

The Flower Biology of the Meliaceae and its Bearing on Tree Breeding

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Introduction

The Meliaceae is a large family, mainly of tropical trees producing many commercially important and well-known, choice hardwoods. Some of the best-known examples in the international timber-trade are American or true mahogany (*Swietenia* spp.), African mahogany (*Khaya* spp.), sapele, utile, gedu nohor (*Entandrophragma* spp.), Central and South American or cigar-box cedar (*Cedrela* spp.), Burma cedar, toon or Australian red cedar (*Toona* spp.) and chikrasy or chittagong wood, *Chukrasia tabularis* A. Juss., besides several others from various parts of the world. Most of the timber-producing species are huge, dominant or emergent trees forming the major constituents of tropical rain-forest, secondary forest or other types of woodland. Timbers from members of the Meliaceae are in fact the backbone of the forest industry of many countries, but continuous exploitation of the natural forest has seriously depleted stocks of desirable specimens, notably in South America and parts of West Africa. Usually it is the best trees which are culled during exploitation so that potential sources of élite or superior genotypes are continually decreasing with consequent depletion of the gene pool. *Cedrela* in Latin America and the Caribbean Islands has been so overcut that some species have been virtually eliminated (A. F. A. LAMB, 1968). Supplies of mature trees of good form for seed production and tree breeding now remain only in remote and inaccessible places. Similarly, in *Swietenia* only trees of a bush-like form now survive in the Caribbean Islands to represent the once famous Cuban mahogany, *S. mahagoni*.

Because of this, several of the more promising and suitable meliaceous species are being grown in plantations to augment or replace natural crops, and a few others are important enough to have been included in the tree-breeding programmes of several Forest Departments. The selection of candidate plus-trees of desirable phenotype and the formation of multiplication-gardens and clonal seed-orchards of these important species, together with the projected breeding programmes, create a need for more knowledge of the phenology and the floral and reproductive biology of the trees. Information of this kind about tropical forest trees is extremely scanty even for the commonest and best-known species and, in many instances, is lacking altogether. As RICHARDSON (1970) has suggested, the lack of precision in the planning of tree breeding programmes emphasizes the need for studies in population genetics and the breeding systems of tropical forest trees. It is alarming that the need for cyto-genetic investigations of their experimental material has only recently been recognized by tropical botanists and foresters.

The purpose of this paper is to summarize the knowledge of the flower biology of the Meliaceae and suggest what genetic systems may be operating in the timber-producing species of the mahogany family. Particular attention is given to the species in the five genera now being intensively worked on by Forestry Departments.

General Observations

A monograph of the Meliaceae has been in preparation for some time at Oxford and a number of interesting discoveries on flower-biology are directly relevant to tree-breeding. A summary of the chromosome cytology of the

family and its bearing on genetic improvement, has been published by STYLES and VOSA (1971). Other facts on pollination-ecology, breeding-systems and forest biology which have come to light will also be useful to the silviculturist and forest geneticist. Probably the only other tropical hardwood species for which comparable information is available is teak, *Tectona grandis* L.f.; in this BRYNDUM and HEDEGART (1969) have studied the flowers and their pollination mechanisms as a prelude to breeding.

Some species of the *Meliaceae* have already been successfully grown in plantations, and others are being tested in trial plots. Perhaps the most important genus investigated is *Cedrela*, with about five species, all native of Central and South America and the Caribbean Islands. *C. odorata* L. has already been widely planted in Mexico, Central and South America and Fiji, and is likely to prove a major exotic plantation-species in Africa, particularly West Africa. According to A. F. A. LAMB (1968) the importance of *Cedrela* to forestry lies in its speed of growth and ease of establishment in plantations. An international provenance trial has been organized by the Commonwealth Forestry Institute, Oxford and *C. odorata* has been included in the tree improvement Programme for Ghana (JONES 1968 and 1969). *C. fissilis* VELL. (syn. *C. tubiflora* BERT.) and forms related to it, are being grown in East Africa and will probably prove important (BURLEY and LAMB, 1971). BRITWUM (1970) has also recently shown that *C. odorata* can be successfully propagated by stem cuttings.

Unfortunately *Cedrela*, within its natural area of distribution in the Americas, is badly attacked by a species of the Mahogany shoot-borer, *Hypsipyla grandella* ZELL., to the extent that planting programmes there are being curtailed or halted until cultivars resistant to the borer can be selected or bred. Some species such as *C. fissilis* VELL. and *C. angustifolia* Sesse & Moc. ex DC. have the reputation of being more resistant and appear worthy of further trial. *Cedrela* planted in Africa is apparently not seriously attacked, as the indigenous species of *Hypsipyla* are different from those occurring in Latin America.

Similarly, *Toona* a genus of large timber trees closely related to *Cedrela*, but having a distribution mainly in Asia and Malesia is also heavily attacked by the shoot-borer throughout its natural geographical range, but apparently not elsewhere. Therefore in Central and South America, foresters have turned their attention to the silviculture and improvement of species in this genus, particularly *T. ciliata* M. J. ROEM. and *T. ciliata* var. *australis* C.DC. (syn. *T. australis* HARMS), both important fast-growing timber trees of Eastern Asia and Australia (GRIJPMA and RAMALHO, 1969, and GRIJPMA, 1970). In Latin America *Toona* seems not to be attacked by the indigenous *Hypsipyla* which is a different species from that (*H. robusta*) occurring throughout its natural range. GRIJPMA and RAMALHO suggest that chemical differences between the two genera may partly explain why the indigenous *Cedrela* is attacked, whereas the exotic *Toona* is not, and that selection and

crossing of resistant forms might provide useful results. Care will be needed with any breeding programme, however, as STYLES and VOSA (1971) have already demonstrated the existence of two cytotypes within *Cedrela odorata* L., and *Toona ciliata* M. J. ROEM. may also be cytologically heterogeneous. Some populations of *Cedrela odorata* occurring mainly in Mexico and South America do have the same chromosome number and karyotypes identical to *Toona ciliata*.

