in turn cause wild swings in the ecology and these swings themselves can sometimes prove to be beyond control through management. In the exotic environments, it is impossible to predict or even conceive of the events that may occur and to know their consequences. Introduction of diversity in the forest through mixed ages, mixed species, rotation of species, silvicultural treatment, and genetic variation may make ecology and management more complex but it will render the crop ecosystem much more stable, robust, and self-perpetuating and provide buffers against disasters. The forester must treat crop protection as part of silvicultural planning.

See also: **Pathology**: Diseases affecting Exotic Plantation Species; Diseases of Forest Trees. **Temperate and Mediterranean Forests**: Northern Coniferous Forests; Southern Coniferous Forests. **Temperate Ecosystems**: Pines. **Tree Breeding, Practices**: *Pinus Radiata* Genetics; Breeding for Disease and Insect Resistance; Southern Pine Breeding and Genetic Resources. **Tree Breeding, Principles**: A Historical Overview of Forest Tree Improvement; Conifer Breeding Principles and Processes. **Tropical Ecosystems**: Southern Hemisphere Conifers.

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TROPICAL FORESTS

Contents

Bombacaceae

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Introduction

The family Bombacaceae contains trees with some of the most enigmatic of all traits, whether it is the

lightness of South American balsa wood (*Ochroma pyrimidale*), the fabled odor of Southeast Asian durian fruit (*Durio zibethinus*), or the unusual architecture of African baobabs (*Adansonia digitata*). Traditionally, the Bombacaceae have been separated as a family, distinct from the Sterculiaceae (cocoas), Malvaceae (cottons), and Tiliaceae (limes). However, detailed analyses of molecular and morphological data have concluded that a single monophyletic Malvaceae should be recognized that encompasses all of the other families. The Bombacaceae cannot be maintained as a separate family since it appears to be paraphyletic with respect to the traditional circumscription of the Malvaceae and, furthermore, the genus *Durio* and its allies are more closely related to the traditional circumscription of the Sterculiaceae.

The traditional Bombacaceae comprises some 25 genera and 250 species of tropical (primarily neotropical) trees (**Table 1**), although some generic limits are controversial. For example, the important timber species *Bombacopsis quinata* is often separated from the genus *Pachira*, whilst the widely planted ornamental genus *Chorisia* may be recognized as distinct from *Ceiba*. The majority of species are found in lowland rainforest, although some genera (e.g., *Adansonia*, *Ceiba*, *Cavanillesia*) show water-storage adaptations for survival in dry, open habitats, for example, small crowns and thick, bottle-shaped trunks.

Table 1 Distribution of genera in the family Bombacaceae

Genus	*Approx. species number*	*Distribution*
Adansonia	15	Africa, Madagascar, Australia
Aguiaria	1	Brazil
Bernoullia	2	Tropical America
Bombax	20	Old-world tropics
Camptostemon	2	Central Malesia, Australia
Catostemma	11	Northern South America
Cavanillesia	3	Tropical America
Ceiba	11	Tropical America and Africa
Coelostegia	5	West Malesia
Durio	28	Myanmar to West Malesia
Eriotheca	19	Tropical America
Gyranthera	2	Panama, Venezuela
Huberodendron	5	Tropical America
Kostermansia	1	Malaysia
Matisia	25	Tropical South America
Neesia	8	West Malesia
Neobuchia	1	Hispaniola
Ochroma	1	Tropical America
Pachira	20	Tropical America
Patinoa	4	Tropical South America
Phragmotheca	5	Tropical South America
Pseudobombax	20	Tropical America
Quararibea	35	Tropical America
Scleronema	5	Tropical South America
Septotheca	1	Peru

The hermaphrodite flowers of Bombacaceae are generally large and showy, being produced during drier periods when the trees lose their leaves. The flowers attract insects (e.g., ants in *Adansonia*), birds and mammals (particularly bats), and are generally highly outcrossed, with pollen moving large distances between trees. The fruits of Bombacaceae are often dehiscent capsules containing wind-dispersed seeds that are surrounded by cotton-like fibers, e.g., *Bombax* and *Ceiba*. *Adansonia* has an indehiscent capsule containing a sour, dry flesh that is dispersed by large mammals, whilst *Durio* seeds are surrounded by a fleshy aril, the odor of which attracts large mammals, e.g., elephants and monkeys, which may also act as dispersal agents. In the neotropics, parrots readily damage fruit capsules to retrieve the oily seeds, and this can be a problem if Bombacaceae species are being grown for their seeds.

