mammals (e.g., squirrels and monkeys) and fish may also be important dispersers.

Economic Uses

Historically, the Lauraceae is a very important economic family, especially the genus *Cinnamomum*, as a source of spices, e.g., cinnamon (*C. verum*), cassia bark (*C. cassia*) and laurel (*Laurus nobilis*), perfume oils, e.g., rosewood oil (*Aniba roseodora*) and sassafras oil (*Ocotea odorifera*), and pharmaceuticals, e.g., camphor (*C. camphora*). However, the most internationally important product produced today is the avocado fruit (*Persea americana*). Lauraceae wood is widely used locally, although a few are internationally important as high-quality timbers for furniture making or for resistance to salt water, e.g., greenheart (*Chlorocardium rodiaei*), Borneo ironwood (*Eusideroxylon zwageri*), and Queensland walnut (*Endiandra palmerstonii*). Some species (e.g., *Ocotea bullata*), once internationally important, are now protected because of past overexploitation.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Medicinal, Food and Aromatic Plants**: Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Tree Physiology**: Physiology of Sexual Reproduction in Trees. **Tropical Forests**: Tropical Moist Forests; Tropical Montane Forests.

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Lecythidaceae

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Introduction

The Lecythidaceae is a pantropical family of trees found in the tropics of Central and South America, southeast Asia, and Africa, including Madagascar (**Table 1**). The family is divided into five subfamilies: (1) the Planchonioideae, with six genera, the best known of which is *Barringtonia*, and 59 species in tropical Asia, Malaysia, northern Australia, the Pacific Islands, and Madagascar; (2) the Foetidioideae, with a single genus, *Foetidia*, and 17 species in Madagascar, Mauritius, and East Africa; (3) the Napoleonaeoideae, with two genera, *Crateranthus* and *Naopoleonaea*, and 11 species in West Africa; (4) the Scytopetaloideae, with a single species, *Asteranthos brasiliensis*, in the Negro and Orinoco river basins of Brazil and Venezuela and six genera and as many as 21 species in Africa; and (5) the Lecythidoideae of the western hemisphere. This article focuses on the New World species of Lecythidaceae.

New World Lecythidaceae range from Veracruz, Mexico (*Eschweilera mexicana*) to Paraguay (*Cariniana estrellensis*). The Caribbean harbors only *Grias cauliflora*, a species found in Jamaica, Central America, and northwestern South America. Several species of *Eschweilera* occur on Trinidad and Tobago, but these islands are South American, both geologically and in their floristic affinities.

Neotropical Lecythidaceae are best known for the Brazil nut of commerce (*Bertholletia excelsa*); for the cannon-ball tree (*Couroupita guianensis*), which is planted as a botanical curiosity in tropical and subtropical botanical gardens; and because species of the family are often ecological dominants in Amazonian forests.

Taxonomy and Genetics

In tropical America, there are 10 genera and 202 known species of Lecythidoideae and a single species, *Asteranthos brasiliensis*, of the African centered Syctopetaloideae. The largest genus is *Eschweilera* with 85 species followed by *Gustavia* (41), *Lecythis* (26), *Couratari* (19), *Cariniana* (15), *Grias* (7), *Corythophora* (4), and *Couroupita* (3). *Allantoma lineata*, *Asteranthos brasiliensis*, and *Bertholletia excelsa* belong to monotypic genera.

Molecular studies have demonstrated that the Lecythidaceae are monophyletic if members of the

Table 1 Subfamilies and genera of Lecythidaceae according to Morton *et al.* (1998)

Subfamily	*Region*	*Genera*	*Number of species*
FOETIDIOIDEAE	Madagascar, Mauritius, and east African tropics	*Foetidia*	17
LECYTHIDOIDEAE	New World tropics	*Allantoma*	1
		Bertholletia	1
		Cariniana	16
		Corythophora	3
		Couratari	19
		Couroupita	3
		Eschweilera	85
		Grias	7
		Gustavia	41
		Lecythis	26
NAPOLEONAEOIDEAE	African tropics	*Crateranthus*	3
		Napoleonaea	8
PLANCHONIOIDEAE	African and Asian tropics	*Abdulmajidia*	2
		Barringtonia	41
		Petersianthus	2
		Chydenanthus	2
		Careya	4
		Planchonia	8
SCYTOPETALOIDEAE	African tropics and *Asteranthos* in Amazonia	*Asteranthos*	1
		Brazzeia	3
		Oubanguia	3
		Pierrina	1
		Rhaptopetalum	10
		Scytopetalum	3

Scytopetalaceae are included. The relationship of *Asteranthos brasiliensis* with the Scytopetalaceae is supported by similarities in embryology, the presence in both of ruminate endosperm, and molecular affinities.

