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Myristicaceae

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Introduction

The Myristicaceae is a pantropical family of trees found in Central and South America, Africa, Madagascar, India, and Asia. The family consists of 20 genera and at least 500 species. Floristic and ecological studies have revealed that the Myristicaceae rank among the top five to ten most common and important tree families throughout the majority of the lowland moist tropical forests of the world, where the family has significant ecological importance. Fruit of the Myristicaceae, particularly the lipid-rich aril surrounding the seed in some species, are important as food for birds and mammals of tropical forests. Numerous species are valued by humans as sources of food, medicine, narcotics, and timber, including *Myristica fragrans*, the source of nutmeg and mace, the spices of commerce.

Throughout the geographical range of Myristicaceae, aromatic leaves, often stellate pubescence, a unique arborescent architecture (**Figure 1**), and sap the color of blood (**Figure 2**) are characteristics that strongly enhance recognition of this family in the field. Species of this family are usually dioecious. Flowers are tiny and found in paniculate inflorescences, with filaments of stamens fused into a column, giving rise to either free or fused anthers (**Figures 3** and **4**). Fruits are one-seeded, dehiscent or indehiscent, and are notable for the typically red arillate covering around the seed.

Taxonomy and Genetics

There are about 500 species of Myristicaceae in 20 genera, restricted to individual continents (**Table 1**). Nutmeg trees first appeared in the earliest botanical works dealing with the East Asian region, and in 1742 Linnaeus established the genus *Myristica*, which remained a broad concept and the only genus in the family until 1856. Warburg produced the first

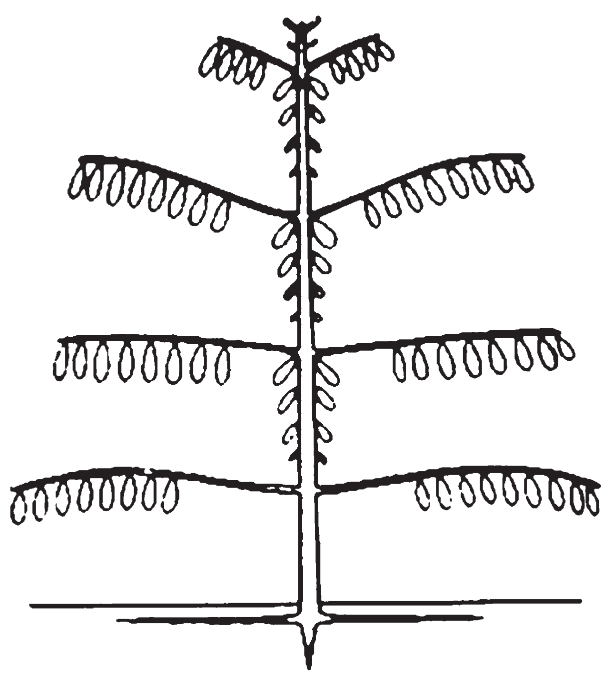

Figure 1 Massart model of tree architecture typical of the Myristicaceae. Modified with permission from Hallé F, Oldeman RAA, and Tomlinson PB (1978) *Tropical Trees and Forests: An Architectural Analysis*. Berlin: Springer-Verlag.

Figure 2 Blood-red sap exuding from trunk of *Compsoneura excelsa* in the Osa Peninsula of Costa Rica. Courtesy of John Janovec.

