

Figure 3.28. Trichomycete gut fungi from the Monteverde region. A. Unbranched *Harpella* sp. bearing cylindrical sigmoid trichospores within the transparent peritrophic membrane of a blackfly larva; this fungal species lives in the midgut of virtually all Monteverde blackfly larvae. B. Released trichospore of *Harpella* sp. with two of four extremely fine appendages barely visible at the basal end. C. Sporulating *Stachylina nana* within the peritrophic membrane of a midge larva. D. Numerous cylindrical bodies of *Amoebidium* sp. attached externally to the anal papillae of a bloodworm living in polluted stretch of Río Guacimal; two released sporangiospores can be seen. Scale bars = 50 μm for A and D, 20 μm for B and C.

BREEDING SYSTEMS OF MONTEVERDE *INGA*

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Inga is the major genus of legume trees in Monteverde. Seven species are canopy or subcanopy trees, occur sympatrically, and have flowers that are similar in structure and appearance (Fig. 3.29). In premontane wet forest (1320–1460 m), *I. brenesii* and *I. punctata* occur in abundance, with occasional *I. mertoniana*, *I. oerstediana*, and *I. quaternata* (*I. hintonii* and *I. longispica* are rare). In the transition forest (1450–1550 m), *I. hintonii* and *I. mertoniana* are common, with occasional *I. quaternata* (*I. brenesii*, *I. longispica*, and *I. punctata* are rare). In the lower

montane rain forest (1550–1800 m), *I. hintonii* and *I. longispica* are abundant, with occasional *I. mertoniana* [Editor's note: *Inga hintonii* was previously identified as *I. densiflora*.]

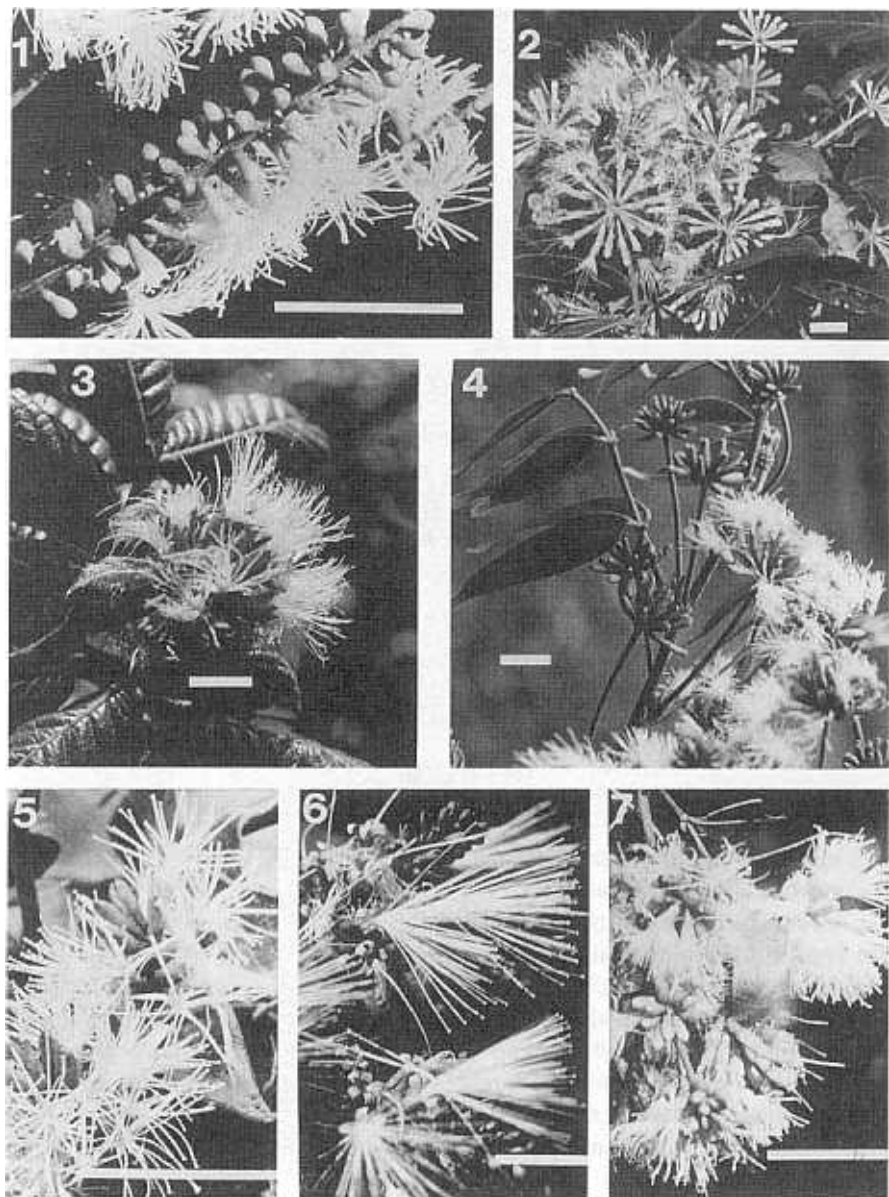
Flowers of *Inga* have reduced perianth parts, numerous white stamens that provide the main visual attraction, and nectar in the floral tube, which is accessible to a wide variety of floral visitors. Flower visitors of Monteverde *Inga* include Hemiptera, Coleoptera, Diptera, Hymenoptera, Lepidoptera, hummingbirds, and bats (Koptur 1983). The most effective

and common pollinators are hawkmoths and hummingbirds. Hawkmoth species visiting *Inga* flowers include *Aelopus titan*, *Agrius cingulatus*, *Pachygonia subhamata*, *Pachylia ficus*, *Perigonia lusca*, *Xylophanes chiron*, and many others (W. Haber, pers. comm.). Hummingbird visitors include *Amazilia saucerrottei*, *Campylopterus hemileucurus*, *Colibri thalassinus*, *Eupherusa eximia*, *Heliodoxa jacula*, *Panterpe insignis*, and *Calliphlox bryantae* (Feinsinger 1978, Koptur 1983; Appendix 9).

