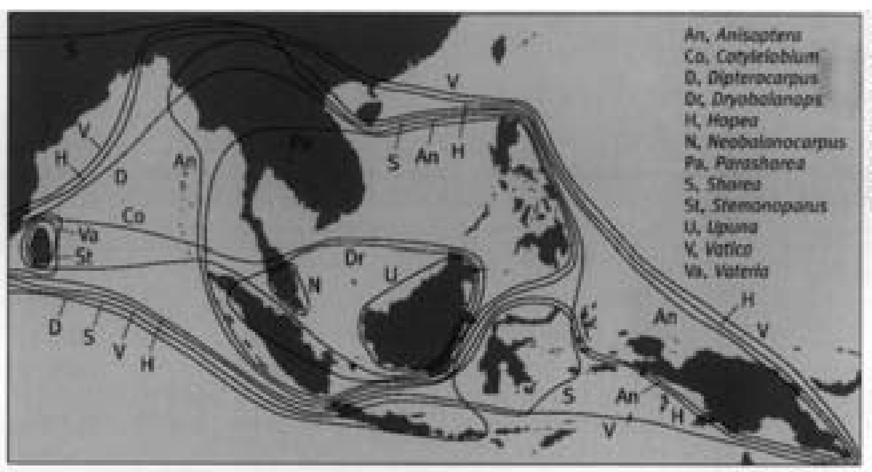
Dipterocarps: Trees That Dominate the Asian Rain Forest

Richard Corlett and Richard Primack

First-time visitors to the rain forests of Indonesia and Malaysia will be amazed to slowly turn around and realize that virtually every giant tree is a member of the dipterocarp family, and yet that they belong to several separate genera and dozens of distinct species. The tree family Dipterocarpaceae (literally "two-winged fruits") plays a dominant role in the ecology and economics of Asian forests in a way that no comparable family plays in other rain forest regions. Dipterocarp trees dominate forests in Borneo, Sumatra, Java, the Malay Peninsula, and the wetter parts of the Philippines, where the majority of the large trees are members of this one family and account for the majority of the biomass. Outside this core everwet area, dipterocarps gradually decline in diversity and abundance. A secondary center of dipterocarp diversity exists in Sri Lanka. In total, there are at least 500 Asian species. Dipterocarp trees also have excellent timber qualities, and they are marketed internationally as luan plywood and as sawn timber under names such as Philippines red mahogany, meranti, keruing, and kapur.

A few species of dipterocarp trees are found in the African tropics and Madagascar, though not in rain forests, and in the highlands of South America, giving testament to the family's origin and spread on the ancient southern supercontinent of Gondwana. The dipterocarps appear to have reached Southeast Asia from Africa via the Indian plate and did not arrive until the middle Eocene (45 million years ago), when a moist corridor between India and Southeast Asia resulted in a major influx of plants with Gondwanan affinities. Despite this relatively late arrival, the dipterocarps underwent a massive evolutionary radiation in Southeast Asia.

Enumerations of research plots in Southeast Asian forests show a conspicuous proliferation of tree species within the individual genera *Shorea, Hopea, Dipterocarpus,* and *Vatica.* In any one forest in the Malay Peninsula, Sumatra, or Borneo, it would be common to find 25 or more species of *Shorea,* and six or more species of the other three genera. Imagine going into a small patch of forest in North America and finding 40 species of oaks and chestnuts. More recently, in



The ranges of dipterocarp genera illustrate that the center of distribution of this tree family lies in Indonesia's Sundaland region Sri Lanka, just off the southern coast of Africa, is a secondary center. Each line encloses the distribution of all species in one genus.

Giant dipterocarp trees, such as this one in Borneo, dominate the forests of Southeast Asia. Photo by Richard Primack geological terms, a few dipterocarp species have managed to disperse from island to island across the narrowing water gap to New Guinea, where they dominate in scattered patches.