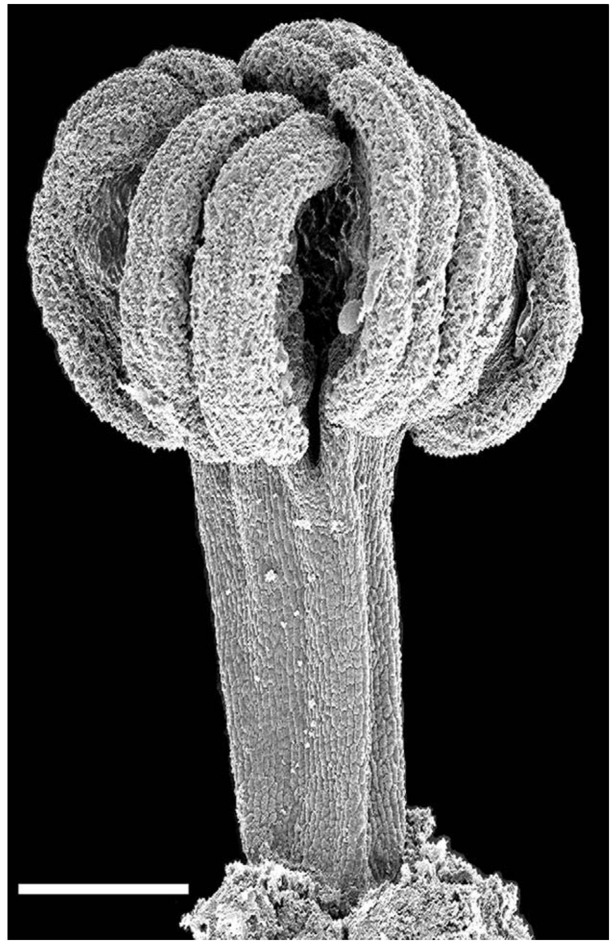

Figure 3 Androecium of *Compsoneura capitellata* from the Peruvian Amazon, showing an elongated column of fused filaments giving rise to anthers. Scale bar = 250 μm. Courtesy of John Janovec.

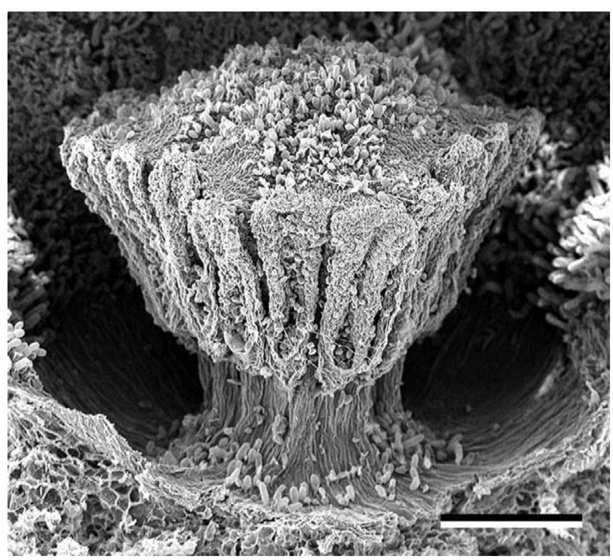

Figure 4 Androecium of *Compsoneura trianae* of western Colombia, showing a reduced column of fused filaments which give rise to a group of anthers fused to central connective tissue. Scale bar = 250 μm. Courtesy of John Janovec.

and last major global treatment and the first phylogenetic tree of the Myristicaceae, and divided the sections of *Myristica* into many of the genera currently accepted. All modern authors include the Myristicaceae within an ancestral lineage of dicotyledonous flowering plants which includes families such as the Magnoliaceae, Canellaceae, Winteraceae, and Annonaceae. Analyses of nucleotide sequences from the chloroplast gene *rbc*L have generated support for this placement. Attempts have been made by Sauquet *et al*. to reconstruct the intergeneric phylogeny within the Myristicaceae. Basic studies of species diversity are needed within each genus to better understand relationships, character evolution, and classification of the family.

