Swietenia (American Mahogany)

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Introduction

The *Swietenia* genus ('true' or American mahoganies) consists of three closely related species (*S. humilis*, *S. mahagoni*, and *S. macrophylla*) whose largely allopatric natural distributions are concentrated in the seasonally dry, lowland neotropics. The latter two species have also been widely planted elsewhere, particularly in tropical Asia and Oceania. The long-established, sustained demand for mahogany timber is largely due to its high stability, durability, easy workability, and beauty. It is used principally in the manufacture of high-quality furniture, flooring, doors, window frames, and decorative veneers. *Swietenia macrophylla*, the only species still with commercially exploitable natural populations, is a massively buttressed, light-demanding canopy-emergent, reaching heights of up to 70 m and diameter at breast height (dbh) of 3.5 m. It occurs principally at low densities of 0.1–3.0 merchantable trees ha^{-1}, although higher densities may occur as a result of catastrophic disturbance, e.g., hurricanes, fires, and floods. The natural ranges of *S. humilis* and *S. mahagoni* are largely deforested; the ecology of these species in natural forest is little known, but is probably similar to that of *S. macrophylla*. All three species are subject to restrictions on international trade under Appendix II of the Convention on International Trade in Endangered Species (CITES), a consequence both of general deforestation and the unsustainable exploitation to which they have been subjected. Sustained production of *S. macrophylla* in natural forests is thought to be feasible. However, due to the species' requirement for high light and relatively low competition in its early years – conditions unlikely to be met under selective logging – it will require intensive methods. The establishment of *Swietenia* plantations has been inhibited by the attacks of mahogany shoot borers (*Hypsipyla* spp.). However, accumulated experience and growing experimental knowledge indicate that, with appropriate pest management methods, mahogany can be successfully grown in plantations.

Taxonomy and Genetics

American or true mahoganies (*Swietenia* spp.) are the most valuable species of the Meliaceae, a pantropical family which includes other high-quality timber trees such as Spanish cedar (*Cedrela odorata*), andiroba (*Carapa guinanensis*), the African mahoganies (*Lovoa*, *Entandrophragma*, *Khaya*), and the Asia-Pacific red cedars (*Toona* spp.) (all of the Swietenioideae subfamily), as well as less closely related species of value, e.g., neem (*Azadirachta indica*) and pride of India (*Melia azedarach*). The genus, named after the Austrian botanist Gerard von Swieten, consists of three largely allopatric species: *S. humilis* (dry-zone, Pacific, Pacific Coast, or Mexican mahogany), *S. macrophylla* (big-leaf, Brazilian or Honduras mahogany), and *S. mahagoni* (Cuban, Dominican, West Indian, or small-leaf mahogany) (**Figure 1**). The latter, restricted naturally to the Bahamas, Cuba, Jamaica, Hispaniola, and southern Florida, is the type species. The first to enter into international trade, its rapid depletion led quickly to commercial displacement by *S. macrophylla*. This has the largest natural distribution of the three, ranging from southern Mexico (23° N) to the southern Amazon of Bolivia and Brazil (18° S). *Swietenia humilis*, the least-known species, is restricted principally to the dry Pacific watersheds of Mesoamerica from the Mexican states of Durango and Sinaloa to northern Costa Rica; although sometimes referred to as Pacific Coast mahogany, it also occurs well inland. Within and outside their natural ranges, the species are generally known as caoba (in Spanish-speaking states except Bolivia, where the name mara is used), mahogany (English-speaking states), and mogno (Brazil), i.e., without the epithets found in the technical literature. Many other names are used locally by indigenous peoples.

Biologically, the three species are rather poorly defined; the current taxonomy is maintained essentially on the basis of the largely allopatric distribution described above, coupled with general morphological differences. The species are not easily distinguished on the basis of leaf and flower morphology, and appear to hybridize readily when in proximity (e.g., *S. humilis* and *S. macrophylla* where their ranges overlap in northeastern Costa Rica; *S. macrophylla* and *S. mahagoni* as exotics in Puerto Rico). Although both common-garden experiments and preliminary studies with DNA markers confirm that the species represent distinct genetic entities, it may be that *S. humilis* and *S. macrophylla*, at least, are no more genetically distinct than regional variants of other species that range over similarly diverse conditions, e.g., Pacific and Atlantic

Figure 1 (a) Mature *Swietenia humilis* tree, Comayagua, Honduras (courtesy of JP Cornelius); (b) *S. macrophylla* saplings in 3-year-old plantations, Quintana Roo, Mexico (courtesy of KE Wightman); (c) foliage of *S. mahagoni*, Puerto Rico. Courtesy of JP Cornelius.