Perhaps the best-known of all meliaceous timbers is the true mahogany, produced by the genus *Swietenia*. Although formerly of great importance to the economies of many Central and Southern American countries, accessible supplies of marketable trees have now almost been exhausted and only trees of poor bushlike form remain over large areas. Because of this, two species *S. mahagoni* (L.) JACQ., a native of the Caribbean Islands and *S. macrophylla* KING, which occurs naturally in Mexico, Central and South America are being raised in plantations in various parts of the world to produce further supplies of this outstanding timber. Fiji now has over 10,000 acres planted with the latter species, and the current annual programme is 2,000 acres (BUSBY, 1967). The potentialities of these and the third species *S. humilis* ZUCC. from the dry Pacific coast of Mexico and Central America, are being investigated by the U. S. Forest Service in provenance trials at Cambalache, Puerto Rico and at Turrialba, Costa Rica. In Taiwan, some experiments in controlled pollination and breeding have already been made. In an interesting series of papers YANG (1965) and LEE (1968, 1970) have described some of the techniques involved, and the characteristics of the progeny of the interspecific cross *S. mahagoni* × *S. macrophylla*. The hybrids appear to combine the best qualities of the two parents, having the faster growth rate of *S. macrophylla* and the denser wood of *S. mahagoni*, while they also seem to show a greater resistance to the well-known mahogany canker. PAWSEY (1970) now suggests that the causal agency of this might be a virus. There is already evidence that the two species hybridise naturally when they occur together in plantations (HUGUET and VERDUZCO, 1952; STEHLÉ, 1958; F. B. LAMB, 1960; BRISCOE and LAMB, 1962; NOBLES and BRISCOE, 1966; CHALBE, 1967). Work is now in progress at Oxford on a cytological and morphological study of putative hybrid material from St. Croix in the U.S. Virgin Islands. STYLES and VOSA (*loc. cit.*) have shown that the three species of *Swietenia* have different chromosome numbers, a situation which is uncommon among tropical, woody plants. The first attempts of YANG (1965) at interspecific crosses failed completely because the flower structure and floral biology of the trees concerned were not fully understood.

Azadirachta indica A. Juss., 'Neem', is a native tree of a small area of India only, but is now extensively cultivated and naturalized in that country and Pakistan. It has already proved to be one of the most important trees for afforestation in the arid zone of Africa and is strongly recommended for the arid parts of Rajasthan in India (BHIMAYA *et al.*, 1964). Moreover, it is one of the few exotic species which have proved successful in plantations in the dry north of Nigeria (GRAVSHOLT *et al.*, 1967) as a source of fuel and building poles and may even provide timber. It has therefore been included in the tree-breeding programme for Nigeria (KEIDING *et al.*, 1964). Vegetative propagation by the forkert budding technique has already been extremely successful and selective breeding may improve poor tree-form. In the Sudan 'Neem' will probably also

prove very suitable for the production of particle board and other wood-based board materials (MUELLER-ECKHARDT, 1967).

Besides the Meliaceae genera and species mentioned above there are other *Meliaceae* of secondary importance which, because they are highly susceptible to shoot-borer predations when grown in monoculture, are not being actively studied at present. Several are already used for enrichment by line, gap and taungya planting in exploited forests in Africa and elsewhere, but RICHARDSON (1970) has criticised foresters in charge of breeding programmes for restricting their attention to too few species and he advocates extension of existing provenance-collections and clone-archives to include more species. The high quality and excellent working properties of the 'secondary' decorative hardwoods in *Meliaceae* are well known and provide sufficient incentive for further investigations on the biology and control of *Hypsipyla* so that more planting of these valuable trees can be done.

These genera and species include *Entandrophragma angolense* (WELW.) C.DC., *E. cylindricum* (SPRAGUE) SPRAGUE, *E. utile* (DAWE & SPRAGUE) SPRAGUE (all three are listed for secondary selection in the forest tree improvement programme proposed for Ghana by JONES (1969)), as well as *Khaya* spp., particularly *K. senegalensis* (DESR.) A. JUSS., *K. anthotheca* (WELW.) C.DC., *K. ivorensis* A. CHEV., and *Lovoa trichilioides* HARMS. Several species of *Khaya* and *Entandrophragma* are being successfully grown in plantations in Honduras and Costa Rica and are generally free from *Hypsipyla* attack. *Soymida febrifuga* A. Juss. is considered by MEIJER (1970) to be worth greater silvicultural attention in Ceylon.

Melia is another genus with distinct forestry possibilities, but one which does not yet appear to have attracted much attention from silviculturists and tree-breeders. *M. bom-bolo* WELW. is extremely quick-growing (MADOUX, 1966) and yields an excellent timber; whilst a provenance of *M. azedarach* L. is proving an important plantation crop in Misiones Province, N. Argentina (Cozzo, 1959).