Ongoing molecular studies of neotropical Lecythidaceae indicate that not all of the genera are monophyletic. *Cariniana*, *Eschweilera*, and *Lecythis*, for example, include several clades that may have to be segregated as separate genera. Other genera, for example *Corythophora, Couratari*, *Couroupita*, *Grias*, and *Gustavia*, form natural groups as they are currently defined.

Ecology

New World Lecythidaceae are often dominant in lowland forests on well-drained soils between 19° N and 25° S latitudes. They rank as the first or second most important family of trees in frequency, density, and dominance in the vicinity of Belém, Brazil; the third most important at La Fumée Mountain, French Guiana; and one of the most important in central Amazonian Brazil.

A 100-ha plot established for the study of Lecythidaceae as part of the Biological Dynamics of Forest Fragments Project in central Amazonian Brazil about 80 km north of Manaus illustrates the ecological importance of Lecythidaceae in Amazonian forests. In this plot, there are 7791 trees of Lecythidaceae equal to or greater than 10 cm in diameter at 1.37 m (dbh, diameter at breast height). Among these trees are 38 different species, or nearly 19% of all of the species of Lecythidaceae known from the Neotropics. In each hectare, there are 45 to 149 individuals and 11 to 24 species. In this forest, where there are about 285 species of trees in all families in this size class per hectare, the Brazil nut family accounts for 12% of the individuals and 6% of the species of trees.

Species of the Brazil nut family diminish in importance at elevations above 1000 m, in periodically flooded forests, and in extremely dry habitats such as the *llanos* of Colombia and Venezuela and the *caatinga* of northeastern Brazil.

Nearly all neotropical Lecythidaceae are trees of either the understory, canopy, or emergent layers. The tallest, for example the forest-dwelling *Cariniana micrantha* and *Couratari stellata*, may reach 55–60 m in height. These genera, both dispersed by the wind, possess species of smaller stature when they are found in more open habitats; for example, *Couratari pyramidata* of the *cerrado* of central Brazil. The smallest is *Eschweilera nana*, a species that often possesses an underground trunk adapting it to survive the frequent fires of the *cerrado*. Individuals of *E. nana* may only reach several meters in height.

Trees of *Bertholletia excelsa* in the 140–150 cm dbh size class have been estimated by radiocarbon dating to be only 270 years old. One of the oldest known trees from the Neotropics is an individual of *Cariniana micrantha* radiocarbon dated at 1400 years old.

Species of Lecythidaceae are not common in secondary vegetation because they are extremely vulnerable to fire. If a forest is cut down and not subjected to fire, many Lecythidaceae will sprout from the cut stumps and flower and set fruit from the new branches. However, if fire follows cutting most Lecythidaceae are killed; hence old slash-and-burn fields throughout the Neotropics harbor few species and individuals of Lecythidaceae. Species of Lecythidaceae are generally indicators of undisturbed habitats.

Pollination Biology

The Brazil nut family provides examples of plant–animal coevolution. The flowers, fruits, and seeds are morphologically and anatomically adapted to the animals that pollinate their flowers and the animals, wind, and water that disperse their seeds.