Various authors have overviewed the geohistorical setting of Central and South America, so far as it is known. Africa and South America began to separate during the Jurassic approximately 140 million years

Table 1 Genera and species of Myristicaceae

Region	*Genus*	*Number of species*
Tropical America	*Bicuiba*	1
	Compsoneura	25, in progress
	Iryanthera	24+
	Osteophloeum	2
	Otoba	8
	Virola	45+
Indo-Asia	*Endocomia*	4
	Gymnacranthera	7
	Horsfieldia	100
	Knema	90
	Myristica	170
	Paramyristica	1
Africa and Madagascar	*Cephalosphaera*	1
	Coelocaryon	4
	Pycnanthus	7
	Scyphocephalium	4
	Staudtia	2

before present (BP). By about 90 million years BP, the two continents were completely separated and life on each took its own course. The center of origin for the Myristicaceae may well be South America, or in a geohistorical context, West Gondwanaland of the early Tertiary or late Cretaceous (about 100–70 million years BP). With this in mind, and since the family is present on all Gondwanaland-based continents that currently have tropical forest (South America, Africa, Madagascar, India, Southeast Asia), it can be hypothesized that the Myristicaceae had diversified before the separation of South America and Africa.

From the point of complete separation (about 90 million years BP), the neotropical Myristicaceae evolved on the South American land mass independently from members of the family which currently occur in Africa or elsewhere on the Gondwanan geoplex. It is truly hard to tell what pathways were taken during such a long period of time. However, the genera of the Myristicaceae have evolved in three major regions (Americas, Africa–Madagascar, and India–Asia).

Ecology

Floristic and ecological studies have revealed that the Myristicaceae rank among the ten and often five most common and thus important tree families in lowland moist tropical forests of the world. In the American tropics, the Myristicaceae is one of the eleven families – along with Fabaceae, Lauraceae, Annonaceae, Rubiaceae, Moraceae, Sapotaceae, Meliaceae, Arecaceae, Euphorbiaceae, and Bignoniaceae – that contribute about half of the species richness of any lowland forests and this pattern is present in some samples of Africa and Asia as well.

The center of diversity of the Myristicaceae in the Neotropics is the Amazon basin, represented by *Virola* with a few species reaching Central America. The genus *Otoba* has its center of diversity and endemism in the Chocó region of northwestern South America. *Otoba* has five species in this area and additional species in Panama and another widespread in Amazonia. *Myristica* has its center of diversity in the Malayan peninsula and New Guinea, and *Knema* is dominant in Borneo. In many forests of South America the Myristicaceae are very conspicuous and form an important element of its rich flora. Some pacific tropical forests in Colombia are dominated by *Otoba gracilipes*, *Virola reidii*, and *V. sebifera*. In an inventory of various types of Amazonia terra firme forests in Peru, *Iryanthera juruensis, I. macrophylla, I. paraensis, I. polyneura, I. tricornis, I. ulei, Virola calophylla*, and *V. pavonis* were the most common species. The importance index values in this study showed that the Myristicaceae was largely higher than the other tree families with a preference of well-drained terra firme soils. More recently, Myristicaceae was found to have exceptional numbers of common species in Manu National Park (Peru) and Yasuni National Park (Ecuador).

Although most species of the family in neotropical forests occur on rich soils, some are restricted to higher-stress habitats. For example, *Virola pavonis* is one of the most important species on the nutrient-poor white sand soils around Loreto, Peru. *Virola surinamensis* is common to swampy areas of lowland Amazon forests where it forms associations with the palm *Maurita flexuosa*. Aerial or stilt roots are one of the adaptations to anoxic, inundated soil exhibited by this species (**Figure 5**). *Virola steyermarkii* is reported endemic for the montane tepui forests in Venezuelan Guayana.

The family is poorly represented at higher elevations. In an analysis of the floristic composition and diversity of Amazonia and the Guiana Shield, it was found that Myristicaceae occurs in high density in terra firme forests of western Amazonia. This diminished in Central Amazonia, eastern Amazonia, and the Guiana Shield, suggesting an increase in the abundance and diversity of the family from the Guianas toward Western Amazonia. This difference may be due in part to richer soils present at western Amazonia in comparison to other sites where a different suite of poor-soil-tolerant plants dominate: Chrysobalanaceae, Burseraceae, and Lecythidaceae among others. In a study of several 1-ha forest plots in Amazonia and Central America, the

Figure 5 Aerial or stilt roots of *Virola surinamensis* growing in a *Mauritia flexuosa* palm swamp of the Peruvian Amazon. Courtesy of John Janovec.

