Chapter (non-refereed)

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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.

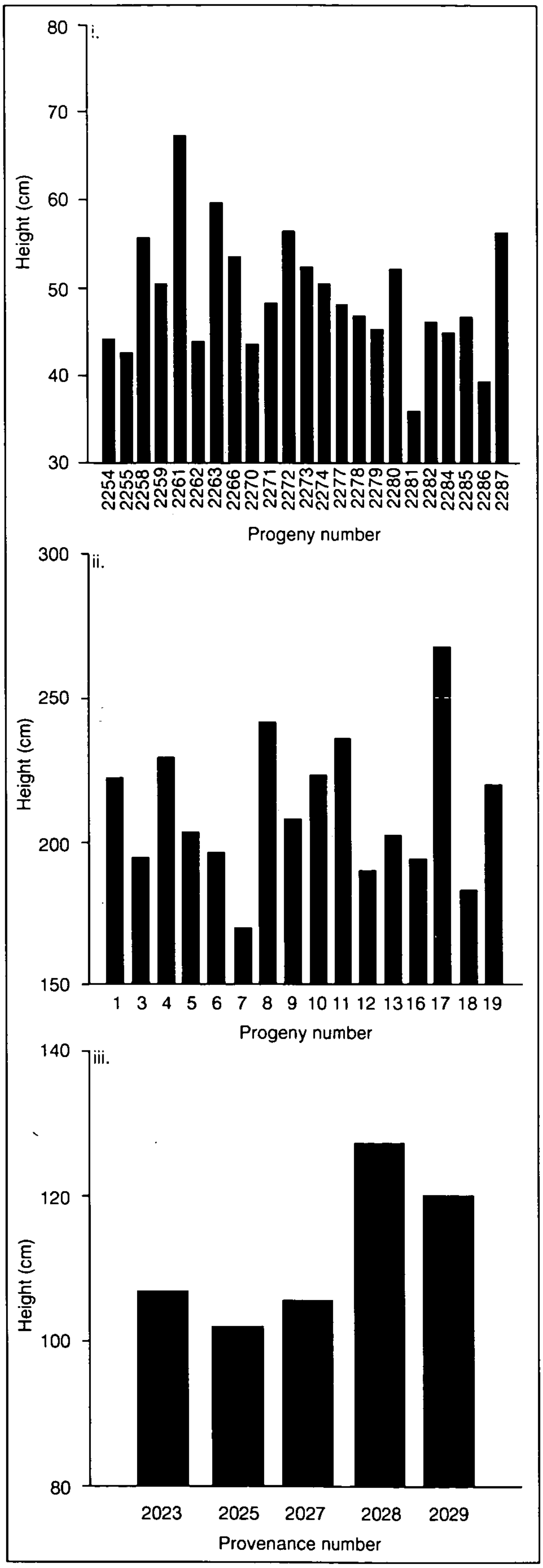

Figure 1. Preliminary results from field trials of *Swietenia macrophylla*, illustrating the extent of genetic variation in height growth

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

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

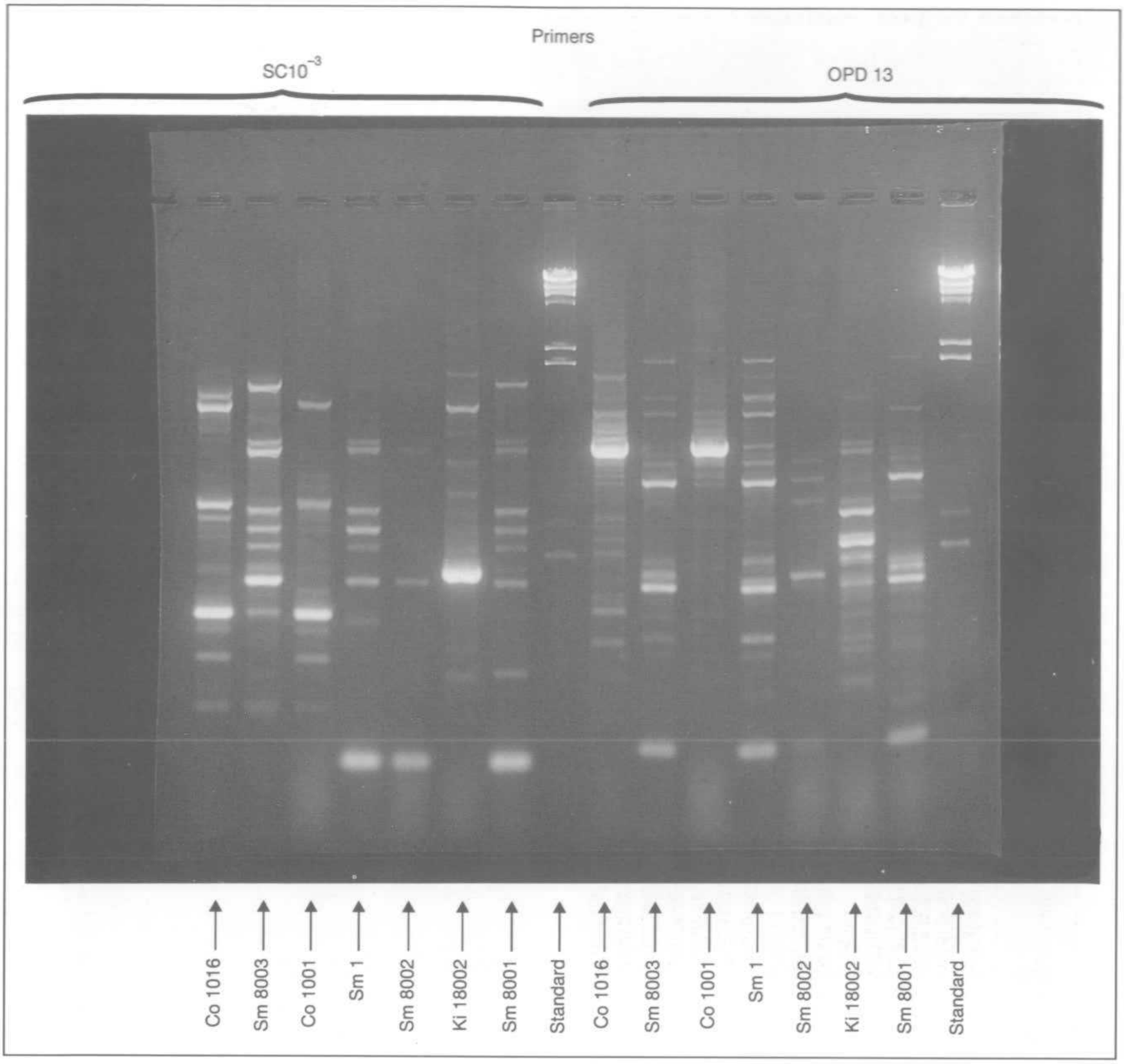

Figure 2. Genetic variation in mahogany species, detected using RAPDs (for details of methods, see text). The Figure presents amplification products of *Swietenia macrophylla* (Sm), *Cedrela odorata* (Co) and *Khaya ivorensis* (Ki) on an ethidium bromide-stained gel, using two primers, SC10^{-3} and 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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