This proliferation of closely related tree species is found in a few other Southeast Asian groups as well, such as *Syzygium,* in the myrtle family, and *Diospyros,* in the ebony family. The proliferation of distinctive but closely related tree species growing together in one place is a special feature of the Asian rain forests, not as common in rain forests elsewhere. Scientists are still debating the arguments to explain this local abundance of closely related tree species. One example of this phenomenon in the temperate zone is the numerous species of morphologically distinct oaks (family Fagaceae) found growing together in the dry forests of southeastern United States.

Why should the dipterocarps in particular be so dominant in Asian rain forests? There is no obvious single answer, but certain common features hint at the reasons behind their success. Dipterocarps tend to have smooth, straight trunks rising to great heights without side branches or forks until the canopy is reached. The base of the tree is often buttressed. These growth characteristics emphasize the strength and stability of individual dipterocarp trees. Because of these growth characteristics and the abundant year-round rainfall, the dipterocarp trees often reach heights of 50 meters (150 feet) or more, which is higher than rain forests elsewhere. Also, trees do not typically fall over or get blown over as is seen in many Neotropical trees. Rather, dipterocarps often die standing, gradually losing their branches until only the trunk remains. As a result, the dipterocarp forest tends to be darker and more stable than forests in Africa (where the trees are shorter and are killed by periodic drought) and the Amazon (where trees may have a greater tendency to fall over and create large canopy gaps soon occupied by sun-loving trees and vines). Once dipterocarp trees reach the canopy and emerge from it, they produce a characteristic crown that is shaped like a cauliflower, with clusters of leafy branches evenly spaced around a dome. A tendency toward lower wind speeds in Southeast Asian rain forests than in the other regions may favor this growth habit.

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Looking up at the cauliflower-like branching pattern of dipterocarp trees, Borneo.

Another possible key to the dipterocarps' success in Asian rain forests and the long lives of individual trees is the presence in all plant parts of an oily, aromatic resin that presumably aids the plant in defense against attack by bacteria, fungi, and animals. This resin often accumulates where the bark is bruised and is encountered as hard, crusty, glass-like pieces on the trunk or on the ground. This resin, called *dammar,* is collected by the local people and used in varnishes or as boat caulking. The value of this resin is illustrated by the kapur tree, also known as the Bornean camphor tree *(Dryobalanops aromatica).* Historically, this species has been one of the main commercial sources of camphor, an essential oil of importance for its use in medicine and as a preservative. The crushed leaves have a distinctive camphor or kerosene-like smell.

Dipterocarps also contain bitter-tasting tannins as a further deterrent to attack. Although nondipterocarp trees also have chemical defenses in their foliage, dipterocarp leaves do seem peculiarly inedible, at least to vertebrates. This is illustrated by the colugo, a leaf-eating, gliding mammal that lives in dipterocarp forests and forages widely in the tree canopy for new leaves but does not eat dipterocarp leaves. The orangutan and proboscis monkey, which also eat young leaves, again do not eat dipterocarp leaves.

The flowers of dipterocarps vary in size, some being small and others being relatively large and showy with five white, yellow, or pink petals and often with numerous stamens. The flowers are also often scented and are adapted for pollination by a variety of insects—thrips, beetles, bees, or moths—depending on the species. Following flowering, a fruit is produced consisting of a single-seeded nut with a membranous winglike calyx that looks like a badminton shuttlecock. The ratio of the fruit weight to the total wing area—known as the wing loading—is much higher in dipterocarps than in most other winged fruits, so they spin to the ground within a few meters of the parent tree. At least this is what usually happens. Certain dipterocarp species have crossed major water barriers to reach New Guinea and the Philippines, which suggests that they sometimes travel long distances. The key to their success must lie in occasional windstorms plucking the winged fruits off the tall trees and transporting them across rivers and seas.