Figure 6 Fruit of *Compsoneura mexicana* from Belize, showing the two-parted dehiscent orange fruit at maturity and the red aril covering a black-mottled seed. Courtesy of John Janovec.

late Alwyn Gentry found that Yanamono and Mishana forest preserve areas in northern Amazonia of Peru presented a higher representation in Myristicaceae than Central America. In La Selva (Costa Rica) and Barro Colorado Island (BCI, Panama) forest plots, Myristicaceae is not one of the most diverse tree families.

Many xeromorphic features (thick cuticle, a dense tomentum, sunken stomata) are present in Myristicaceae in spite of its present-day humid tropical forest distribution. This may be indicative of a wider ecological amplitude than the current distribution. The presence and type of pubescence are useful for differentiating the genera in the family; this character has been used since the pioneering studies of this family prior to 1900. It has been hypothesized that the hairs function as protection against herbivory and regulate the physiology of the water in the plant.

Most species of Myristicaceae are trees occupying the middle-story of canopy in the forests. For example, *Virola surinamensis* is a large tree, attaining 30 m in height and 1 m in diameter at breast height (dbh), generally with a straight, cylindrical trunk above the buttressed roots. Other species in the family reaching or exceeding the canopy are: *Virola duckei*, *V. pavonis, Otoba glycicarpa*, and *Osteophloeum platyspermum*. Most *Iryanthera* and *Compsonera* species are treelets or medium-sized trees.

One of the most noteworthy features of the Myristicaceae is its branching architecture corresponding to the Massart model (**Figure 1**). This branching pattern may enable the family to better survive the dynamic conditions of tropical forests. This is especially important during younger stages of growth and establishment for efficient use of forest resources, to allow recovery from traumatic events, and for adjustment to environmental changes in the struggle to reach the canopy.

The small, pale flowers common in the family are presumed to be pollinated by small insects. *Myristica fragans* is pollinated by small nocturnal beetles. Both the male and female flowers are strongly scented and pollen is the only reward. *Compsoneura sprucei* (= *C. mexicana*) has been reported to be pollinated by thrips, based on studies in Costa Rica. In the Asian tropics, *Myristica myrmecophylla* has an association with ants that may play a role in pollination.

The principal dispersers of the family are thought to be birds because of the attractive arillate seeds (**Figure 6**). But this assumption has been challenged in recent studies showing that spider monkeys act as principal dispersers of *Virola calophylla* in the southern Peruvian Amazon. In the Old World, rodents occasionally act as dispersers. Observations in Belize suggest that rodents may act as secondary dispersers, which may account for the camoflauge mottling found on seeds of *Compsoneura mexicana* (**Figure 7**), which are difficult to see in the leaf litter on the forest floor.

Figure 7 Black mottled seeds of *Compsoneura mexicana* from Costa Rica. Courtesy of John Janovec.

Silviculture

As a family primarily of trees, many species of Myristicaceae have been studied in experimental plantations. In Brazil, *Virola surinamensis* has been studied with silvicultural methods. However, few of these studies have been adopted by the industry and an unfortunate consequence is that much of the lumber is coming from the forests. In the Peruvian Amazon it is becoming more common to see timber from *cumala*, the vernacular name for species of Myristicaceae. Some of the more valuable species are: *Otoba glycicarpa*, *Virola pavonis*, *V. duckei*, and *Osteophleum platyspermum*. Seeds remain viable for a limited period of time and germinate in damp, shady environments offered only by tropical old growth forest. Seed germination trials conducted using *Compsoneura* and *Virola* seeds from Central America showed that some seeds can take up to 6 months to germinate in a greenhouse setting.