Flower Biology

TROUP (1921) and MARSHALL (1939) describing the silviculture of the indigenous *Meliaceae* of India and Trinidad respectively, do not seem to have noticed anything peculiar about the flower of the species they were dealing with and presumably took them to be hermaphrodite or perfect, with each flower having fully-functional male and female parts. Both however, observed that only one or two fruits developed in each inflorescence. Numerous general taxonomic works and local floras dealing with the *Meliaceae* (such as those of HOOKER 1862, HARMS 1940, KEAY 1958) and even monographic accounts of single genera (EARLE SMITH, 1960; F. B. LAMB, 1966; GRIPMA, 1970) state that the flowers are always hermaphrodite. That this is not true for most of the family was established by WHITE and STYLES (1963) from their observations in South eastern and Central Africa. Most of the species examined had functionally unisexual flowers, but each male or female flower had well-formed though sterile rudiments of organs of the opposite sex. Individual trees can have flowers of both sexes or of one only but are functionally either monoecious or dioecious¹. Only very rarely, it appears, do some species have

¹ The terms monoecious and dioecious should in the strict sense be applied to the staminate or male and pistillate or female flowers occurring on the same or on two different individual plants; but are now applied to the plants themselves or even the species.

functionally bisexual, hermaphrodite flowers, and these may also be accompanied by male flowers and so can be called polygamous²⁾. This situation is important to tree-breeders because for those species with functionally unisexual flowers, the troublesome technique of emasculation can be dispensed with in controlled-pollination experiments. Moreover the functional monoecious or dioecious condition has a practical importance because the flowers of nearly all species are small and difficult to handle. Both JONES (in press) and KLAHN (1961) point out that this situation will influence the size and management of seed orchards. In the case of those genera with polygameous flowers (*Melia* and *Azadirachta*), great care will be necessary in selecting the correct type of flower for pollination experiments.

A more extensive and complete study of all known genera has now been made over the entire range of distribution of the family by PENNINGTON, STYLES and WHITE. The facts reported by WHITE and STYLES (1963) have been checked and found to be correct for most genera, and it now appears that only *Turraea* and related genera (which are of no economic importance) have hermaphrodite flowers alone. Studies in the forest on living specimens of *Swietenia* by LEE (1967), on *Cedrela* by JONES (in press), on *Trichilia* by DE WILDE (1969) and by STYLES (unpublished data), further corroborate these findings. Table 1 shows the sex-distribution of flowers of the important timber genera in *Meliaceae*. It will be noticed that the genera of subfamily *Swietenioideae* which, as circumscribed by PENNINGTON, STYLES and WHITE includes the *Cedreloideae* of previous workers, are composed of species with both male and female flowers on the same individual (monoecious), and most often these occur together in the same inflorescence. This subfamily contains the important timber trees of *Cedrela*, *Toona*,

²⁾ Polygamous means that a species has unisexual and bisexual flowers on the same or different individuals. This condition is more strictly referred to as andromonoecious.

Swietenia, *Entandrophragma*. In the subfamily *Melioidae* most species have male and female flowers on different individual trees (dioecious) or have polygamous flowers (male and hermaphrodite flowers on the same plant). Although in this subfamily only two genera (*Azadirachta* and *Melia*) are of increasing importance in forestry, others may become so in the future. Where the sexes are dioecious, care will be necessary to make sure that the correct proportion of male to female trees is maintained in seed orchards. Chromosome and karyotype studies carried out on seedlings have not yet revealed differentiated (heteromorphic) sex chromosomes, so that the sex of a particular tree cannot be ascertained until it produces flowers. This fact would greatly increase the value of such grafting techniques as have been shown to accelerate flowering.

The Structure of the Flower³⁾

Many botanists describing the flowers of this family have assumed them all to be perfect and hermaphrodite. This is because each flower seems to possess both male and female reproductive organs. Although both anthers and pistils are present in any flower, in the functionally male flowers the anthers are large, yellow and full of pollen which is released in the normal way by longitudinal dehiscence at anthesis. In such flowers, however, although the ovary or pistil may look normal in size and shape (usually cylindrical or globular), the ovules it contains are minute and rudimentary, brownish in colour and abortive. They do not completely fill the loculi of the ovary as they do in functionally female flowers. Such a sterile ovary is known as a pistillode and is incapable of developing further. In

³⁾ All genera in *Meliaceae* except *Cedrela* and *Toona* have flowers with the filaments of the androecium partially or completely joined to form a staminal tube. The anthers are borne either within the tube, partially exerted from it or on the margin. Staminal appendages of various shapes and sizes are often present, alternating with or opposite to the anthers.

Table 1. — Sex-Distribution in Flowers of *Meliaceae* (important timber species only).