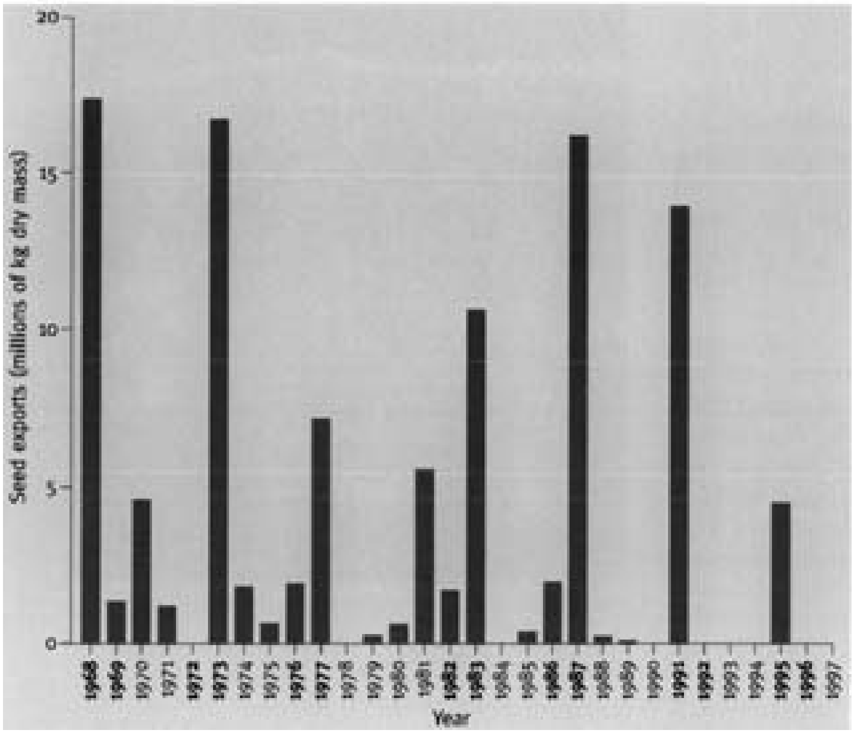
A further reason for the success of the dipterocarps in the everwet areas of Southeast Asia may be the way most of the dipterocarp species over a wide region flower and fruit simultaneously only once every two to seven years. In an entire forest only a few dipterocarp trees will flower in an ordinary year, but during a so-called "mast" year almost every large tree reproduces.

Individual plant species have mast years in all rain forests, but only in Southeast Asia do the mast years of so many species coincide over such a large area. The trigger for the initiation of flower development may be a brief episode of low nighttime temperature caused by strong radiative cooling under cloudless conditions during a drought two months before flowering. However, these meteorological conditions do not always trigger mass flowering, showing that other factors are also important, presumably including the amount of resources the trees have accumulated since the last event.

Flowers of a dipterocarp species, Hopea ponga, *from India.*

Two main advantages to this type of masting behavior have been suggested. First, in the Asian everwet climate, with no distinct wet and dry seasons, plants need some cue to trigger the onset of reproduction. In this way, all the individuals of a species can flower at the same time, and cross-pollination among trees of the same species can occur. The multiyear seasonality of the El Niño cycle provides the distinct set of conditions needed to coordinate reproduction, and it is used by almost every species of dipterocarp in these forests.

Second, and perhaps more important, mass fruiting at long intervals may prevent the build-up of the populations of insects, birds, and mammals that would destroy the large and highly nutritious, oil-rich fruits. Synchronization of fruiting by many dipterocarp species across large areas is necessary for this to work, otherwise nomadic seedeaters, such as wild pigs, could simply move to wherever the trees were fruiting and destroy the whole crop. Thus, it is only in the mast years that any seeds survive long enough to germinate and grow into seedlings. And during these flowering years, dipterocarp trees make a full commitment to reproduction. Dipterocarps invest so much energy in reproduction during flowering years that they



*Dipterocarp trees mass-flower once every two to seven years with little or no flowering during the intervening years. This is illustrated by the export figures for illipe nuts (*Shorea *spp., section Pachycarpae), oil-rich seeds of a common group of dipterocarp species, from West Kalimantan, Indonesian Borneo, from 1968 to 1997. Years with El Niño–Southern Oscillation (ENSO) events are shown in bold; strong flowering years are associated with ENSO events. From L. M. Curran & M. Leighton, 2000.*

stop growing; in practice, they often have several years of growing without reproducing, followed by a heavy flowering year with no growth.