Central American ecotypes of *Cedrela odorata* and *Cordia alliodora* (Boraginaceae). The taxonomic significance of observed interspecific variation in chromosome number is questionable because wide intraspecific variation in chromosome number has also been reported.

The little provenance work that has been carried out (*S. macrophylla* and *S. humilis* only) suggests substantial genetic variation between widely separated provenances, but little differentiation between populations at a more local scale (e.g., within the Yucatan peninsula of Mexico). Joint consideration of randomly amplified polymorphic DNA (RAPD) studies in Mesoamerica and allozyme work in Bolivia suggests that neutral genetic variation shows a similar trend. Quantitative and molecular (allozymes, RAPDs, microsatellites) data indicate abundant genetic variation at the within-population level, as is common in tropical trees. Long-distance pollination has been demonstrated in *S. humilis*, and probably occurs in all three species, contributing to the maintenance of genetic variation even in apparently isolated populations. Sporadic tree improvement activities have been implemented, e.g., clonal seed orchards in Mexico and Fiji (*S. macrophylla*), and seedling seed orchards and progeny tests in Costa Rica, Mexico (*S. macrophylla*), and Honduras (*S. humilis*). The absence of large, sustained planting programs explains the lack of more intensive breeding activities.

Swietenia macrophylla and, to a lesser extent, *S. mahagoni*, have been widely planted outside their native ranges, particularly in Southeast Asia and Oceania; plantations established in Fiji, Indonesia, Philippines, Solomon Islands, and Sri Lanka total more than 190 000 ha. There are also increasing areas of *S. macrophylla* plantations within the natural range, particularly in southern Mexico and

Guatemala. Worldwide, however, mahogany remains a minor plantation species, with total area less than one-twentieth that of teak. In large measure, this can reasonably be attributed to the problem – real or perceived – of mahogany shoot-borer attack.

Ecology

Swietenia macrophylla

Typically, *Swietenia* are species of relatively low-altitude (≤ 1400 m), seasonally dry forests, and are largely absent from or rare in perhumid regions within their natural ranges. These factors are responsible for an interruption in the natural range of *S. macrophylla*, formed by the coast-to-coast humid and/or high-altitude belt that runs diagonally from northeastern Costa Rica to north-Pacific Panama. Similarly, *S. macrophylla*'s arc-shaped range in South America traces the seasonal tropical forests along the northern, western, and southern rims of the Amazon basin.

Big-leaf mahogany is one of the giants of the tropical forest, reaching heights of up to 70 m and diameter (above often massive buttresses) of 3.5 m. Trees of such dimensions are probably more than 400 years old and are now rarely found; across its range, the average merchantable big-leaf mahogany tree is likely to be 20–30 m tall with dbh of 60–120 cm. Young trees have narrow, shallow crowns and may remain unbranched for 6–8 m. The mature crown, composed of a few, large primary branches, tends to be irregular or umbrella-shaped. The thick bark of older trees is deeply furrowed and sometimes nearly black. The pinnately compound leaves are deciduous; trees tend to be leafless for weeks rather than months. The small, unisexual flowers emerge with the leaves, and appear to be pollinated by small bees and moths. In natural forest, trees of 14 cm dbh may flower, but only trees >30 cm with exposed crowns are likely to do so consistently. The species is monoecious and tends to be fully outcrossing, at least in relatively undisturbed conditions. It is unknown whether this is due to genetic self-incompatibility, abortion, selection against inbred zygotes, or dichogamy. Mahogany fruits are woody capsules, each containing 25–60 wind-dispersed, samaroid seeds (**Figure 2**). These measure 1–2 cm (up to 13 cm including the wing) and generally land within 50 m of the mother tree. Maximum seed production occurs in large but vigorous trees of 90–130 cm dbh, which can produce up to 800 fruit capsules in a single year. Germination of mahogany seed is maximal under shaded, closed-canopy conditions, where seedlings show remarkable persistence. Nevertheless, they will not grow vigorously without higher light levels.

Figure 2 Opened capsule and seeds of *Swietenia macrophylla*. Courtesy of KE Wightman.

