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.

Further Reading

- Chalmers KJ, Newton AC, and Waugh R (1994) Evaluation of the extent of genetic variation in mahoganies (Meliaceae) using RAPD markers. *Theoretical and Applied Genetics* 89: 504–508.
- Francis JK (1991) Swietenia mahagoni Jacq., West Indies Mahogany; Meliaceae, Mahogany Family. International Tropical Forestry Report no. SM 46, pp. 1–7. Asheville, NC: US Department of Agriculture Forest Service Southern Station.
- Grogan J, Barreto P, and Veríssimo A (2002) Mahogany in the Brazilian Amazon: Ecology and Perspectives on Management. Belém, Brazil: Imazon. Available online at www.imazon.org.br.
- Lamb FB (1966) Mahogany of Tropical America: its Ecology and Management. Ann Arbor, MI: University of Michigan Press.

- Lugo A, Figueroa Colón JC, and Alayón M (eds) (2003) Big-Leaf Mahogany: Genetics, Ecology, and Management. New York: Springer-Verlag.
- Mahroof RM, Hauxwell C, Edirisinghe JP, et al. (2002) Effects of artificial shade on attack by the mahogany shoot borer, *Hypsipyla robusta* (Moore). Agricultural and Forest Entomology 4(4): 283–292.
- Mayhew JE and Newton AC (1998) The Silviculture of Mahogany. Wallingford, UK: CAB International.
- Negreros-Castillo P and Mize C (1993) Effects of partial overstory removal on the natural regeneration of a tropical forest in Quintana Roo, Mexico. *Forest Ecology and Management* 58: 259–272.
- Newton AC, Baker P, Ramnarine S, et al. (1993) The mahogany shoot borer: prospects for control. Forest Ecology and Management 57: 301–328.
- Robbins C (2002) Mahogany Matters: The US Market for Big-Leafed Mahogany and its Implications for the Conservation of the Species. Washington, DC: TRAFFIC North America. Available online at: http://www.worldwildlife.org/forests/attachments/mahogany.pdf.
- Stevenson NS (1927) Silvicultural treatment of mahogany forests in British Honduras. *Empire Forestry Journal* 6: 219–227.
- Various authors (1996) Papers arising from a meeting on 'The future for the genus mahogany in its native forests'. Botanical Journal of the Linnean Society 122(1): 1–87.
- Veríssimo A, Barreto P, Tarifa R, and Uhl C (1995) Extraction of a high-value natural resource in Amazonia: the case of mahogany. *Forest Ecology and Management* 72: 39–60.
- Weaver PL and Sabido OA (1997) *Mahogany in Belize: A Historical Perspective.* General Technical Report no. IITF-2. Asheville, NC: US Department of Agriculture Forest Service, International Institute of Tropical Forestry/Southern Research Station.
- White GM, Boshier DH, and Powell W (1999) Genetic variation within a fragmented population of *Swietenia humilis* Zucc. *Molecular Ecology* 8: 1899–1909.

Teak and other Verbenaceae

P J Wood, Commonwealth Forestry Association, Oxford, UK

© 2004, Elsevier Ltd. All Rights Reserved.

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*

and *Vitex* (Viticöideae) and *Gmelina*, *Lantana*, and *Lippia* (Verbenöideae).

Teak

Teak is arguably the most famous timber in the world (Figure 1). The combination of the wood's strength, durability, and stability, as well as its availability in long lengths gave it a key role not only in shipbuilding for the European empires in south and southeast Asia since the seventeenth century, but much further back in trade to Mesopotamia in the third millenium BC. In its natural habitats in India, Myanmar, Thailand, and Laos teak occurs mixed with many other species, but since the sixteenth century the species has been heavily exploited, as well as encouraged and replanted, so that today simplified monocultures of teak are the rule rather than the exception. Teak is thought to have been introduced in the fourteenth century from India to Indonesia by Hindu monks. The large-scale plundering of teak forests in the colonial era gave rise to early concerns for its regeneration and protection among some colonial administrators, so



Figure 1 Tectona grandis.

that sustained management of teak in India, Myanmar, and Indonesia probably has the longest history of any tropical tree species.

Teak occurs naturally as a component of many forest types ranging from moist to dry, though in all cases in a monsoonal climate. Like many other members of the Verbenaceae it is insect pollinated. Major phenotypic and genotypic differences have been identified in different parts of the natural distribution which have been used in tree breeding programs across the tropics, especially in south and southeast Asia.

Global areas of teak forest in 1998 were approaching 28 million ha, of which some 25 million ha were reported as natural forest (**Table 1**).

Other Species of Tectona

In addition to *Tectona grandis* four other species of the genus have been identified: *T. australis*, *T. hamiltoniana*, *T. philippinensis*, and *T. ternifolia*. These are, however, of low social or commercial importance, though they form important components of different natural ecosystems.

