stands of dipterocarps remain and the shrub vegetation resulting from the fire is now being converted to timber plantations for construction wood. At first, fast-growing light-demanding tree species are used, followed by line planting with dipterocarps.

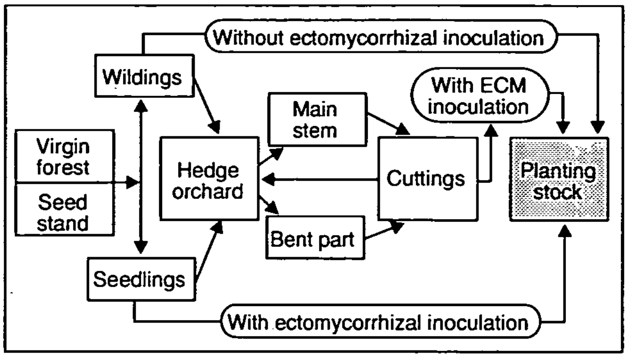

Figure 1. Production of dipterocarp planting stock in the Longnah timber estate of PT. INHUTANI I

Because sources of wildlings are scarce around Longnah, some of the PT. INHUTANI staff were trained at the TROPENBOS-Kalimantan project and subsequently applied the project's propagation techniques in the field. They set up a large hedge orchard (more than 1 ha) and many propagating tanks for rooting the cuttings. To start up the hedge orchards, they partly used wildlings collected from beneath healthy trees of the faster-growing light-red *Shorea* (meranti) species, and their unit is now capable of producing more than 300 000 cuttings a year. The trees developing from the cuttings are growing well. PT. INHUTANI I is making use of a permanent nursery with roofed rooting facilities, shaded areas with screen wire, electricity supply, etc.

However, it is now also possible to produce the dipterocarp cuttings under much more modest conditions appropriate to the average forestry concession. A simple water bath can be constructed out of wooden boards that surround a hole in the ground. The lining of this hole and the boards are covered with a sheet of plastic, and the propagation brushes can then be put on the edges of the boards. Normally, a temporary nursery will be located where a road crosses a river, where vegetation is still present, providing the right light environment. If the nursery is located along a river, use can be made of water power to rotate a water wheel which can in turn pump air to the rooting tanks. The soil is mostly rather wet along the rivers, and the air humidity as a consequence is also high. Operation is, therefore, possible without covering the rooting tank with a plastic sheet. Examples of such nurseries have now been set up and demonstrated to be practical.

PROSPECTS FOR GENETIC IMPROVEMENT

Although rare, hybridisation in dipterocarps does occur (P S Ashton, personal communication). Some of the induced or naturally produced hybrids show heterosis. One example in East Kalimantan is a probable hybrid between

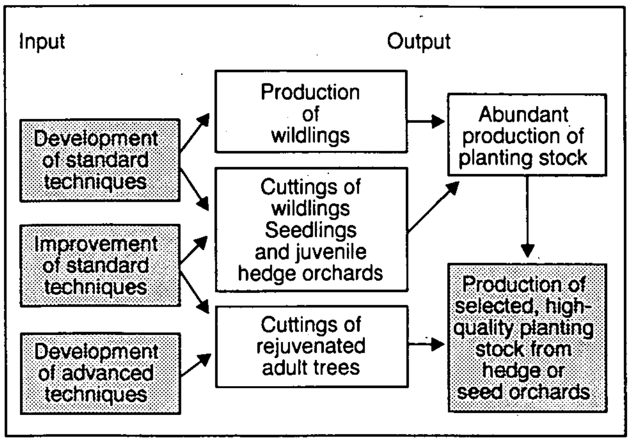

Figure 2. Research approach for vegetative propagation at the Wanariset I Dipterocarp Research Station

Dipterocarpus confertus and *D. tempehes.* The tree shows intermediate morphology between the two mentioned species and was considered a hybrid by Ashton (personal communication). The hybrid is growing faster than plants of either of the two original species, has good self-pruning, and has a very straight stem. At the same time it does not seem to suffer from shoot-borers as is common in both the original species (Smits *et al.* 1990), although shoot-borers were found within a few metres from the hybrid. Vegetative propagation may prove useful in the near future to propagate such promising individuals, although it may not be so relevant in the case of *Dipterocarpus* species, as their wood contains much resin and the trees are generally slower-growing than the light-red *Shorea* species.