Inga flowering phenologies are not uniformly spaced throughout the year. Most species bloom at the wet/dry season interface, and usually more than one species is in flower in a forest at any time of year. Simultaneously blooming species often attract the same pollinators, regardless of flower size. Differences in seasonal flower-

ing phenology and floral behavior (flower opening times and patterns of flower opening) provide some separation of visitors among co-occurring species, reducing the potential negative consequences of pollinator sharing.

Despite producing multitudes of flowers in many compound inflorescences, most *Inga* trees set very little fruit (Koptur 1984). *Inga* pollen grains are released in polyads (clusters of 16, 24, or 32 pollen grains), which increases the efficiency of compatible pollination. Observations of visitor activity on *Inga brenesii* and *I. punctata* indicate that each flower receives an average of more than two visits per day. Examination of stigmas showed that, in all species, far more flowers had received pollen than normally set fruit. Hand pollination of six species revealed them to be self-incompatible.



Figures 3.29. Flowers of *Inga* spp. (1) *I. longispica*. (2) *I. quaternata* = *I. nobilis*. (3) *I. brenesii* = *I. sierrae*. (4) *I. mortoniana*. (5) *I. hintonii* = *I. micheliana*. (6) *I. oerstediana*. (7) *I. punctata*. Scale bars = 2 cm.

For three *Inga* species studied in detail, cross-pollinations between individuals of the same species were more successful in setting fruit when the parent trees were at a distance greater than 1 km away from each other than when they were closer than 0.5 km (Koptur 1984), suggesting that near neighbors are likely to be more closely related and therefore less compatible for

cross-pollination. A similar distance effect was documented for the hawkmoth-pollinated species *Luehea candida*; distant parents produced more viable seeds (Haber and Frankie 1982). This phenomenon may be widespread among tropical trees, which emphasizes the importance of long-distance pollinators such as hawkmoths and hummingbirds.

SEX RATIOS AND THE DISTRIBUTION OF MALE AND FEMALE TREES

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About 20% of tropical plant species are dioecious, that is, have individual plants that fall into one of two distinct sexual types or morphs (Bawa 1980, Renner and Ricklefs 1995). In the simplest cases, the pistillate (female) morph is capable of developing fruits but does not produce pollen whereas the staminate (male) morph produces flowers that have functional stamens but not pistils. Sex expression in plant populations can be more complicated, however. For example, there can be three sexual morphs (male, female, and hermaphrodite). Sometimes the differences between morphs can be extremely subtle; for example, two individual plants of the same species may have flowers that look similar, but functionally one plant acts as a male while the other acts as a female (Haber and Bawa 1984). Alternatively, different plants of the same species may produce morphologically dissimilar flowers that are equally hermaphroditic (Levin 1974). The study of patterns of plant reproduction in sexually polymorphic species addresses several questions. What is the ratio of male, female, and hermaphroditic plants in a plant population, and how is it affected by population age structure? Do males and females tend to occur in different habitats? Is sex expression constant within an individual over the course of its life, or within a population between years?

Ocotea tenera (Lauraceae), an understory tree found in small light gaps and along forest edges, has two sexual morphs, which correspond functionally to male and female. Although male flowers contain pistils as well as stamens, fewer than 0.01% of male flowers produce fruits. (Because some male plants set a small number of fruits, the species could be considered gynodioecious; an uncommon third, hermaphroditic morph also exists [Gibson and Wheelwright 1996]). The species has been the focus of a study of reproduction and growth in Monteverde since 1979

(Wheelwright 1993, Gibson and Wheelwright 1995). The adult sex ratio of natural populations of *O. tenera* in Monteverde is about 1:1, which is typical of the small number of dioecious tropical tree species that have been studied (Melampy and Howe 1977, Opler and Bawa 1978, Ackerly et al. 1990).

Surprisingly, functionally male and female *O. tenera* trees appear to be distributed throughout the forest in a peculiar way. A tree's nearest conspecific neighbor is more likely to be of the opposite sex than one would expect by chance (Wheelwright and Bruneau 1992); the sexes show "negative spatial association" (Bierzychudek and Eckhart 1988). Although one can readily appreciate the selective advantages of being located next to an individual of the opposite sex—greater fruit set or greater success as a pollen donor—it is difficult to imagine how such a spatial pattern could arise under natural conditions.

In 1981 and 1984, I established two experimental populations of *O. tenera* by planting seedlings of known parentage (but unknown sex), arrayed in a Latin square experimental design. When the plants became sexually mature 5 years after germination, males outnumbered females. However, in the experimental populations, the spatial distribution of the sexes proved to be random. During their first 6 years of reproduction, 11% of the young trees altered their functional sex at some point. In a natural population of older trees monitored since 1980, as many as 40% of trees may have changed functional sex at least once in their reproductive lives. In some cases, changes in functional sex could be traced to the production of distinct floral morphs by the same tree in different years. Although sex switching is not common in plants, it occurs in some temperate-zone plant species (Freeman et al. 1980, Lloyd and Bawa 1984). (Some botanists consider changes in sex expression over time as "temporal monoecy" rather than sex switching [M. Grayum, pers. comm.].)