Two particular patterns of frequency and abundance of big-leaf mahogany have been widely noted. First, and more rarely and locally, mahogany may form relatively dense aggregations of up to 40–50 mature trees ha^{-1}. These formations, reported particularly from the Yucatan peninsula, seem to derive from the resistance of mature mahogany trees to hurricanes and fires, both relatively common in the Caribbean region. Such catastrophic disturbances favor the species by opening the canopy and destroying seed trees and advance regeneration of other species. The copious seed rain of surviving mature mahogany trees can then lead to seedling densities of up to 1000 ha^{-1}. The annual height growth of young seedlings, which may exceed 2 m during the first 5 years, is sufficiently rapid to permit high adult stocking. The second, more common pattern is of low densities of 0.1–3.0 merchantable trees ha^{-1}, found in small aggregations. It occurs in much of Quintana Roo, Mexico, the Chimanes region of lowland Bolivia, seasonally flooded forest in the Peruvian Amazon, nonriverine, upland or terra firma landscapes in western Amazonia, and southeast Pará, Brazil, and seems to reflect absence of (recent) catastrophic disturbance. Studies demonstrate that, under spatially smaller and/or lower-intensity disturbance (resulting, for example, from flooding or tree-fall of mahogany and other large trees such as *Hura* and *Manilkara*), advance or postdisturbance regeneration of mahogany will almost always die due to lateral canopy closure or competitive effects of exploitative gap-invaders. This seems to explain the low density of mahogany in such forest: that is, conditions dictate that, of the lifetime seed fecundity of individual trees, only a small proportion – on the order perhaps of 1 in 0.25 million dispersed seeds – survives to adulthood. The survival of even this proportion is presumably facilitated by the ability of seed to germinate in closed-canopy conditions and the relative robustness and shade tolerance of mahogany seedlings.

Although mahogany is tolerant of a wide range of soil types (derived from alluvial, volcanic, metamorphic, and calcareous material) and conditions (deep, shallow, acid, alkaline, well drained, and gleyed), edaphic or hydrologic factors certainly also partly determine distribution patterns. However, the relative roles of disturbance and such factors are unknown. Physiographic associations at the population level remain poorly described and understood across the natural range. Big-leaf mahogany was first observed in riparian situations in coastal Belize. Similarly, descriptions from South America emphasize the species' association with river floodplains in the upper reaches of the western Amazon basin. From Bolivia, Brazil, Ecuador, and Peru many observers have noted highest densities on drier, firmer, and infrequently flooded soils slightly above seasonally inundated floodplains. Nonriverine associations have also been described, e.g., in interfluvial and upland ecosystems in Belize, where mahogany will even invade stands of *Pinus caribaea* on drier sites with high understory light levels.

Swietenia humilis and *S. mahagoni*

As little natural forest remains within the generally highly (human-) populated natural ranges of *S. humilis* and *S. mahagoni*, their ecology in natural conditions is to some extent a matter of conjecture. However, the close similarity between all three species suggests a similar ecological role and regeneration ecology to that of *S. macrophylla*. *Swietenia humilis* is found in farmers' fields, fence lines, riparian strips, and in some of the few remaining areas of relatively intact natural forest. *Swietenia mahagoni* is found principally in remnant stands on inaccessible terrain. Large individuals of either are rare. For *S. mahagoni*, this may be due to past exploitation (in Jamaica, a harvested specimen reached 3.7 m in diameter, and 200-year-old avenue trees in the US Virgin Islands have attained 2.0 m). Consistent with its epithet, no such *S. humilis* individuals seem to have been recorded. Common-garden provenance and species trials suggest that both *S. mahagoni* and *S. humilis* are adapted to drier conditions than *S. macrophylla*, as their respective distributions would suggest.

Conservation Status

None of the species is in imminent danger of biological extinction. Nevertheless, there is justified concern about the current conservation status of all three. *Swietenia humilis* and *S. mahagoni* are both commercially exhausted, as illustrated by current imports of *S. macrophylla* to the Dominican Republic, formerly a producer of *S. mahagoni*. They were listed in CITES Appendix II in 1975 (*S. humilis*: all parts and derivatives except seed, pollen, seedlings, or tissue cultures) and 1992 (*S. mahagoni*: logs, sawnwood, veneer, and plywood). As pioneers – considered potentially invasive in exotic locations – both species are well equipped to survive in the highly disturbed conditions where they now generally occur. However, their continued persistence is likely to depend on the nurturing of regeneration by farmers.