Adaptation of Lecythidaceae for pollination has taken place, for the most part, in the male part of the flower. There are two types of flowers, radially and bilaterally symmetrical and three different rewards offered to pollinators – fertile pollen, sterile pollen, and nectar (**Figure 1**). Radially symmetrical flowers, such as those of *Gustavia superba* (**Figure 2**), offer only fertile pollen as a reward; consequently the pollinator reward and the pollen that effects

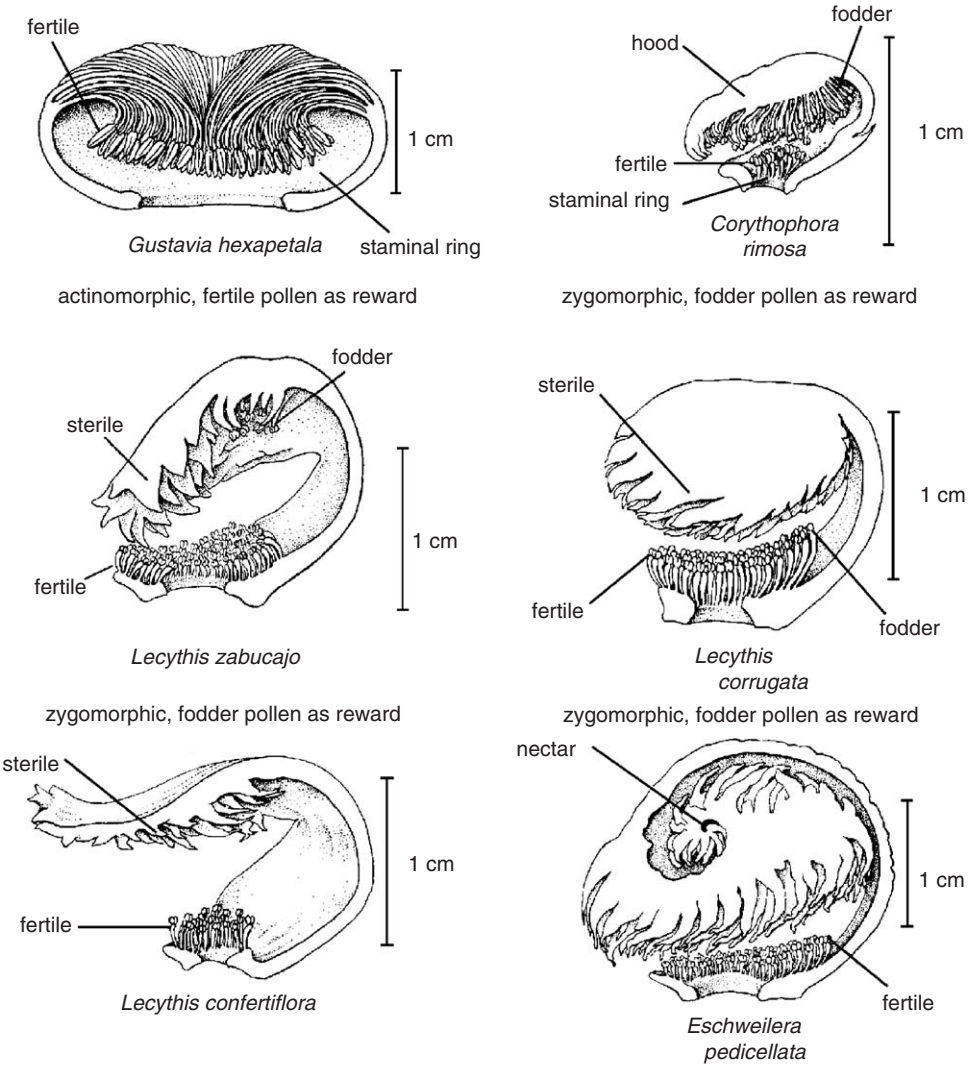

Figure 1 Examples of flower symmetry and pollinator rewards of Neotropical Lecythidaceae. Adapted with permission from Mori SA (1989) Diversity of Lecythidaceae in the Guianas. In: Holm-Nielsen LB, Nielsen IC, and Balslex H (eds) *Tropical Forests*, pp. 319–332. London: Academic Press. Illustration prepared by Bobbi Angell.

Figure 2 Radially symmetrical flowers of *Gustavia superba*. The pollinator reward in this species is nondifferentiated pollen. Photograph © SA Mori.

Figure 3 Bilaterally symmetrical flowers of *Lecythis pisonis*. The pollinator reward in this species is fodder pollen. Photograph © CA Gracie.

fertilization are morphologically and physiologically identical. Female bees visit the flower without restriction, collect pollen that is subsequently eaten by their larvae, and pollen is haphazardly deposited on their bodies. When the bees move to a flower of another tree, the pollen is deposited onto the stigma of that flower and eventually effects fertilization.