Other Important Genera

The genus *Gmelina* is represented by over 57 species that occur mostly in the Indo-Malaysian and Australasian regions. The most commercially important species is *Gmelina arborea*, widely planted in many parts of the humid and subhumid tropics for general-purpose timber and the subject of important breeding and conservation programs. The pantropical genus *Vitex* contains several hundred species, some of which are of commercial importance.

Table 1 World teak area statistics

Country/zone	Teak area reported, 1998 (ha × 10 ³)	Plantations as % of teak area reported	Country/zone area as % of world area
Myanmar	14225	1.6	51
India	10000	10	36
Thailand	2 100	4.8	7.8
Laos	22	11	<1
Indonesia	1 100	100	3.5
Other Asia	159	100	4.5
Africa	124	100	<1
Latin America	47	100	<1
Total	27777		

Note: these figures should be regarded as a general guide only. *Source*: Derived from Behagel I (1999) State of teak plantations in the world. *Bois et Forêts des Tropiques* 264(4).

The genera *Lantana*, *Lippia*, and *Clerodendron* are also pan-tropical, contain several hundred species, and are important components of many forest ecosystems. They comprise trees, shrubs and lianes. Species of *Lantana* are important weeds and *Lippia* species are important sources of medicine.

See also: Silviculture: Treatments in Tropical Silviculture. Tree Breeding, Practices: A Historical Overview of Forest Tree Improvement; Tropical Hardwoods Breeding and Genetic Resources. Tropical Forests: Monsoon Forests (Southern and Southeast Asia). Wood Use and Trade: History and Overview of Wood Use.

Further Reading

- Behagel I (1999) State of teak plantations in the world. Bois et Forêts des Tropiques 264(4).
- Champion HG and Seth SK (1968) A Revised Survey of Forest Types of India. Delhi, India: Government of India, Nasik Press.
- Dawkins HC and Philip MS (1998) Tropical Moist Forest Silviculture and Management: A History of Success and Failure. Wallingford, UK: CAB International.
- Kadambi K (1972) Silviculture and Management of Teak. Nacogdoches, TX: Stephen F. Austin State University.
- Krishna Murthy AVRG (1975) Bibliography on Teak: Tectona grandis Linn F. Jughal Kishore, India: Dehra Dun.
- Mathur KBL (1973) *Teak Bibliography*. Delhi: Government of India.

Tropical Pine Ecosystems and Genetic Resources

J Burley and R D Barnes, University of Oxford, Oxford, UK

© 2004, Elsevier Ltd. All Rights Reserved.

Introduction

The genus *Pinus* (family Pinaceae) is one of the most widely distributed genera of trees in the northern hemisphere (Figure 1). The species often dominate the natural vegetation types in which they occur and provide some of the most important timber trees in the world. *Pinus* comprises approximately 100 species, of which about half occur naturally within the northern tropics. The tropical pines consist of two categories: first, those that occur naturally in the tropics, e.g., *P. oocarpa* (Figure 2) and, second, nontropical pines that are planted for wood production or shelter in the tropics, e.g., *P. elliottii* and *P. taeda* (Figure 3 and Table 1). This definition is

taken from the account of the tropical pines given in *Tree Crop Ecosystems* (Barnes *et al.*, 2001; see Further Reading) and on which this contribution is based.

There are virtually no natural pine forests in the southern hemisphere (Figure 1). It is not surprising, therefore, that the tropical pines have been used most extensively as exotics in the southern tropics, where some 6 million ha of plantations have been established to produce structural lumber and long-fibered pulp for particleboard, kraft paper, and newsprint manufacture (Figure 3). Unlike other crops, it is not usually economic to modify the plantation environment artificially through fertilization or irrigation. However, the extensive gene pool of tropical pine species has made it possible to establish plantations that are many times more productive than the natural forests over a great range of environmental conditions.

Taxonomy and Variation in Natural Populations of Tropical Pines

The pines are evergreen, resin-yielding, small to very large trees, usually with a single stem and strong apical dominance. If open-grown, most branches are retained and the bole tends to be conical but, under forest conditions, lower branches are shed and clean cylindrical boles are produced. Bark varies from rough and furrowed (Figure 4) to smooth and scaly (Figure 2). All pines have mature needles in fascicles (bundles) of from one to six, enclosed in a deciduous or persistent basal sheath. The fascicles are dwarf short shoots and are important in their identification. The needles contain resin canals running along their length which vary in number and position and which are also important for species identification. Needles may possess one or two vascular bundles, upon which the two major divisions of the genus are based, viz., Haploxylon and Diploxylon. Stomata (pores for gas exchange) are borne in lines on all surfaces, varying in number between species and within subspecies and ecotypes of single species.

All pines are monoecious with male and female strobili borne on the same individual tree. The female strobilus is usually terminal or subterminal and is composed of two series of spirally arranged scales, a very small bract scale and a much larger ovuliferous scale. The latter bears two pendulous ovules on its upper surface. The mature cone shows considerable variation in size, degree of woodiness, shape and size of the individual scales, and position of the apophysis and umbo (the exposed part of the scale when the cone is closed). In the Haploxylon group of