DOMESTICATION OF TROPICAL TREES: AN APPROACH SECURING FUTURE PRODUCTIVITY AND DIVERSITY IN MANAGED ECOSYSTEMS

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SUMMARY

In recent years, progress has been made with domestication of *Triplochiton* scleroxylon, an important timber tree of the moist West African forests. Seed viability has been extended from a few weeks to many months by appropriate drying and cold storage. Seed supply is irregular, but the successful development of vegetative propagation methods has provided an alternative, regular supply of planting stock. Rooted cuttings have the further advantage that they can readily be tested to identify promising clones of good form. To this end, experiments on the physiology of branching have allowed the development of a screening technique which can predict later branching habit from tests on small plants. The occurrence of precocious flowering in glasshouse conditions has allowed progress towards control over reproduction, and cross-pollinations with deep frozen pollen have produced viable seeds from clones only 2-5 years old.

The possibility of similarly domesticating many other tree species is discussed in relation to the need for improved selections for use in diverse managed ecosystems. Obtaining sustained yields of food and wood products on land formerly under moist tropical forest clearly depends on learning how to combine increased output from currently under-utilized species with soil improvement and *ex situ* conservation.

RESUMÉ

Triplochiton scleroxylon est un arbre des forêts d'Afrique occidentale dont le bois est très important. On peut rendre les graines plus viables en les faisant sêcher ou en les mettant dans une pièce froide pendant quelques semaines ou même pendant quelques mois. Il est quand même difficile de les obtenir régulièrement. Les boutures, qui ont pris racine, ont l'avantage sur les graines par ce qu'elles sont plus disponibles et on peut les développer à partir d'un bon clone. Elles fleurissent très jeunes quand on leur offre les conditions semblables à celles d'une serre où il est possible de contrôler la reproduction avec du pollen congelé et cela a déjà produit des graines viables à partir des clones âgés de deux à cinq ans.

La domestication d'autres arbres deviendra possible par cette méthode et avec l'amélioration de la terre il y aura plus de bois et plus de la nourriture dans les forêts tropicales.

RESUMEN

En anos recientes se han hecho progresos en el cultivo de *Triplochiton scleroxylon*, un importante arbol maderero de los bosques humedos del Africa occidental. La viabilidad de la semilla ha sido extendida de unas pocal semanas a varios meses madiante tecnicas apropriadas de secado y alma cenamiento en frio. El abastecimiento de semillas es irregular, pero el exitoso desarrollo de metodos de propagacion vegetativa ha proveido de una laternativa, el abastecimiento regular de 33

material vegetativo para plantacion. Estacas con raices tienen aun la ventaja que pueden ser probadas para identificar clones prometedores de buena forma. Para este fin, se han llevado a cabo experimentos en la fisiologia de la formacion de ramas que han permitido el desarrollo de una tecnica de proyeccion que puede prede predecir el desarrollo futuro de ramas mediante pruebas en plantas pequenas. La ocurrencia de floracion precoz en condiciones de invernacula ha permitido progresar hacia el control sobre la reproduccion y polinizaciones cruzadas usando polen congelado, han producido semillas via bles de clones de apenas 2.5 anos.

Es discutida la posibilidad de uncultivo similar de muchas otras especies arboreas en relacion a la necesidad de selecciones mejoradas para vso en diversos ecosistemas bajo cultivo. La obtencion de rendimientos sostenidos de alimentos y productos madereros en tierras anteriormente bajo bosque tropical humedo, depende claramente en aprender como combinar el incremento en la produccion de especies corrientemente subutilizadas con el mejoramiento del suelo y la conservacion *ex situ*.

Introduction

The forests of the humid tropics currently amount to around 9 million Km^2 . If the current rate of destruction, approaching 50 ha min⁻¹ (Myers, 1980), were to continue unchecked it can be projected that all but the most inaccessible parts will disappear within the next 60 years, with the concurrent loss of thousands of plant and animal species. The situation is already serious, but attitudes are fortunately changing through the actions of governments and a variety of international agencies. As a result, a nominal 1.5% of the world's tropical forests has already been designated for conservation, and it is the intention that this should be raised to 10% under the Man and the Biosphere programme. Essential as this *in situ* conservation is, it needs to be augmented by *ex situ* conservation (see FAO, 1975; Frankel & Hawkes, 1975), as part of the overall process of domestication in the management of the remaining 90% of the forest land.

Exploitation of natural forest and the needs of the future

The exploitation of tropical timbers has been and still is highly selective, with characteristically only about 5% of the trees being extracted at any one time (Myers, 1980). This process is also very wasteful, for although some of the remaining trees are used for fuel, many are burnt on site or left to rot. The consequent sudden release of nutrients is rarely efficiently utilized in such disturbed sites before they are lost from the soil.