Utilization

Economically, the most important species, *Myristica fragrans*, is Asiatic and is widely cultivated as the source of nutmeg (the ground seed) and mace (the dried aril). This species is also cultivated in areas of Central America and the Caribbean. Some species are used in the timber industry, such as *Virola surinamensis* in Brazil, and *Otoba gracilipes*, *V. reidii*, and *V. sebifera* in Colombia. In the American tropics, species of the Myristicaceae have been valued as sources of food, medicine, and narcotics. Amazonian Indians utilize the dried sap and ground inner bark of numerous Myristicaceae species (*Osteophloeum platyspermum*, *Virola calophylla*, *V. cuspidata*, *V. duckei*, *V. elongata*, *V. pavonis*, *V. sebifera*, and *V. surinamensis*) to make hallucinogenic snuffs used in spiritual ceremonies and as medicine in the treatment of various ailments. In the Venezuelan Guayana region, the wood of *Iryanthera lancifolia* is used for lumber and the reddish sap of *Virola surinamensis* is used to seal wounds. *Virola surinamensis* is also valued as timber, especially in the plywood industry. Some species yield essential oils and fats that have been used in perfumery and in making candles. It has been suggested that nutmeg produces hallucinations when ingested by humans, but this has been criticized as a myth.

See also: **Ecology**: Reproductive Ecology of Forest Trees. **Medicinal, Food and Aromatic Plants**: Medicinal and Aromatic Plants: Ethnobotany and Conservation Status. **Tree Physiology**: Tropical Tree Seed Physiology. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Moist Forests; Tropical Montane Forests.

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Tropical Dry Forests

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Introduction

Tropical dry forests occur in nearly every tropical country. This forest type provides critical habitat for large mammals and migratory birds, and patches of dry forest can support a high proportion of endemic plant and animal species, as well as being highly valued for agricultural and production forestry uses. Consequently, conservation and understanding of these forests need emphasis, yet conservationists and scientists still frequently overlook this ecosystem.

Distribution and Definition

Dry forests comprise 42% of all tropical forests – the largest proportion of any forest type. They can be found as large continuous tracts, particularly in India, Mexico, eastern South America, northern Australia, and Africa, or in smaller, more local areas. Smaller tracts grow in rainshadows of tropical islands, Central America, and western South America (**Figure 1**). Coastal environments support dry forest when elevation is too low to generate rainfall from orographic uplift of ocean air masses.

Tropical dry forests occur in frost-free areas where annual precipitation is 500–2000 mm, mean annual biotemperature is $>17°C$, and potential evapotranspiration exceeds precipitation (**Figure 2**). Rain falls in one or two seasons each year, depending on the latitude of the forest, and forests experience 3–10 dry months (<50 mm rainfall) each year. The most important characteristic is the highly variable length of the dry season, seasonal distribution of rainfall, and amount of rainfall. Perhaps the only real constant from site to site is the occurrence of a dry season. Savannas often grow under the same climatic conditions as dry forests, but sparse tree cover and frequent fire in savannas allow grass to dominate.

Typically, dry forests have a closed canopy, but this may not be the case in the driest parts of their range, or if disturbance is prevalent. Due to their variability in climate and appearance, many names are applied to dry forests. These include: deciduous forest, semideciduous forest, semi-evergreen forest, woodland, and dry seasonal forests. Local names are also used: caatinga in Brazil, miombo in southern Africa, and chaco in parts of South America. Southeast Asia has a specific type of dry forest – deciduous dipterocarp forests – dominated by about six species of Dipterocarpaceae.

As a consequence of prolonged dry seasons, tropical dry forests are less complex than wet or temperate forests (**Table 1**). They have one to three canopy layers and short canopies with relatively low leaf area index (3–7) and leaf biomass (2–7 tonnes ha^{-1}). In mature forest, the stems can still be quite narrow, with common diameters in the range of 3–15 cm, and stem densities can exceed one stem per square meter. Trees are frequently multistemmed. Among dry forests, most structural features vary by two to ten times (**Table 1**), with the upper limits overlapping the lower limits in wetter forests, leading to inconsistencies in the scientific literature when classifying forest types. Climate features such as the amount of rainfall or the length of the rainy season can explain canopy height and biomass, but other structural characteristics,