In contrast, species of Lecythidaceae with bilaterally symmetrical flowers offer two types of rewards, differentiated pollen and nectar. *Lecythis pisonis* (**Figure 3**), the *sapucaia* of the Amazon and the coastal forests of eastern Brazil, is a bilaterally symmetrically flowered species with both sterile and fertile pollen in the same flower. The fertile pollen is located in the staminal ring and sterile pollen is found in the staminal hood. Large, female bees, often of the genus *Xylocopa*, land on the staminal hood to collect sterile pollen from the hood. While collecting this pollen, the bee is dusted on the head and back with fertile pollen from the staminal ring. Experiments have demonstrated that the pollen purposely collected by the bee never germinates while that accidentally deposited onto the head and back always does. It is the latter pollen that is brushed off the head and back of the bees onto the stigmas of subsequent flowers visited that effects fertilization.

Eschweilera pedicellata (**Figure 1**) is a bilaterally symmetrically flowered species that offers nectar as a reward to the pollinators which are usually robust male and female euglossine bees. Both sexes visit flowers of this kind of Lecythidaceae because the nectar reward is utilized as an energy source for adult bees. In this type of flower, the staminal hood usually closes the flower; moreover the hood is internally coiled and nectar is produced at the apex of the coil (**Figure 1**). The nectar is secreted from vestigial stamens that no longer bear anthers.

Although the most important pollinators of Lecythidaceae are bees, at least two species (*Lecythis barnebyi* and *L. poiteaui*) and perhaps a third (*L. brancoensis*) are pollinated by bats, and some species of *Grias* are suspected to be pollinated by beetles. The bat-pollinated species have nocturnal flowers, display their flowers at the periphery and above the canopy, and emit an aroma dominated by sulfur-bearing compounds that is similar to rotting cabbage, all features of flowers visited by bats. The putative beetle-pollinated species of *Grias* emit aromas dominated by fatty acids similar to those produced by other beetle-pollinated plants.

Dispersal Biology

Neotropical species of the Brazil nut family have fruits that either do not open (indehiscent) or open via a lid at maturity (dehiscent). The seeds of different species are dispersed by animals, the wind, or water.

Several examples will give an idea of the wide variation in dispersal systems found in the New World Lecythidaceae. Species of *Gustavia* and *Grias* possess indehiscent fruits with the seeds often surrounded by a pulp eaten by animals, including humans. For example, *Grias neuberthii* has a fleshy mesocarp surrounding a fibrous endocarp, and, in that regard, is similar in structure, but not shape, to a peach. The fruits are sold in western Amazonian markets for their edible mesocarp. The endocarp, however, facilitates flotation of the fruit once the mesocarp has been eaten by animals, and it appears

that this species may be secondarily dispersed by water currents.

In *Couroupita guianensis* (**Figure 4**), the mature fruits fall from trunk and crack open upon impact with the ground to expose a bluish-green, foul-smelling pulp, in which are embedded numerous, small seeds. In the Brazilian Amazon, peccaries have been reported to eat the pulp and swallow the seeds and it is presumed that the seeds pass through the peccaries' digestive tracts and subsequently germinate some distance from the mother trees, thereby effecting seed dispersal. The pulp is often fed to domestic pigs and poultry and seeds have been reported to germinate in the feces of these animals. This is the only genus of Lecythidaceae known to have numerous, long hairs arising from the seed coat. It is hypothesized that these hairs protect the seeds from digestive juices as they pass through the peccaries' digestive tracts.

Bertholletia excelsa, the Brazil nut of commerce, has a very specialized dispersal system. At maturity the fruits drop to the ground with the seeds trapped inside because the size of the fruit opening is smaller in diameter than the size of the seeds (**Figure 5**). Rodents, especially agoutis (*Dasyprocta* spp.) gnaw through the woody fruit walls by enlarging the small opening of the lid, chew through the thick and bony seed coat to consume the embryos of some of the seeds, and cache other seeds for future consumption. Some of the cached seeds are forgotten, and it is these that germinate 12–18 months later to form the next generation of trees. The fruits are so rot resistant that after the seeds have been removed by animals, they accumulate water and serve as breeding sites for an assemblage of anuran and insect species.