Producing successful crops of seedlings only every two to seven years could be a major disadvantage in responding to the short-term recruitment opportunities that occur following the death of adult trees. Therefore, another important element in the success of dipterocarps is the ability of seedlings of some species to survive for many years under the dense, shady canopy of established trees. The resources provided by a large seed are an obvious advantage here. This effectively creates a "seedling bank" that can respond to opportunities created by an opening in the canopy overhead. In forests in Borneo, the seedlings of some dipterocarp species last for more than fifteen years on the forest floor after a single fruiting event. The variation among dipterocarp species in how well the seedlings can survive in deep shade and in how rapidly they can increase their growth rate in response to an increase in light levels allows the family as a whole to take advantage of a wide range of conditions.

Dipterocarp seedlings may also have an increased chance of survival as a result of a special form of the mutualistic relationship between roots and the fungi called mycorrhizae (literally, "fungus roots"), in which the plant receives mineral nutrients and water from the fungus in exchange for carbohydrates. Almost all plants form mycorrhizae, but unlike most other rain forest trees, dipterocarps are ectomycorrhizal—that is, the fungus forms a sheath over the outside of the roots. Ectomycorrhizal trees and their seedlings are linked by a network of fungal hyphae that transfer nutrients from decaying organic matter to the plants. As soon as it germinates, a dipterocarp seedling may be able to plug into the existing network and may obtain resources from its nearby parent, although this has not yet been convincingly demonstrated. Whether this suggested ectomycorrhizal advantage exists or not, it is very striking that the same fungal association occurs in the oak family, which often dominates Southeast Asian montane forests, and in legume trees in the subfamily Caesalpinioideae, which form extensive stands dominated by single species in parts of Africa and South America. Ectomycorrhizal associations are also the norm in low-diversity, temperate-zone forests. It is striking too that many of these ectomycorrhizal tree species follow a pattern of heavy fruiting at multiyear intervals—mast fruiting—that is similar to that shown by the Southeast Asian dipterocarps.

Many of these elements of the dipterocarp strategy for rain forest success seem to fit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An assortment of dipterocarp fruits, Borneo. Species vary widely in the size and shape of the wings.

together. Wind-dispersed fruits are only practical in the rain forest for very tall trees that emerge from the forest canopy: there is too little air movement inside the forest. Large seeds produce seedlings that can establish and survive in deep shade. What is food for a seedling is also food for a beetle, rat, pheasant, or a pig, but mast fruiting at long time intervals can satiate these seed predators so that many seeds escape consumption to grow into seedlings.

Even in the rain forest, however, there are exceptions to some of these generalizations, including dipterocarp trees too small to emerge from the canopy and species that flower every year. Their strategies for survival must be different and require further research. Moreover, in areas outside of the everwet zone, such as in Thailand and the Western Ghats, a hilly region of southwestern India, dipterocarps flower and fruit on annual cycles in response to seasonal weather changes. In the rain forest at Sinharaja, in southwest Sri Lanka, which has a brief annual dry period, some dipterocarps have annual cycles while other show synchronized masting at multiyear intervals.

Over the last few decades, many scientists have speculated about how one family of trees could be so dominant in the forests of Southeast Asia. Careful comparisons are now needed among rain forest regions to determine if dipterocarp trees really are different in their growth habitats, masting behavior, and seed biology from rain forest trees in other plant families. Of special interest would be comparative studies of the animal communities: do dipterocarp forests really have lower densities of insects and other animals due to the absence of flowers, fruits, and seeds during the long periods between masting years? Our ability to answer these questions is being facilitated by the network of rain forest plots being established by the Center for Tropical Forest Science, a joint project of the Smithsonian Institution and the Arnold Arboretum. Perhaps in the years to come we will be able to understand the amazing dominance of the dipterocarp family.

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Richard Corlett, a professor at the University of Hong Kong, is investigating the role of seed dispersal in rain forest recovery after deforestation. Richard Primack, a professor at Boston University, is currently conducting research on the effects of climate change on plants and birds. Both authors have worked and traveled in Asian forests and are the co-authors of a recent book on rain forests, cited above, from which this essay is adapted.