Genus	Species	Distribution
SWIETENIOIDEAE: flowers unisexual, sexes monoecious.		
Carapa	<i>C. guianensis</i> AUBL., <i>C. procera</i> DC.	C. & S. America, Caribbean; W. & E. Africa
Cedrela	Most	C. & S. America, extensively cultivated throughout tropics
Chukrasia	<i>C. tabularis</i> A. JUSS.	India, Ceylon
Entandrophragma	<i>E. angolense</i> (WELW.) C.DC., <i>E. cylindricum</i> (SPRAGUE) SPRAGUE, <i>E. utile</i> (DAWE & SPRAGUE) SPRAGUE	Africa, cultivated in C. America
Khaya	All	Africa, cultivated in C. America
Lovoa	<i>L. trichilioides</i> HARMS., <i>L. swynnertonii</i> BAK. f.	W. & E. Africa
Soymida	<i>S. febrifuga</i> (ROXB.) A. JUSS.	India, Ceylon
Swietenia	<i>S. macrophylla</i> KING, <i>S. mahagoni</i> (L.) JACQ.	C. & S. America, cultivated extensively throughout tropics
Toona	Most	India, Far East, Australia, cultivated throughout tropics
MELIOIDEAE: flowers unisexual, sexes dioecious.		
Dysoxylum	<i>D. fraserianum</i> BENTH., <i>D. muelleri</i> BENTH.	N. Zealand, Australia
Ekebergia	<i>E. capensis</i> SPARRM.	S. & E. Africa
Guarea	<i>G. cedrata</i> (A. CHEV.) PELLEGR., <i>G. thompsonii</i> SPRAGUE & HUTCH.	W. & E. Africa
Synoum	<i>S. glandulosum</i> A. JUSS.	Australia
Trichilia	<i>T. dregeana</i> SOND., <i>T. lanata</i> A. CHEV.	E. & W. Africa
Turraeanthus	<i>T. africanus</i> (WELW. ex C.DC.) PELLEGR.	W. Africa
MELIOIDEAE: individuals polygamous, flowers ♂ & ♀.		
Azadirachta	<i>A. indica</i> A. JUSS.	India, Pakistan, cultivated in Africa
Melia	<i>M. azedarach</i> L., <i>M. bombo</i> WELW., <i>M. dubia</i> CAV.	Cultivated throughout tropics and subtropics

fact although the pistillode appears normal to an unpractised eye, the style-head, large and capitate in most species, is generally thinner and less glandular, and the style is longer than in functionally female flowers. After shedding their pollen the male flowers shrivel and fall to the forest floor (LEE, 1967 and STYLES, unpublished data). TROUP (1921) probably confused petals with whole male flowers when he wrote of the flowering of *Toona ciliata* M. J. ROEM (syn. *Cedrela toona* ROXB. ex ROTTL.) that "the petals quickly fall, whitening the ground around the tree". Thus this flower-drop is a normal occurrence and is not, as might be thought, due to nutritional deficiency or to failure of pollination.

The flowers which are functionally female often have slightly smaller petals than the male flowers and, although stamens with anthers are always present, they remain small, darker yellow and seem not to produce fertile pollen. In some species the anthers appear to dehisce, but no grains can be detected in the anther sacs. These sterile anthers are termed antherodes and are generally about half the size of fertile ones. The functional ovary, on the other hand, contains large ovules which are fleshy and translucent and completely fill the loculi of the ovary. The latter is surmounted by a short style and thickened style-head, the stigmatic surface having very evident glandular papillae. Immediately after fertilisation the ovary starts to develop, and in fully-open flowers it generally appears globose and brown or black in colour. In young flower-buds, however, an ovary is indistinguishable from a pistillode, and likewise an anther from an antherode (Fig. 1, A—D).

The detection of male and/or hermaphrodite flowers in genera of the *Melioidae* such as *Azadirachta* and *Melia*, has proved difficult. The pistillode and ovary in the two types of flower are practically indistinguishable externally

and, as in most of the *Melioidae* the ovules in both types are very similar in size, shape and general appearance. The occurrence of the two types of flower can probably only be ascertained with certainty by studying living trees. In this way LEE (1967) has shown convincingly that *Melia azedarach* (Persian Lilac) has both hermaphrodite and male flowers in the same inflorescence. After anthesis the male flowers shrivel and drop off whilst the hermaphrodite flowers form fruits normally after pollination. *Azadirachta indica* (Neem) is probably similar to *Melia* in its polygamy, and simple field experiments are now being done in Nigeria to confirm this.

The Inflorescence

Because the flowers of the *Meliaceae* are frequently inaccessible and difficult to observe in the crowns of tall trees, little is known of their biology. They are usually borne in large, much-branched and complex inflorescences, often with primary, secondary, tertiary and even quaternary branches. In *Cedrela*, *Toona* and *Khaya* the inflorescences may reach 90 cm. in length but they are less complex in *Swietenia* and in some genera in *Melioidae* such as *Azadirachta*. This type of inflorescence has been variously called a panicle, compound cyme or cymose panicle, but more correctly should be termed a thyrses (LEE, 1967). Although the number of branches is variable and the central axis is indeterminate in growth (i. e. racemose), each ultimate branchlet always ends in a cymule of 3 (or very rarely 2) flowers and thus is a 2- or 3- flowered dichasium. A precise knowledge of the structure of the inflorescence of the monoecious species may prove important since there appears to be a definite arrangement of male and female flowers within it. Thus, when dealing with such small flowers, a knowledge of the expected position of flowers of