In some areas, particularly in West Africa, Central America and parts of India and S.E. Asia, the demand for timber has greatly exceeded natural production and this deficit has stimulated interest both in the establishment of exotic species in plantations and a reconsideration of the value of indigenous species previously regarded as of little or no potential. Thus in West Africa where only 10 species were exploited in the 1950's (contributing 70% of timber exports) more than 40 are utilized today, as for instance in Nigeria (Spears, 1980). Similar reappraisals could be made in:- (i) Malaysia, where there are at least 4,100 species of trees (Whitmore, 1972) and (ii) Amazonia, where only 50 of 2,500 tree species are used, although about 400 are thought to have some direct commercial value (Myers, 1980).

Although difficult to quantify, there is little doubt that fruits (including nuts), gums, resins, oils, tannins, fibres, latex, dyes and medicinal products produced by the different components of moist forests, could be utilized to a great extent

(Robbins & Matthews, 1974; Jong *et al*, 1973; Okafore, 1980). Many of these forest products are of increasing economic importance (Grainger, 1980), although movement to international markets is often restricted by inadequate storage, transport and infrastructure. Unlike the extracting of timber trees, the mainly non-destructive harvesting of these forest products has little or no detrimental effect on tropical forests. Indeed increased interest in these products could contribute positively to the mixed assemblages of plants grown in the tropics.

Domestication of under-utilized timber species

Domestication implies the collection of seeds or plants, ideally from the entire natural range of the species, and in time, the selection, propagation and breeding of variants best suited to the needs of man. Because this is a lengthy process, commercial cultivation usually starts before the crop is fully domesticated. This is particularly so in trees because of their long life-cycles, where it is the selection processes which often put a constraint on the rate of improvement achieved during domestication.

For forestry plantations, the first steps are usually taken through provenance testing, where seeds collected from several locations are compared often outside their natural range.

Many of the candidate species for domestication, however, have seed problems which hinder both provenance testing and commercial forestry, these problems ranging from short periods of seed viability, damage from pests and pathogens to irregular and infrequent flowering. In all these instances, the lack of a dependable supply of seed can be overcome through vegetative propagation. This technique, which has been widely and successfully used to domesticate horticultural crops, has the added advantage that by producing genetically identical trees it allows promising genotypes to be easily identified. However, with a few notable exceptions (*Cryptomeria* and *Populus*), it has only recently been considered for timber species (see Longman, 1976), in spite of the obvious potentials.

1. Experience with Triplochiton scleroxylon

In 1971 the U.K. Overseas Development Administration, having been persuaded of the significance of vegetative propagation, initiated a co-operative programme with staff of the Forestry Research Institute of Nigeria (FRIN), Ibadan, aiming to investigate and develop techniques for conserving and improving indigenous West African hardwoods, and in particular *Triplochiton scleroxylon* K. Schum. (Sterculiaceae), the source of the light-weight hardwood "Obeche". In 1974, a second project was established at the Institute of Terrestrial Ecology near Edinburgh, U.K. In concentrating on physiological principles, the latter project complemented the former more practically orientated project, the two together providing a model probably suitable for the conservation and domestication of other tropical trees.

Until recently, T. scleroxylon was one of the commonest high forest trees in many of the moist lowlands of West Africa accounting for up to 13% of the trees present (Hall & Bada, 1979). Although a pioneer species, it was able to maintain itself in established forests in areas with annual rainfall between 1,100-1,800 mm (Leakey *et al*, in press *b*). In the 1950's and 1960's "Obeche" formed 60% of Nigeria's roundwood exports, its good peeling properties being favoured by plywood manufacturers.

Despite the demand, few plantations were established before 1975 because the inherently short-lived seeds were generally scarce, frequently attacked by weevils

(Apion ghanaense) and parasitized by smut fungus (Mycosyrinx spp.). Since 1975, the development of techniques to extend the viability of sound seeds by dry storage at -18° C (Bowen *et al*, 1977) together with the modification of standard horticultural techniques in order to root leafy cuttings taken from young trees (Howland, 1975 *a*), have dramatically changed the availability of planting stock. Together these techniques have enabled gene banks and clonal trials to be established at 8 different sites in Nigeria, with a concentration at Onigambari Forest Reserve (Howland & Bowen, 1977; Longman *et al*, 1979 *a*). The gene banks at Ore, Nimbia and Afaka include material from seed collections from Sierra Leone to Cameroun spanning a large part of the natural range of *T. scleroxylon*.