The largest fruited species of Lecythidaceae is *Lecythis pisonis* (**Figure 5**). After fertilization by carpenter bees (*Xylocopa* spp.), the fruits reach the size of a human head after nearly a year of development. This species, distributed in the Atlantic forests of eastern Brazil and in eastern Amazonia, opens via a lid that drops when the seeds are mature. The fruit opens while still in the tree crown and the seeds remain attached to the inner fruit wall by a funicle, which, in turn, is surrounded by a fleshy, white outgrowth called an aril. Bats, including *Phyllostomus hastatus*, remove the seeds with the attached aril on the same night that the fruits open. After the aril

Figure 4 The indehiscent fruits of *Couroupita guianensis*. Peccaries eat the pulp of the fruits of this species. Photograph © CA Gracie.

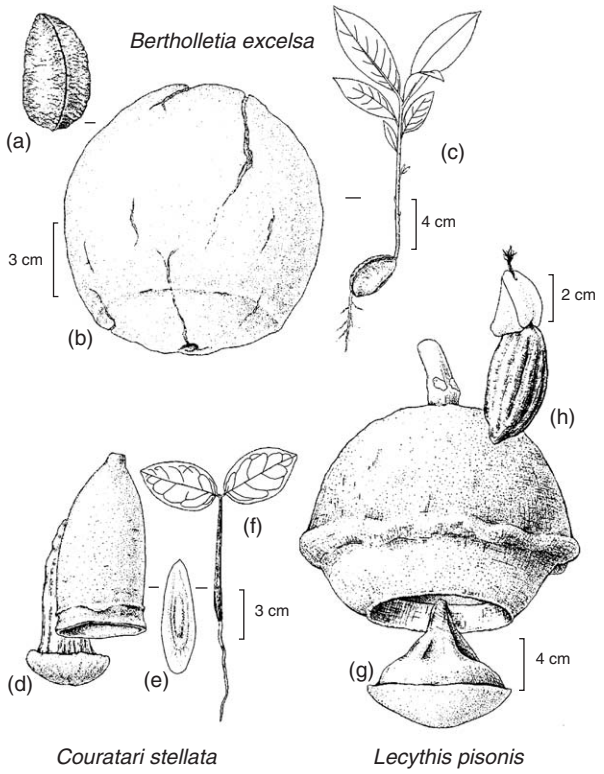

Figure 5 Fruits, seeds, and seedlings of *Bertholletia excelsa* and *Couratari stellata* and fruit and seed of *Lecythis pisonis*. Adapted with permission from Mori SA (1989) Diversity of Lecythidaceae in the Guianas. In: Holm-Nielsen LB, Nielsen IC, and Balslex H (eds) *Tropical Forests*, pp. 319–332. London: Academic Press. Illustration prepared by Bobbi Angell.

is eaten, the bats drop the intact seeds either in flight or under their roosts.

All species of *Cariniana* and *Couratari* (**Figure 5**) are dispersed by the wind. The woody, cylindric fruits open to release seeds that are either winged at one end in *Cariniana* or winged all around the seed in *Couratari*. Species of these genera are either very tall forest trees or smaller trees of open habitats; consequently seeds falling from the fruits are exposed to the wind. The seeds of these genera are very light and possess embryos with leaflike cotyledons that enable the seedlings to begin photosynthesis immediately upon germination of the seeds, thereby compensating for the lack of nutrients in the seeds.

Water dispersal, although relatively uncommon, takes place in two different ways. In some species, the seeds fall from the fruit, float on the water because of the corky seed coats, and are carried away by currents. A common Amazonian tree found in periodically inundated forest, *Eschweilera tenuifolia* (**Figure 6**), is dispersed in this fashion. In *Lecythis rorida*, the entire fruit falls into the water and floats away with the seeds inside. The morphologically most similar species to *L. rorida* is *L. chartacea*, a species that normally grows in nonflooded forest away from the river. *Lecythis chartacea* has fruits that open at maturity to reveal seeds subtended by an aril that is most likely sought after by animals that, in turn, disperse the seeds. The seeds of *L. rorida* lack an aril, which would serve no purpose in water dispersal.