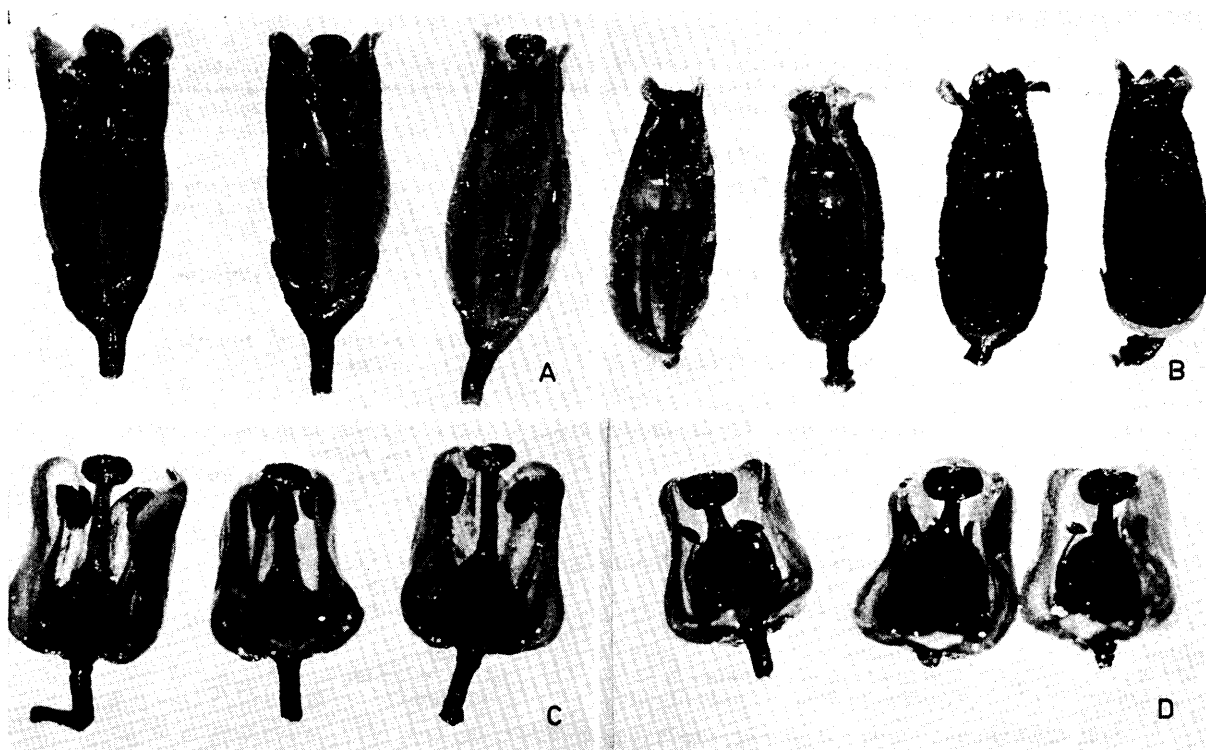


Fig. 1. — (Photos) — *Cedrela odorata* L.: Section of (A) male flower showing pistillode and anthers; (B) female flower, showing ovary and antherodes (from PENNINGTON and SARUKHÁN 9650 (Mexico)). — *Toona ciliata* M. J. ROEM.: (C) male flower, showing pistillode and anthers; (D) female flower, showing ovary and antherodes (from STYLES 266 (Uganda)). (all $\times 4.5$).

different sexes may reduce the difficulty of locating them during pollination procedures. The flowers of some genera in the *Melioidae*, such as *Guarea*, *Turraeanthus* (Avodiré) and *Dysoxylum*, are much larger than those of *Swietenioideae*, but most of them are dioecious. In those species in which the sexes are monoecious, male flowers always greatly outnumber females in the inflorescence and in dioecious species, specimens from male trees are much more frequent than those from female trees. These observations have been substantiated by JONES (in press) on *Cedrela*. Moreover, LEE (1965) has found that whole trees of *Swietenia mahagoni* usually have about ten times as many male as female flowers. There is, however, considerable variation in this proportion and there could be more females than males. Thus LEE found on eight inflorescences of this species 360 pistillate flowers to 204 staminate flowers. Both LEE and JONES record that some inflorescences may be composed either entirely of male (and more rarely) of female flowers. This has not been seen in the monoecious species in *Meliaceae* but in the herbarium it is rarely possible to dissect every flower in a single inflorescence. Very probably, the tendency towards maleness or femaleness of any particular tree is affected by nutrition and other environmental factors. According to LEE the greater tendency to either maleness or femaleness among trees of *S.*

mahagoni changes from year to year. KLAHN (1961) cites a number of examples from among temperate hardwoods where the degree of maleness or femaleness apparently varies between trees in a single population of the same species. The proportion of male to female flowers can also vary during the flowering period itself.

Among the dioecious species also, there appears to be a greater preponderance of male over female specimens in preserved collections. Observations in Mabera forest, Uganda, failed to reveal one female tree of *Trichilia prieureana* among the first 48 examined.

DE WILDE (1968) states with reference to the African species of *Trichilia*, which are all strictly dioecious, that the male flowering specimens preserved in herbaria far outnumber specimens with female flowers. For one species, *T. emetica* VAHL, he estimated a sex-ratio of three male-flowered individuals to one female, although he possibly might have expected a 1 : 1 ratio. He further observed male flowering and female fruiting trees of *Trichilia monadelpha* (THONN.) J. J. DE WILDE (syn. *T. heudelotii* PLANCH. ex OLIV.) in the forest, and records that the male trees flowered several times during a three-month period and may do so many times during the year. The fruiting, female trees on the other hand appeared to flower once or possibly at the most twice per year; no female trees were found bearing