Initially stem cuttings of T. scleroxylon were rooted at FRIN on mist propagators, but subsequently shaded polythene frames were used, with the cuttings sprayed twice a day to maintain humid conditions (Howland, 1975 a). Leafy single-node cuttings from seedlings, coppice shoots and managed stockplants have been successfully rooted with or without applying auxins. However, rates of rooting and numbers of roots per cutting were increased by applying the auxin IBA (indole-5-butyric acid) (Howland, 1975 b). More recently, different clones have been found to have different auxin requirements (Leakey, et al, in press a). As a result, and to achieve at least 60% success within 6-8 weeks, it is recommended that cuttings are dipped quickly in 0.2% alcoholic solution or treated with 40 μ l of a 50:50 mixture of IBA with a second auxin NAA (α naphthalene acetic acid). After evaporating the alcohol with the help of a fan, cuttings are set in coarse sand with temperatures at the base of the cutting preferably being maintained at about 30°C. To maximise rooting, the leaf of each cutting should be trimmed to about 50 $\rm cm^2$, this presumably optimising the balance between photosynthesis and transpiration (Leakey et al, in press a). The ability of cuttings to root is additionally dependent upon the condition of the stockplants, the most easily rooted cuttings being those from lateral shoots of plants cut back to about 10-20 cm from the ground (Howland, 1975 c; Leakey, in litt.). The rooting ability of cuttings from such stockplants was greatest when subsequent regrowth was restricted to two shoots each yielding 5-6 single-node cuttings. This number, possibly because of competition for nutrients (Leakey, in litt.), could probably be increased by irrigating and applying fertilizers (Howland, 1975 c). Cuttings from shaded shoots seem to root better than those from exposed shoots (Leakey, in litt.).

Now that T. scleroxylon can be readily propagated by cuttings, fuller advantage can be taken of within-species variation by identifying and multiplying genetically superior individuals, as has happened for many years in horticultural and agricultural crops. In field trials now being managed and observed in Nigeria, attempts are being made to analyse the components of growth of promising clones (Howland et al. 1978; Ladipo et al, in press). Interestingly, branching habit and height growth seem strongly related; the tallest clones have fewest primary branches per metre of mainstem. From one experiment, data taken 18 months after planting, suggests that selection of the 10 tallest out of 100 clones might give a genetic gain of 16.5% (Ladipo et al, in press), whereas the choice of the best provenance might give a 9.3% gain. Clearly the potential for improvement is considerable and warrants the screening of many more clones. As a supplement to field trials which are expensive and time consuming, it may become feasible to predict inferior and superior clones at an early age by a simple test based on an understanding of the processes determining branching habit. Patterns of branching depend on at least two physiological processes: -(i) apical dominance, the ability of a terminal bud to inhibit the growth of axillary buds on the current year's growth and (ii) apical control, the influence

of one or more shoots on the extension growth of other, usually more proximal, shoots. Experiments with *T. scleroxylon* indicate that these processes operate to different extents between clones and that genetic and environmental influences on apical dominance can be separated (Leakey & Longman, *in litt.*). Current studies (Ladipo, Leakey & Grace, unpublished) are investigating the apical dominance relationships in small decapitated plants, and comparing these with growth and branching habits of the same clones in plantations. If the fairly strong correlations found so far are confirmed, then it should be possible to screen large numbers of clones in nurseries when 3-6 months old. Experience with *Terminalia superba* Engl. & Diels, another West African hardwood, suggests that it would also be wise to screen clones for wood quality as the genetic differences in various wood characteristics are not always closely related to morphology and growth (Longman *et al*, 1979 *b*).

Having developed methods of vegetative propagation and made considerable progress with techniques to allow early selection of superior clones, the next phase of domesticating *Triplochiton scleroxylon* is to develop the capacity for easily-managed controlled breeding. This necessitates methods of inducing flowering when required in small and preferably young plants. In the wild, *T. scleroxylon* does not normally flower until 15 or more years old when the occasional occurrence of severe 'short dry' seasons is thought to stimulate flowering (Jones, 1974; Howland & Bowen, 1977). Three approaches have been made to the study of flowering and reproductive biology:— (i) phenological and development of natural flowering (Jones, 1974; 1975); (ii) establishment of adult clonal material (in the nursery and field) by grafting/budding, and also by rooting adult cuttings (Howland & Bowen, 1977); and (iii) stimulation of precocious flowering (Leakey *et al*, 1981).