The woody fruits of Lecythidaceae are viewed as a way to protect the seeds from predispersal predation. The thick and woody fruit walls of *Cariniana micrantha*, however, do not deter brown capuchin monkeys (*Cebus* spp.) from opening the lids just before the fruits would naturally open and eating the seeds. The monkeys tear the fruits from the branches, knock them against the larger limbs and trunk, consume seeds, and then drop the fruits with a few remnant seeds to the ground. In one year, 99.5% of the entire seed production of a tree in central Brazilian Amazon was destroyed by brown capuchins.

Figure 6 Trees of *Eschweilera tenuifolia* growing in periodically inundated forest on the Rio Negro, Brazil. The seeds of this species drop into the water and are carried away by currents. Photograph © SA Mori.

Silviculture

The methodology for growing Brazil nuts in large plantations has been developed by the Brazilian agricultural research institution, EMBRAPA, in Belém and a great deal of literature exists about starting plantations from seeds and about grafting high-yield clones onto established root stocks. Nevertheless, most of the Brazil nuts reaching the international market are still gathered from wild trees, perhaps because native pollinators are not as abundant in the disturbed habitats of plantations as they are in more mature forests.

Utilization

The Brazil nut is the economically most important species of Lecythidaceae. Brazil nuts are gathered only from *Bertholletia excelsa*, a species of nonflooded forest native to Guyana, Surinam, Amazonian Colombia, Venezuela, Peru, Bolivia, and Brazil. Brazil nut trees are cultivated as a curiosity in tropical botanical gardens and sporadically in experimental plantations outside of the original range of the species. The edible seeds of the Brazil nut, along with the latex of rubber (*Hevea brasiliensis*) are often cited as the most important products of extractive reserves in Amazonia and these products are heralded as a way to conserve tropical diversity while at the same time sustaining human populations.

Brazil nut trees flower during the dry season into the wet season and are only found naturally in regions with a 3–5-month long dry season. Toward the end of the rainy season, the leaves of Brazil nut trees begin to fall. As the dry season approaches, new growth flushes of leaves and inflorescences are produced at the apex of the current growth. The flowers open shortly below daybreak and the petals and attached androecium fall in the afternoon of the day they open. Robust nonsocial or semisocial bees of *Bombus*, *Centris*, *Epicharis*, *Eulaema*, and *Xylocopa* are the pollinators. Both sexes of these bees visit the flowers for nectar. Although the Brazil nut is mostly self-incompatible, a small amount of self-compatibility does occur; therefore, the bee pollinators are usually essential for carrying pollen from one tree to the next as most of the fruit set results from their visits.

Brazil nuts are an economically important crop because the seeds are retained within the fruit when

the fruit falls to the ground. The fruits, which weigh from 0.5 to 2.5 kg and contain 10 to 25 seeds, are easily harvested from the ground. A few other species, such as *Lecythis pisonis* (**Figure 5**), produce seeds equally as good to eat and as nutritious as the Brazil nut. However, they appear only sporadically in local markets because the fruits open and the seeds are carried away by bats before they can be harvested. These species are generally harvested by climbing the tree and cutting the entire fruit shortly before the fruit would naturally dehisce, a system that does not lend itself to the easy gathering of massive numbers of seeds by human collectors. Two closely related species, *L. minor* and *L. ollaria*, also yield edible seeds, but the seeds sometimes accumulate selenium, and, if too many of them are eaten, hair and even finger nails may be temporarily lost as the possible result of mild selenium poisoning.

A few species of *Gustavia* and *Grias* are grown in backyard gardens for the pulp surrounding the seeds that can be eaten raw or cooked. The best known are *Gustavia speciosa*, known as *chupa* in Colombia and *chopé* in Peru, and *Grias neuberthii*, the *sacha mangua* of Peru.

For the most part, the Brazil nut family is not known for high-quality timber. However, species of *Cariniana* have long straight boles and excellent timbers. The best known are *albarco* (*C. pyriformis*) of northwestern South America and the *jequitibás* (*C. estrellensis* of eastern Brazil and *C. legalis* of southwestern Amazonia and eastern Brazil). Brazil nut trees also produce high-grade timber, but they are protected by law because of their greater value as producers of edible seeds.