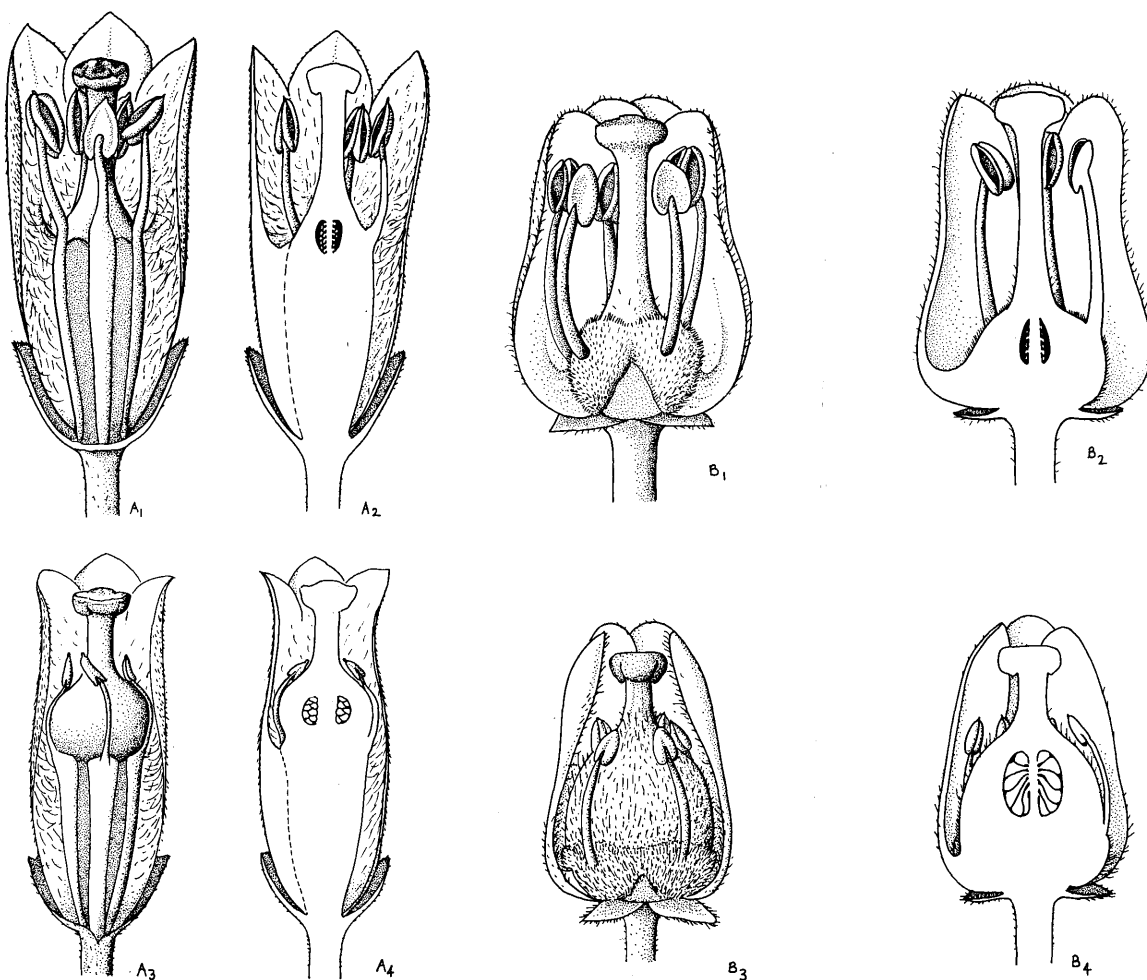


Fig. 1. — (Drawings) — (A 1) Whole ♂ flower of *Cedrela odorata* with 2 petals removed to show fertile anthers; (A 2) 1/2 section of same flower showing pistillode and abortive ovules; (A 3) whole ♀ flower with 2 petals removed to show antherodes; (A 4) 1/2 section of same flower to show ovary and ovules (all ×6, from PENNINGTON and SARUKHÁN 9650). — (B 1) Whole ♂ flower of *Toona ciliata* with 2 petals removed to show fertile anthers; (B 2) 1/2 section of same flower showing pistillode and abortive ovules; (B 3) whole ♀ flower with 2 petals removed to show antherodes; (B 4) 1/2 section of same flower to show ovary and ovules (all ×6, from STYLES 266).

fruit in different stages of development. The greater frequency of flowering in male trees probably explains their greater frequency in collections, as being more often conspicuously worth collecting.

Concerning the sex-distribution within the inflorescence of the monoecious species of mahoganies, the male and female flowers (or in *Melia* and *Azadirachta*, male and hermaphrodite flowers) are not randomly distributed. As mentioned previously most inflorescences are composed of cymules of three, or very rarely, two flowers which are themselves arranged on a cymose plan (see Fig. 2 a and b). In *Cedrela*, *Toona* and *Swietenia* and probably all other *Swietenioideae* it is usually found that where male and female flowers are borne together on the same inflorescence, only the centre flower of a cyme or of a three-flowered cymule is female, whereas the lateral flowers are male. Sometimes, however, cymules may have only male flowers or, more rarely, all may be female. In *Melia* and *Azadirachta*, it appears that only the central flower of each cyme or cymule is hermaphrodite and that the lateral ones are male.

Phenology and Breeding System

The monoecious condition may encourage outbreeding but does not necessarily ensure outbreeding as effectively as dioecism or as an efficient incompatibility system. The chances of cross-fertilisation are, however, enhanced in some of the monoecious *Swietenioideae* by the fact that male and female flowers do not open at the same time (that is the sexes are dichogamous). Inflorescences on preserved specimens often have a few capsules developing, whereas

the majority of the flowers are still in the bud stage. This observation is supported by the field observations of LEE on *Swietenia* and by JONES on *Cedrela*. In species of both these genera the central female flower always opens first, so that the first flowers to open in any thyrses and probably over the entire tree, will be female. Opening of female flowers is then followed by the opening of male flowers. JONES (in press) further observed that more female flowers then open before the flowering period is complete but only rarely does there seem to be a mixture of the two sexes open in any one individual tree at the same time. In *Melia* and *Azadirachta*, hermaphrodite flowers open first and are followed by male flowers.