A start with provenance trials has been made in East Kalimantan and additional trials of some seven species will be established soon. In addition, some 50 different clones of two *Shorea* spp. have been selected with good potential growth for testing on a larger scale. Research is also continuing on the rooting of mature shoots by air layering, and on other aspects of tree improvement (Figure 2).

CONCLUSIONS

Recent developments in Indonesia have shown that there are good prospects for use of vegetative propagation techniques in tropical forestry. These techniques are not solely suitable for typical plantation species like *Eucalyptus* spp. and *Gmelina arborea*, but can also be used for indigenous species such as the dipterocarps, in a cost-effective way. The research results reported here suggest that in the future vegetative propagation of dipterocarps may be applied to the production of highly productive clones, providing a completely new economic outlook on the use of dipterocarps in plantation forestry, as well as the enrichment of natural stands.

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Some wild Malaysian species – domestication through agroforestry
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An attempt to establish indigenous tropical forest trees of economic potential on mining wasteland at the Kenya coast
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CONSEFORH – conserving and developing forest genetic resources in Honduras
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Neem decline in West Africa
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The domestication of *Coula edulis*, a multipurpose species of the humid tropical forests of Africa: the germination problem
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Native tree species for improvement of secondary forest vegetation
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Agroforestry *vs* forest destruction in eastern Bolivia
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Survival and growth of seedlings of four tropical dry forest tree species, *Hymenaea courbaril, Swietenia macrophylla, Manilkara chicle* and *Cedrela odorata* in Costa Rica
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Studies in the nitrogen nutrition of *Acacia auriculiformis* seedlings
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Multipurpose trees: the requirements of the local community
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Sesbanias: model woody legumes for biotechnological development
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Early growth and survival of four open planted dipterocarps in peninsular Malaysia
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***Leucaena salvadorensis:* conservation and utilisation in Central America**
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Floral biology and vegetative propagation of the African plum *(Dacryodes edulis)*
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Application of clonal technology for tree improvement in India – ITC Bhadrachalam experience
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Low-technology propagation of tropical trees: appropriate technology for rural development
(R R B Leakey, J F Mesén, P N Shiembo, D Ofori, T Nketiah, A Hamzah, Z Tchoundjeu, C Njoya, P Oduol, A C Newton, J McP Dick & K A Longman, Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK)

***Calliandra calothyrsus* and the domestication of close relatives**
(D MacQueen, Oxford Forestry Institute, Department of Plant Sciences, University of Oxford, South Parks Road, Oxford 0X1 3RB, UK)

Selection for resistance to the mahogany shoot-borer in Central America and the Caribbean
(A C Newton, J F Mesén, P Baker & R R B Leakey, Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK)

Nodulation and characteristics of rhizobial isolates trapped with various legume genera in a semi-arid tropical soil
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Study of *Inga* genetic resources in Central and South America
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The effects of moisture content on the low temperature responses of *Araucaria hunsteinii* seed and embryos
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Strategies for the selection of salt tolerance in tropical woody legumes
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Ecophysiology of seeds and storability problems in seven valuable tropical rain forest tree species from south-eastern Mexico
(M C Rodriguez-Hernandez & C Vazquez-Yanes, Centro de Ecologia, National University of Mexico, Apartado Postal 70-275, Ciudad Universitaria, 04510 Mexico DF, Mexico)

The forestry management and plantation project
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Infection process and root nodule development in *Anadenanthera falcata* Speg.
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Domestication of indigenous fruit trees in Cameroon
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Nutrient cycling and competition: the potential for management in agroforestry
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Shrubby forage legumes for the acid soils of Latin America
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The selection of *Khaya senegalensis* for use as shade trees and line plantations
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Effect of the *Rhizobium* inoculation in *Prosopis pallida* seedlings
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Comparative evaluation of agroforestry trees on vertisol soils under low rainfall
(I Verinumbe, F L Sinclair, W P Adderley & D A Jenkins, Department of Biological Sciences, University of Maiduguri, PO Box 1069, Maiduguri, Nigeria)

Optimisation of agroforestry systems with traditional tree crops in SW province, Cameroon
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Domestication of rainforest trees in Cameroon
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Application of vegetative propagation techniques for Dipterocarpaceae in East Kalimantan, Indonesia
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