In parts of Central America, e.g., northern Costa Rica and adjoining parts of Nicaragua, *S. macrophylla* also is increasingly rare. In South America, particularly in Brazil and Peru, substantial stocks remain. However, intensive logging in recent decades has led to virtual local extinction over large areas of the natural range in both these countries and Bolivia. Growing concern over the impact of logging – on the species itself, on associated forest types, and on forest-dwelling indigenous peoples – led in the 1990s to a sometimes acrimonious debate, centered around successive proposals to include *S. macrophylla* in CITES Appendix II. The third such proposal was approved in November 2002, and applies to mahogany logs, sawn timber, and veneer.

Silviculture

Natural Stand Management

To date, with the exception of relatively small areas of forest certified by the Forest Stewardship Council in Mesoamerica, mahogany has been 'mined' rather than managed; with exhaustion of merchantable stems in one area, loggers have moved on to new 'deposits' in other regions or countries. Selective logging for mahogany tends to cause relatively little canopy disturbance. As discussed above, in natural, unlogged forest, rare recruitment to adulthood in tree-fall gaps may be adequate to maintain low-density populations. However, the probability of replacement arising from a specific canopy opening (e.g., one logging event) is vanishingly small, even supposing that, contrary to frequent practice, trees are not felled before seed dispersal. Consequently, sustained production of mahogany in selectively logged forests is likely to require intensive management and more complete ecological information. Recently initiated experimental management in Acre, Brazil reflects these requirements, emphasizing knowledge of local distribution patterns and population structures; retention of hollow adult trees and highly fecund individuals for seed production and maintenance of genetic structures; acceleration of diameter increment of retained trees through vine cutting and crown liberation thinnings; and artificial regeneration in treated (cleaned, burned) logging gaps with regular postharvest cleaning. Such management has the potential to increase mahogany densities substantially in 'natural' forest. In the longer term, this could permit the use of classic shelterwood regeneration systems, as has been proposed for some mahogany plantations.

Mean periodic annual diameter increments reported in the literature range from 0.36 to 0.91 cm year^{-1} in Belize over an 8-year period; an estimated 0.38–1.09 cm year^{-1} in Mexico's Yucatan peninsula, with highest increment growth by 15–30-year-old trees; 0.26–0.9 cm year^{-1} in Bolivia over a 2-year period, with fastest rates by trees 20–80 cm dbh; and 0.19–0.59 cm year^{-1} in southeast Pará, Brazil over 3 years, with increment rates declining with increasing diameter and maximum increment rates of individual trees approaching 2 cm year^{-1}. Mean rotation lengths required to grow merchantable trees from seed range from an estimated 85 years in Pará (50 cm dbh) to 122 years in Mexico (55 cm dbh), with fastest-growing trees reaching merchantable size in 50–55 years.

Plantations

The choice of species is the first decision to be faced by the potential mahogany planter. In relatively moist sites with short (2–4 months) dry seasons, *S. macrophylla* is the species of choice. Research carried out in Puerto Rico and the US Virgin Islands suggests that *S. mahagoni* or, if available, the F_1 hybrid, should be preferred to *S. macrophylla* in dry forest. Within its native range, *S. humilis* is probably the safest choice. However, consideration should be given to *S. macrophylla* in moist or irrigated sites within the range of *S. humilis*. Whatever species is used, seed should be derived from a local (or locally tested) source. *Swietenia macrophylla*, particularly, occupies an ecologically variable range, and long-distance seed transfers should be avoided. Germination capacity of fresh seed is 80–95%, although drying of seed on ventilated screens in partial sunlight for 2–3 days is recommended to reduce rot. Unopened capsules can also be dried in the sun to encourage opening. Mahogany seed is orthodox and may be stored for long periods at 4–5% moisture content and -20°C, with little or no loss of viability. If necessary, seed may also be stored in ambient conditions for 7–8 months (approximately 50% decline in viability). Seed is usually dewinged to facilitate planting, although such seed may have lower viability after storage. It should be planted flat or with the winged end pointed down. No pretreatment is necessary. Germination is hypogeal, beginning in moist soil after 2 weeks and finishing 4 weeks later. Seedlings develop a strong taproot. Planting stock can also be produced vegetatively, e.g., in nonmist propagators.