When self-pollinated, flowers of *T. scleroxylon* only produce fruits very occasionally and in these instances their seeds do not germinate. By contrast viable seeds have been produced by cross-pollination (Howland and Bowen, 1977), even when the parent trees were only 2-5 years old and less than 1m tall (Leakey *et al*, 1981). Pollinations were equally successful when done with pollen stored dry at -25° C, conditions which extended viability from less than 1 week to at least 25 weeks. The progeny of these controlled pollinations between precociously flowering clones will be used to study the factors influencing floral initiation in *T. scleroxylon*. It is hoped this will lead to the development of reliable techniques for flower induction, which can be applied to clones with superior vegetative growth. The folly of selecting precocious and heavily flowering variants for commercial plantings, as seems to have happened with teak, must be avoided because of the likely adverse effects on form and timber productivity.

The results of the complementary projects discussed in this paper illustrate how the constraints retarding the domestication and use of species like *T. scleroxylon* can be minimized. The stage has now been reached where it is possible to recommend selected clones for more extensive trials.

2. Experience with other timber producing species.

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Thirty-three species of tropical trees with known potential for forestry have been vegetatively propagated at I.T.E. using the techniques developed for *T. scleroxylon* (Table 1). Generally they were easy to root; although the Dipterocarps (*Shorea* spp. and *Vateria seychellarum*) proved to be more difficult than the others.

With some of the species, the source of the cutting greatly affected its growth after rooting, in addition to altering its rooting ability. For example, lateral shoot

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cuttings of Agathis and Araucaria grew plagiotropically, whereas mainstem cuttings grew erectly. In Cordia alliodora the early growth of rooted cuttings from lateral branches was similar to that of mainstem cuttings, but later decreased in vigour. These differences highlight the need for (i) good stockplant management and (ii) a thorough knowledge of the characteristics of individual species before extensive plantings of clonal material are made. Additionally it should be remembered that cuttings from mature shoots of many tree species are not only difficult to root but have the tendency to grow plagiotropically and are unsuitable for commercial forestry.

If genotypes tolerant to insect attack could be identified, the use of vegetative propagation could be extended to the important species of *Khaya*, *Entandrophragma*, and *Chlorophora*. Moreover it should not be restricted to those species with problems preventing their extensive use in plantations, for it is clear that, for example *Gmelina arborea* and *Tectona grandis*, could both benefit from selection for improved form, removing their marked tendency for heavy branching and precocious flowering, respectively. Similarly the use of the techniques described above for *T. scleroxylon* could also be extended to arid-zone species (Leakey & Last, 1979).

TABLE 1

Tropical tree species vegetatively propagated at the Institute of Terrestrial Ecology, Edinburgh, with actual, or potential, value as timber species.

MOIST FOREST

West Africa

Ceiba pentandra (L.) Gaertn. Chlorophora excelsa (Welw.) Benth. & Hook. Nauclea diderrichii (De Wild. & Duv.) Merr. Terminalia ivorensis A. Chev. Terminalia superba Engl. & Diels Triplochiton scleroxylon K. Schum.

East & Central Africa Dalbergia melanoxylon Guill & Perr. Vateria seychellarum Dyer

Central & South America Albizia caribaea (Urb.) Britton & Rose Cedrela odorata L. Cordia alliodora Cham. Ochroma pyramidale Urb. Swietenia mahogani Jacq. Tipuana tipu (Benth.) Kuntze Toona ciliata M. Roem.

DRY FOREST

Acacia senegal L. Afzelia africana Smith Azadiracta indica A. Juss. Prosopis juliflora (Swartz) D.C.

S.E. Asia & Australasia

Agathis australis (D. Don.) Salisb. Agathis dammara (A.B. Lam) L.C. Rich. Agathis macrophylla (Lindl.) Mast. Agathis obtusa (Lindl.) Mast. Agathis robusta (Moore) Bailey. Agathis vitiensis (Seeman) Benth. & Hook. Araucaria hunsteinii K. Schum. Gmelina arborea Roxb. Shorea albida Sym. Shorea albida Sym. Shorea contorta Vidal Shorea curtisii Dyer ex. King. Shorea leprosula Miq Shorea macrophylla (De Vries) Ashton

Domestication of species for fruit and other forest products

The domestication of forest species for fruit and other products is not a new concept. Indeed many plantation crops (coffee, cocoa, tea, citrus, coconut, oil palm and rubber) have been or are being improved by selection, but the potential of others is still largely untapped (National Academy of Sciences, 1975; 1979). In addition to trees which produce fruits, resins, latex etc., there are many which have medicinal properties (Irvine, 1961), only a few of which have been utilized commercially. In some instances variants may exist in plants occupying similar geographical ranges, as for example with the acridone alkaloids found in *Oricia suaveolens* and *Teclea verdoorniana* and other members of the West African subfamily Toddalioidea (Rutaceae) (Waterman, *et al*, 1978; Fish *et al*, 1978). If such variation becomes useful pharmaceutically there is little doubt that selected clones could be multiplied vegetatively.