Only minor medicinal properties have been reported for the family. The most significant chemical use of Lecythidaceae is as an arrow poison derived from *Cariniana domestica*. The poison, extracted from the bark, kills small animals by disrupting their blood-clotting mechanisms thereby causing excessive bleeding when the animals are hit by poisoned arrows.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems. **Medicinal, Food and Aromatic Plants**: Edible Products from the Forest. **Silviculture**: Managing for Tropical Non-timber Forest Products; Treatments in Tropical Silviculture. **Tropical Forests**: Tropical Moist Forests; Tropical Montane Forests.

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Monsoon Forests (Southern and Southeast Asia)

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Introduction

Tropical forests are of two major types – rainforest and monsoon or seasonal forest, close to the equatorial region. Monsoon forests are also known as mixed forests, along the borders or part of tropical rainforests in southern and southeastern parts of Asia. The forest type is characterized by a dry period of 3–5 months, when plant growth is limited by water stress, whereas in typical tropical rainforests this phenomenon does not exist. In general, monsoon forests are more nanic in stature than typical rainforests and many tree species in the forest formation remain leafless during the dry season; this is otherwise known as deciduous species. Because of this, more sunlight reaches the understory, promoting the growth of rich heliophilous ground flora, in addition to several lianas. However, woody epiphytes are comparatively few in number in monsoon forests, compared to rainforests. The monsoon vegetation of South and Southeast Asia is subject to much degradation, especially due to fire in the drought season, as well as shifting cultivation and several other factors. In order to conserve the forest type and its biodiversity, protected areas have been established in almost all countries in the region.

Definition and Terminology

In the early twentieth century, based on climatic and vegetational parameters, monsoon forests were described as more or less deciduous or leafless during the dry season and tropophilous in nature, i.e., alternating in hygrophilous and xerophilous characters, regulated by the monsoon climate. In typical rainforest areas of the Asian continent there is evenly distributed and heavy rainfall throughout the year, whereas in certain countries within the continent (Cambodia, India, Myanmar, Sri Lanka, Thailand and Vietnam), rainfall is seasonal with an annual dry period of about 3–5 months. In those countries, monsoon forests are quite common, apart from the evergreen and semievergreen rainforests. Due to the dry period and consequent deciduous nature of many tree species constituting the upper story of the vegetation, the subcanopy flora is fairly rich with woody climbers, shrubs, and herbaceous ground flora. At the same time, because of the dry climate and the deciduous nature of the forest formation, monsoon forests are poor in biomass content as compared to rainforests. Monsoon forests are also subjected to seasonal fire, promoting the development of savannas or grasslands, containing thorny or unarmed, stunted trees and shrubs. Because of the complex nature of monsoon forests, they are also designated as mixed forests, and vegetation types like moist and dry deciduous forests, savannas, scrubs, and thorn forests all belong to this category. Often, tropical rainforests merge or penetrate into monsoon forest formations, especially along water courses and wet habitats and the continuity of the two forest types is also restricted by repeated fire, resulting in the formation of savannas, which separate the two forest types. Such extensions of rainforests into monsoon forests are called gallery forests. **Figure 1** shows different categories of tropical forests in South

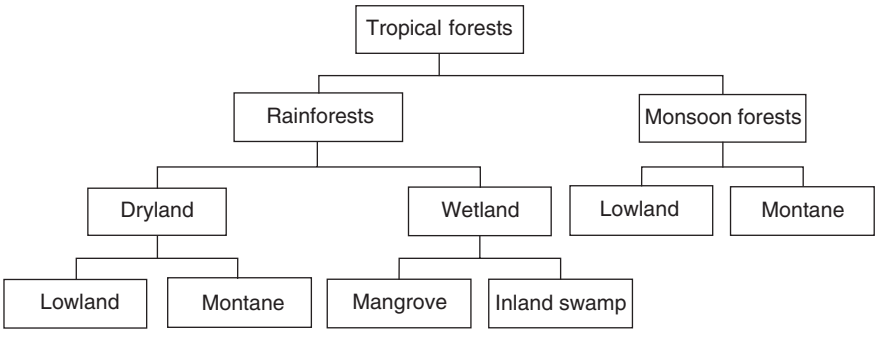

Figure 1 Categories of tropical forests in South and Southeast Asia.