Common substrates for poly-bag production include mixtures of forest soil with sand and a variety of composted organic materials. However, results vary greatly depending on nutrient concentrations and proportions in local materials. In container nurseries, common mixtures include 50% sphagnum moss, 25% vermiculite, and 25% perlite mixed with a slow-release fertilizer. Substrates should be kept partially shaded and moist during the first weeks of germination. Seedlings are ready to plant when the base of the stem has lignified and reached a minimum diameter of 8 mm. Seedlings from 20 to 80 cm, produced after 3–6 months in the nursery, may be planted successfully. The use of bare-root stock and striplings is inadvisable because subsequent field growth may be retarded. Direct seeding in the field is a viable option, but requires high soil moisture, early competition control, and the use of abundant seed.

Plantations can be successfully established on cultivated fields (e.g., in taungya) or recently cleared areas. Weed competition must be controlled carefully but can also be managed to provide lateral shade (**Figure 1b**). This encourages height growth, reduces soil exposure, promotes biodiversity (species richness), and may reduce and/or mitigate *Hypsipyla* attack. Close spacing (2×2 m or 3×3 m) allows greater flexibility in selection of final crop trees – an important consideration when *Hypsipyla* is present – and quicker canopy closure. Wider spacing, or deployment in mixed plantations or agroforestry systems, permits biological and product diversification, intermediate income generation and may form part of the integrated management of *Hypsipyla*. Mahogany has also been successfully used in line (enrichment) planting, although this approach requires careful management of the overstory. Fertilization during the first two to four growing seasons (increasing to 200 g per plant of a complete granular fertilizer) can be effective. Well-tended plantations of any of the species on well-drained, fertile sites can easily reach average heights of 6 m in 3 years. Maximum mean annual increments for well-managed, conventionally spaced (i.e., 1111–2500 trees ha^{-1} at establishment) plantations reach 25 m^3 ha^{-1} year^{-1}. First thinning should usually take place after 5–10 years. Commercial sizes (>50 cm dbh) can be reached in 20–30 years.

Abundant regeneration has been observed in *S. macrophylla* and *S. mahagoni* plantations, suggesting that planting may be unnecessary for establishment of second and subsequent rotations. Suggested silvicultural systems include the uniform shelterwood and group selection systems. Under the latter, trees are removed in groups in order to open canopy gaps sufficiently large for continued development of new and advance regeneration. In the former, a regeneration felling is carried out 4–6 years before final felling. The resulting advance regeneration is released by the final felling of the seed trees. In either system, intensive tending would be necessary, as in natural forest.

Mahogany's relatively fast growth, ease of nursery production, and high value suit it to plantation production. However, these advantages must be weighed against the serious pest problem of the mahogany shoot-borer (**Figure 3**). The larvae of the pyralid moths *Hypsipyla grandella* (neotropics) and *H. robusta* (old tropics) feed on the pith of mahogany shoots, principally while succulent or semisucculent. *Hypsipyla* attack approaches 100% in many plantations. Unless pruned, affected trees often develop into multiple-stemmed individuals of little commercial value. Attack may also reduce growth rate because of stalling for a variable period before dormant axillary buds respond. The problem has led to widespread avoidance of mahogany and related species both by tree planters and development projects. Nevertheless, there is no doubt that mahogany can be successfully cultivated in plantations. Tree mortality due to *Hypsipyla* is very unusual, and deformations caused by *Hypsipyla* up to at least 3 m height can be relatively easily corrected by biannual or annual pruning. The length of clean stem laid down between attacks, which depends both on growth rate and speed of post-attack lateral bud break, can be increased by both genetic selection and environmental manipulation (including appropriate site selection). There is evidence that lateral shading can both reduce *Hypsipyla* oviposition and stimulate vertical growth. Finally, selective thinnings in higher density plantations can be employed to favor the best-formed trees. A combination of all these control tactics should form the basis of an integrated pest management system.

In the neotropics, mahogany plantations can also be severely attacked by leaf-cutting ants, leading to growth reduction and, in young seedlings, death or forking. Leaf-cutters may be efficiently controlled using specific insecticides. Where these are unavailable or prohibitively priced, attack may be minimized by providing alternative browsing sources (interplanted or in neighboring areas) and avoiding clean-weeding. Other pest problems, such as Ambrosia beetle (*Crossotarsus externedentatus* and *Platypus gerstaeckeri*) and termite attack in Fijian plantations, have also been noted.