Much basic information remains to be acquired regarding the developmental and reproductive biology of many tree species which could be domesticated as producers of a wide range of forest products. In many instances the approach developed for *T. scleroxylon* could be adapted to meet the needs of particular species. In other groups, notably perhaps the fruit trees, budding and grafting may be a more suitable method of propagating desirable clones, as illustrated by Okafor (1978, 1980) who has studied some 150 Nigerian species spanning 103 genera and 48 families.

Plantations in the tropics

As areas of natural forest in the tropics decrease, and the tendency towards semipermanent agriculture increases, both the diversity and indeed the functioning of these ecosystems are at risk. Moreover the world's timber demand by 2025 AD is expected to be of the order of 300 million m^3 ann um^{-1} . For this to be one quarter satisfied, current planting programmes will need to be increased by 300% (Spears, 1980). If such an increase were achieved, the pressure on the surviving natural forest would be lessened, but the extensive reliance on plantations will itself represent a substantial loss of diversity. This loss of diversity may increase the risks of attack by pests and pathogens, but to a considerable extent this could be minimized by increasing the number of species grown commercially. In particular the domestication of more indigenous species could usefully supplement the plantations of *Pinus, Eucalyptus, Tectona* and *Gmelina* which have been widely planted over the

TABLE 2

Tropical tree species vegetatively propagated at the Institute of Terrestrial Ecology, Edinburgh, with potential for producing minor forest products or conferring amenity.

Fruit

Casimiroa edulis La Llave Chrysophyllum cainito L. Citrus halimii B.C. Stone Shorea macrophylla (De Vries) Ashton Tamarindus indica L.

Pharmaceutical

Teclea verdoorniana Exell & Mendonca

Multi-purpose (gum/fodder/tannins etc.) Acacia senegal L. Ceiba pentandra L. Gaertn (Kapok) Prosopis juliflora (Swartz) D.C.

Amenity

Delonix regia Raf. Caesalpinia spinosa (Mol.) Kuntze Tabebuia pallida (Lindl.) Miers last 20 years. In addition to growing a wider range of species, foresters should probably also learn from the experience of tropical farmers who traditionally practice mixed-cropping. There are several examples from the temperate zone where even-aged monocultures have been severely attacked by pests and pathogens, and if such plantations are inserted into complex tropical ecosystems the risks are likely to be greater. Already in Nigeria some stands of *T. scleroxylon*, established since 1975, have been defoliated by the grasshopper *Zonocerus variegatus* while in Ghana caterpillars of *Lamprosema lateritalis* have repeatedly attacked stands of *Pericopsis elata*, and other caterpillars have defoliated *Mansonia altissima*.

The arguments presented by foresters and the timber industry when advocating pure plantations are strong. Monocultures tend to give large yields; they are easier to manage and harvest, and produce uniform products for processing (Dyson, 1965). However there is increasing evidence that, particularly in moist tropical forest, they have many disadvantages in relation not only to pests, but in nutrient cycling, accelerated erosion etc. Additionally the advocation of monocultures, assumes that forestry is only to be practiced by large enterprises. With the increasing interest in agroforestry, however, it is clear that the farmer, without need for great capital investment or large forces of paid labour could become a significant producer of timber and other forest products, especially if he were supplied by a Co-operative nursery with selected material of a wide range of useful indigenous and exotic species. By combining the cultivation of these trees with agricultural crops (Okigbo, in press) it is probable that the production of both can be extended into areas with infertile and degraded soils. The area suitable for such land use may thus prove greater than that foreseen by Spears (1980). A greater diversity of produce would undoubtedly help many rural communities.

In conclusion, a more enlightened attitude to the untapped resources of the rapidly disappearing tropical forests of the world is necessary if supplies of food, timber, fuel and other forest products are to be available for future generations. A range of techniques discussed here is facilitating the domestication of T. scleroxylon. Additionally the prospects for other tree species appear hopeful, with some sort of the problems restricting their use now being easier to resolve. The usefulness of clones must not, however be abused; variation should be maintained by the judicious selection of numbers of superior clones, but perhaps even more importantly, their utilization should be sought within integrated systems of land-use which recognize the need to conserve both soil fertility and biological variation within and between species.

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