Flowering among the high forest species of *Meliaceae*, in Africa at least, appears to be seasonal and simultaneous in most of the trees in a population, although sporadic flowering of individual trees at any time of year is not unusual. But copious flowering does not necessarily mean that viable seed is set.

The work of CORNER (1958), FEDOROV (1966) and ASHTON (1968) makes it evident that great controversy and confusion still exists about the possible genetic systems operating among the larger rain forest trees, of which the timber species of *Meliaceae* form a considerable proportion. Scarcely any forest studies have been made of pollination mechanism, while for many of the supposed entomophilous types the pollinating agents have not been fully identified, nor has their behaviour when visiting flowers been carefully observed. Until more is known of the incompatibility systems operating among individuals and the structure of populations has been worked out, it seems premature to attempt an assessment of how much in-breeding or out-

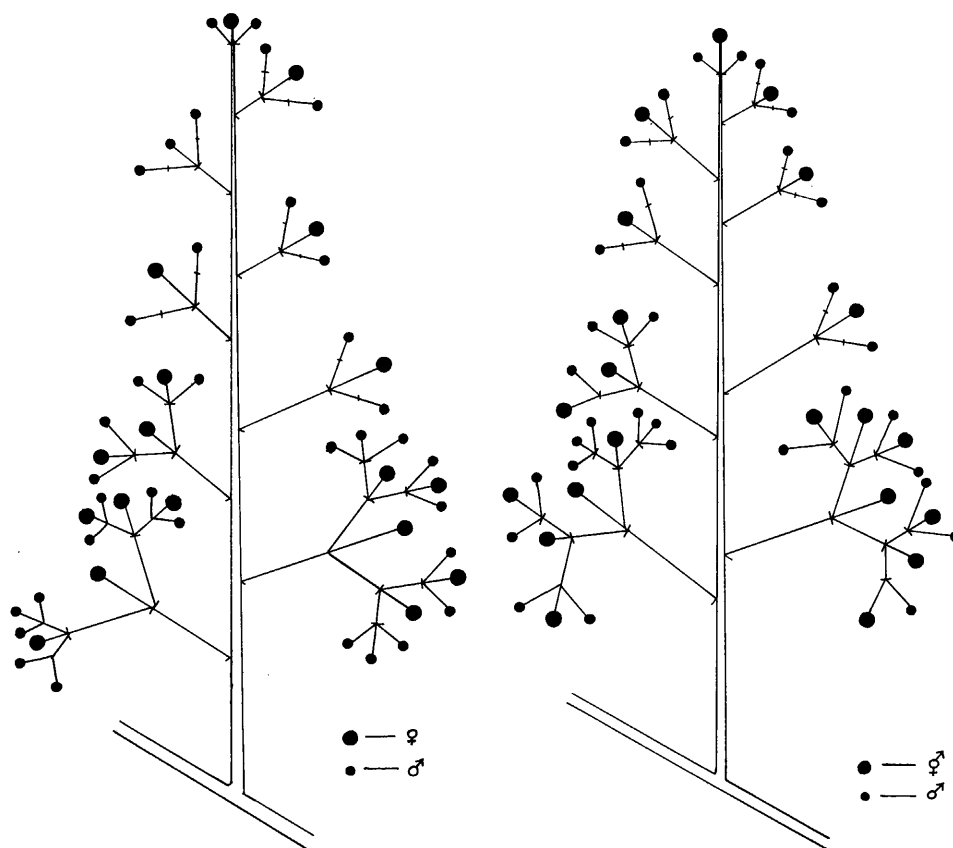


Fig. 2. — (a) Diagram of thyrses of *Cedrela odorata* L., showing positions of male and female flowers. — (b) Diagram of thyrses of *Melia azedarach* L., showing positions of male and hermaphrodite flowers.

breeding might occur. Indeed, knowledge of the reproductive biology of rain forest trees is deplorably inadequate.

The structure of Meliaceae flowers suggests they are entomophilous. Most species have a sickly-sweet perfume which in some can be extremely powerful, permitting their detection from a considerable distance. Although no insects have yet been seen to pollinate the taller forest emergents, bees do visit the flowers of the small (dioecious) savanna tree *Trichilia emetica*. YANG (1965) published a photograph of an unnamed insect, removed from a flower of *Swietenia*, with pollen-grains attached to its legs. That some cross-pollination and therefore out-breeding can occur is shown by obvious and frequent hybrids occurring between *Swietenia macrophylla* and *S. mahagoni* grown together in close association. On the other hand LEE (1965), who has made the only studies of breeding behaviour in the family, thinks that trees of these two species of *Swietenia* may be completely self-compatible, as he obtained 83% fertile seed from one tree of *S. mahagoni* which he had self-pollinated.

The apparent preponderance of male over female trees in the dioecious species of *Meliaceae* is puzzling. It could make pollination more likely and hence may have been established by selection. On the other hand nothing is known in *Meliaceae* of sex-reversal which is well-documented in several other families. In sex-reversal, at some point during a single flowering season, or at different times of the year, an individual tree or a part of it which at first produced male flowers, produces others which are female, or hermaphrodite. VERMOESEN (1922) mentions an instance of a tree of *Trichilia retusa* which had produced only male flowers, giving rise to others later (presumably either female or hermaphrodite) which set young fruits. These could, as DE WILDE (1968) points out, have been purely malformations of male flowers into galls (resembling fruits). Thus it is clear that many problems exist which can only be solved by controlled experiments or direct observations over long periods. Silviculturists have special opportunities to collect information on the important economic species which can be vital to future tree-breeding.