Economically, the most important species is *Ochroma pyramidale*, which is the source of commercial balsa wood. However, other genera (e.g., *Bombax*) may also be used where light, low-quality timbers are needed. *A. digitata* is an important multipurpose African species, with a complex mythology surrounding it. Uses of *Adansonia* include fruit pulp as a drink, young leaves as a vegetable, seeds as fruits and sources of oil and tartaric acid and bark for rope and cloth. *Pachira fendleri* (synonym: *Bombacopsis quinata*) is used as a living fence in Central America and *Ceiba pentandra* is the commercial source of kapok. *Durio zibethinus* is an important fruit tree in Southeast Asia, where the fruit is said to 'smell like hell but taste of heaven.'

See also: **Tropical Forests**: Tropical Dry Forests; Tropical Moist Forests.

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Combretaceae

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The Combretaceae, based on morphological and molecular data, is a monophyletic family comprising 19 genera (approximately 510 species) of subtropical and tropical trees (to 50 m), shrubs, or lianas (**Table 1**). In general, forests have a predominance of trees and lianas whilst in grasslands shrubby species are more common. Shrubby species may be suffructices, the aerial shoots of which are frequently grazed or burned, making the plants appear annual. The two most important genera are *Terminalia* and *Combretum*. *Terminalia* species are important constituents of primary and secondary forests; for example, in Malaysia the genus is common in evergreen and semideciduous rainforest, and swamp and riverine forests, whilst *T. catappa* (native to tropical Asia and Pacific region) is a common constituent of littoral forests, sandy beaches, and eroding rocky shores, often as street or garden trees rather than for commercial forestry. *Combretum* species are commonly lianas, often found in riverine habitats and on the margins of primary and secondary forests. The species of the two closely related genera (*Laguncularia*, *Lumnitzera*) are mangrove species, whilst species of the more distantly related genus *Conocarpus* are mangrove associates. For example, the adaptations of *Laguncularia racemosa* to salt-water flooding include salt glands, vivipary, and pneumatophores.

Table 1 Distribution of genera in the family Combretaceae

Genus	*Approx. species number*	*Distribution*
Subfamily Strephonematoideae		
Strephonema	6	West tropical Africa
Subfamily Combretoideae		
Anogeissus	8	Tropical Africa and Asia
Buchenavia	20	West Indies, tropical America
Bucida	8	Tropical and subtropical America, West Indies
Calopyxis	23	Madagascar
Combretum	250	Tropics and subtropics (excluding Australia)
Conocarpus	2	Tropical America and Africa, Arabia
Dansiea		Australia
Getonia	1	Indo-Malaysia
Guiera	1	North Tropical Africa
Laguncularia	2	Tropical America, West Africa
Lumnitzera	2	East tropical Africa to Pacific
Macropteranthes	3	Australia
Meiostemon	3	South-east and tropical Africa, Madagascar
Pteleopsis	9	Tropical Africa
Quisqualis	16	Old-world tropics
Terminalia	150	Tropics worldwide
Terminaliopsis	2	Madagascar
Thiloa	3	North South America

The Combretaceae are part of the Myrtales (together with Vochysiaceae, Myrtaceae, Melastomataceae, Memecylaceae, Lythraceae, and Onagraceae), a monophyletic order, of uncertain position within the Rosids, based on morphology, embryology, anatomy, and DNA sequence data. The family Combretaceae is distinguished from the other families in the Myrtales by the occurrence of characteristic hairs, unilocular, inferior ovaries with apical placentation and flattened, ribbed, or winged drupes with large fibrous seeds. However, the relationships of the Combretaceae within the Myrtales are uncertain. Traditionally, the occurrence of combretaceous hairs in some Myrtaceae has suggested a close relationship of the Combretaceae to this family, although the Combretaceae may be closely related to the Lythraceae or Onagraceae.

The flowers of Combretaceae are often clustered in globular or spicate inflorescences, and typically produce nectar to attract insects, birds, and small mammals. For example, the long tubes of *Quisqualis* flowers presumably make pollination possible only by long-tongued insects. In the majority of species, flowers are hermaphrodite and outcrossing is promoted by protogyny. However, other mating systems are found in the family; for example, *Conocarpus erectus* is dioecious, *Laguncularia racemosa* has populations of male and hermaphrodite individuals and *Terminalia* species have male and hermaphrodite flowers on the same individual.

Combretaceae fruits of savanna and grassland species are often winged and adapted for wind dispersal, whilst forest species often have wingless fruits which are either fleshy and animal-dispersed or spongy and water-dispersed. Mangrove species (e.g., *Laguncularia*) have viviparous fruits that germinate on the parent plant. Combretaceae fruits can be