Utilization

Mahogany has been one of the world's most traded timbers for the last four centuries. Currently, it is used principally in furniture manufacture, flooring, doors, window frames, and decorative veneers. Free-on-board sawnwood prices in the early 2000s have been around US$1000 m^{-3}. At the same time, retail prices in the USA were around US$5–6 board $foot^{-1}$, equivalent to more than US$2000 m^{-3}. The sustained demand for mahogany is largely a result of its excellent properties: extraordinary dimensional stability, high strength (particularly for its relative lightness), workability and exquisite, subtle beauty. These qualities, combined with centuries of use, have also

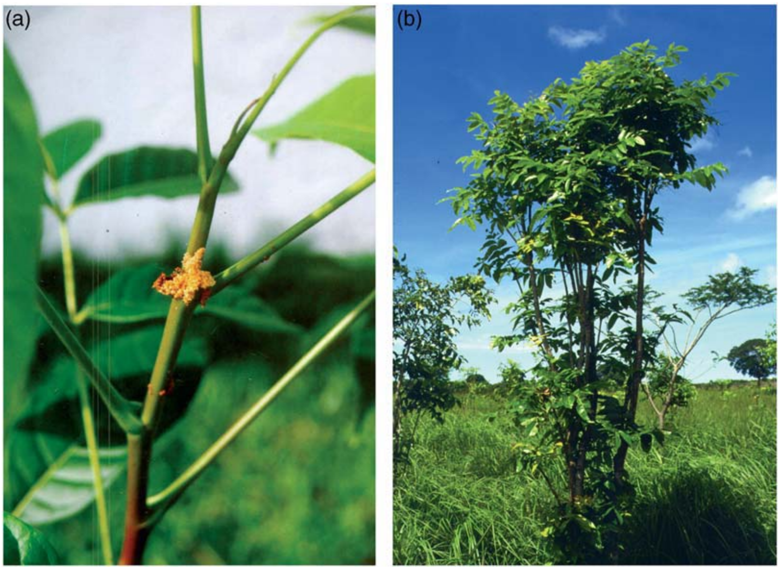

Figure 3 (a) *Hypsipyla*-attacked *Swietenia macrophylla* shoot in Turrialba, Costa Rica; (b) attacked *S. macrophylla* sapling, Guanacaste, Costa Rica; note multiple leaders due to lack of post-attack pruning. Courtesy of JP Cornelius.

given rise to an associated cachet – reflected in the many different woods commercially sold as mahogany, including not only other Meliaceae, but also Dipterocarpaceae (*Shorea* spp.) and various eucalyptus – that in itself sustains demand.

Wood quality, particularly density, appears to be related to environmental conditions, particularly as they affect growth rate; faster growth appears to be related to lower density. This factor, rather than inherent genetic characteristics, may also explain an apparent tendency of both *S. humilis* and *S. mahagoni* to have higher-density wood than *S. macrophylla*. The drier conditions in the natural ranges of *S. humilis* and *S. mahagoni* are probably less conducive to fast growth than those of typical *S. macrophylla*.

Exploitation and trade have shown three distinct phases: early exploitation of *S. mahagoni* in the Caribbean; cutting and substantial commercial exhaustion of *S. macrophylla* in Mexico and Central America; exploitation from the mid twentieth century of South American sources, particularly in Bolivia, Brazil, and Peru. The exploitation history of *S. humilis* is little known. It may be that mahogany exploitation is now entering a fourth phase, as international and domestic pressures lead producing states to adopt increasingly stringent management and trade regulations.

See also: **Harvesting**: Forest Operations in the Tropics, Reduced Impact Logging. **Operations**: Nursery Operations. **Plantation Silviculture**: Forest Plantations; High Pruning; Treatments in Tropical Silviculture. **Sustainable Forest Management**: Causes of Deforestation and Forest Fragmentation; Overview. **Tree Breeding, Practices**: Tropical Hardwoods Breeding and Genetic Resources. **Tropical Forests**: Tropical Dry Forests; Tropical Moist Forests.

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Teak and other Verbenaceae

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Introduction

The family Verbenaceae contains over 3000 species of trees, shrubs, herbs, and lianes in some 86 genera, virtually all of which are tropical or subtropical and a number of which are economically important tree species. It contains what is probably the most prized and famous of all timbers, teak (*Tectona grandis*). Other important tree genera include *Clerodendrum*