Finally, as KLAHN (1961) reminds us, insect-pollinated tree-species in seed orchards probably require numbers and distribution of clones and spacing of individuals which differ from that appropriate for wind-pollinated species. A knowledge of pollination-mechanisms are important in theoretical evolutionary studies and of direct practical interest to silviculturists and tree-breeders. Until more information is available about the incompatibility mechanisms that may operate among individuals of the species large scale breeding programmes should proceed with caution.

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Summary

Work being done by Forest Departments on breeding species of *Meliaceae* is reviewed. The structure and biology of the meliaceous flower are described with emphasis on phenology and sex dimorphism. Tentative suggestions on pollination mechanisms and breeding systems of the high

forest timber species are made. The urgent need for further forest observations is stressed.

Zusammenfassung

Bisherige Züchtungsarbeiten bei Arten der *Meliaceae* werden besprochen. Die Struktur und Biologie der Meliaceenblüte werden beschrieben, insbesondere ihre Phänologie und ihr Geschlechtsdimorphismus. Über Bestäubungsmechanismen und Züchtungssysteme bei wertvollen Holzlieferanten finden sich Hinweise. Weitere forstliche Beobachtungen sind erforderlich.

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Supernumerary Chromosomes in *Picea sitchensis* (Bong.) Carr.

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Introduction

In many genera of *Gymnospermae* the basic chromosome number is 11 or 12 (DARLINGTON and WYLIE, 1955). In addition to the relative constancy of the basic chromosome number, polyploidy is rare (KHOSHOO, 1958) and supernumerary chromosomes (with the possible exception of DARK, 1932) have never been recorded. This uniformity even extends to the pattern of secondary constrictions within chromosomes of nine species of *Pinus* (PEDERICK, 1970).

However, karyotypic stability is more apparent than real in some cases. For example, MIKSCHÉ (1967) showed that for eleven diploid species within the *Pinaceae* ($x = 12$) and two species within the *Cupressaceae* ($x = 11$), there is a range of $\times 2.9$ in DNA content between equivalent cells. Indeed, a similar variation exists within the species *Picea glauca* and *Pinus banksiana* when seed samples from different geographical locations are compared (MIKSCHÉ, 1968). This variation in cellular DNA content has a regular geographical basis at least for the western populations of *Picea glauca* where the DNA content is higher in seed from the most northerly provenances. Since nuclear volume generally increases with DNA content (SUNDERLAND and McLEISH, 1961; SPARROW and EVANS, 1961; PARODA and REES, 1971), we might expect that a similar relationship between latitude and DNA content exists for *Pinus silvestris* and *Picea sitchensis* since in these species nuclear volume increases with latitude (MERGEN and THIELGES, 1967). Recently, MIKSCHÉ (1971) has confirmed this relationship for *Picea sitchensis*, plants derived from more northerly provenances again having higher DNA contents. He considers that his data combined with the observation by BURLEY (1965) that total length of the A-chromosome karyotype of *Picea sitchensis* increases with latitude, imply that structural variations have occurred within the chromosomes which result in the geographical variations in RNA content.

In this report we describe the presence of supernumerary (B) chromosomes in seed derived from eight provenances of *Picea sitchensis*. This is the first definite report of B-

chromosomes in the *Gymnospermae* and further calls into question the karyotype uniformity of the group.

Materials and Methods

(i) Seed Sources. Seed samples were provided by the Forestry Commission Research Station, Alice Holt Lodge, Wrecclesham, Farnham, Surrey. A summary of the provenances is contained in table 1.

(ii) Cytological Techniques. Seed was germinated on moist filter paper in petri dishes for 10–14 days at 20° C. At this time the radicle was 1–2 cms long. Mitotic spindle inhibition was achieved by immersing the seedlings in a saturated aqueous solution of paradichlorobenzene for eight hours, with aeration. Radicles were subsequently fixed in CARNOY's fluid (6 alcohol : 3 chloroform : 1 acetic acid, v/v/v) overnight at 4° C. A few drops of concentrated ferric chloride solution were then added to the fixative as premordant and the material returned to the refrigerator for a further two days. Squash preparations of individual radicle tips were made after macerating in 2% orcein (G. T. GURR) dis-

Table 1. — Origins of the eight seed samples of Sitka spruce.

Sample No.	Source	Map reference		Altitude
		N	W	
22	Masset, Q. C. I.	54°	132° 20'	< 500
23	Skidegate, Q. C. I.	53° 16'	132°	< 500
24	Ucluelet, Vancouver Is.	49° 10'	125° 55'	< 500
25	Washington State	General		
26	Washington State	General		
27	Radnor Exp. 20 (Siskiyou, Calif.)	58° 18' (41° 30')	3° 11' (123° 30')	1200 (200)
28	Radnor Exp. 20 (Siuslaw, Oregon)	58° 18' (44° 05')	3° 11' (123° 50')	1200 (150)
29	Radnor Exp. 20 (Olympia Mt. Washington)	58° 18' (47° 50')	3° 11' (123° 40')	1200 (200)

¹⁾ R. B. M. participated in this work during the course of an honours B.Sc. degree at Aberdeen University.