

INTERACTIONS AMONG *INGA*, HERBIVORES, ANTS, AND INSECT VISITORS TO FOLIAR NECTARIES

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Inga is a large genus (ca. 400 spp. in the neotropics) of mimosoid legume trees, many species of which bear extrafloral nectaries (Fig. 8.1), including all of those that occur in Costa Rica (ca. 30 spp.) (León 1966). In Monteverde, 8–10 species occur. In the MCFP (1520–1600 m), *I. densiflora*, *I. longispica*, *I. mertoniana*, and infrequently *I. tonduzii* occur. In the middle woods (1460–1520 m), *I. densiflora* and *I. mertoniana* are common, with occasional *I. quaternata* and rarely *I. brenesii*, *I. longispica*, and *I. punctata*. In the lower woods (1320–1460 m), *I. brenesii* and *I. punctata* are the most abundant, with occasional *I. mertoniana*, *I. oerstediana*, and *I. quaternata*, and rarely *I. densiflora* and *I. longispica*.

Inga have compound leaves, with foliar nectaries located between each pair of opposite leaflets (Fig. 8.15). These nectaries secrete nectar from the first unfolding of a new leaf until the leaf is fully mature. They provide an incentive for insects to visit the leaves to collect nectar. Two guilds of nectary visitors (ants and parasitic insects) provide protection against herbivores. How do these and other defenses of *Inga* vary over an elevational gradient? *Inga* leaves provide food for many herbivores, including large vertebrates such as Howler Monkeys (*Alouatta palliata*; Milton 1978), sloths (Montgomery and Sunquist 1978), snails, and a variety of insects, including katydids, beetles, sucking insects, leaf-miners, and caterpillars. Individual leaves are long-lived, some surviving three years or more.



Figure 8.15. Ants (*Camponotus substitutus*) visiting foliar nectaries of *Inga densiflora* in Turrialba, Costa Rica. Photo by S. Koptur.

Experiments with saplings of two species (*I. densiflora* and *I. punctata*) in wet forests at elevations lower than Monteverde (600 m, near Turrialba) revealed that ants protect developing leaves against herbivores (Koptur 1984a). Ants collect the nectar and disturb herbivores they encounter on the foliage, attacking and eating some of the slow and soft-bodied ones and generally inciting all insect herbivores to “move along.” Extrafloral nectar is produced throughout the day and night, and ants continually visit nectaries at these lower elevations. This benefits the plants because many leaf-feeding herbivores are active at night. The same species of *Inga* occur over a wide elevational range in Costa Rica; for example, *I. densiflora* ranges between 600 and 1500 m. Nectar-feeding ants are less abundant and less active at higher elevations (see Chap. 4, Insects and Spiders), but the nectaries of most *Inga* trees secrete nectar. What is the function of this extrafloral nectar when there are no ants to protect the plants?

This nectar is used by a variety of insects, including adult wasp and fly parasitoids. Parasitoids complete their life cycle within or on the body of one host and ultimately kill it. Female parasitoids lay their eggs in herbivore eggs or larvae, and their own larvae develop inside the egg or body of the host larva. The feeding caterpillar transforms the leaf material into food for the parasitoid larvae living within it. The parasitoid larvae emerge from their host and pupate; new adult parasitoids hatch from the pupae. They leave behind an empty shell of a caterpillar that is a “dead end,” even though it might still look alive, for it does not live to reproduce. Some parasitoids are egg parasitoids and emerge as adults without the herbivore egg hatching. In either case, the numbers of herbivores are reduced by parasitoids, which potentially benefits both the *Inga* individual that secretes the nectar and other trees in the area that may have been attacked by those herbivores (Koptur 1991).

Caterpillars of many lepidopteran herbivores of *Inga* are parasitized to a much greater extent at higher elevations, where ants are not abundant (Koptur 1985), than at lower elevations. Chemical analyses of foliage from trees of the same species at different elevations reveal that upland individuals have substantially greater amounts of tannins in their leaves than their lowland counterparts. Tannins bind proteins, and caterpillars eating more tannins in their *Inga* leaves may take longer to develop (also development

is slower at cooler temperatures of higher elevations), thus spending more time being vulnerable to parasitoids and predators. Tannins may therefore enhance parasitoid protection of upland *Inga*. Alternative explanations for this increased tannin content, such as greater pressure from fungal pathogens or other environmental factors, have not yet been studied.

Although the antiherbivore properties of higher elevation *Inga* are a fairly effective complex of fac-

ultative defenses (parasitoids and tannins) in the absence of ant protection, they are not as effective as ant defense in limiting damage to foliage. Upland *I. densiflora* leaves are damaged substantially more after six months than their lowland, ant-defended counterparts. Nonetheless, the extrafloral nectaries that make *Inga* leaves easy to recognize are also important in antiherbivore defense of *Inga* at all elevations.

A FLY LARVA DIRECTLY ALTERS FLORAL SEX IN *CENTROPOGON SOLANIFOLIUS*

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Some interactions between plants and insects are obvious to the observer (e.g., leaf damage by folivores). Other interactions are more subtle. I studied an interaction in which the larva of a fly, *Zygothrica neolinea* (Drosophilidae), lives inside unopened flowers of *Centropogon solanifolius* (Campanulaceae; Weiss 1996). The larva eats the developing pollen and reduces or eliminates the flower's ability to act as a male without affecting its female function. *Centropogon* is a genus of mostly Andean herbs, shrubs, and vines with brightly colored hummingbird-pollinated flowers (Standley 1938, Stein 1992). The bright orange flowers of *C. solanifolius* grow along the cloud forest trails in Monteverde.

My studies of *C. solanifolius* flowers began in ignorance of the fly. I set out to investigate whether removal of pollen from protandrous flowers shortens the duration of the male phase of the flower. Protandrous flowers have a temporal separation of sexual functions: they are first male and provide pollen; in the subsequent female phase, the stigma becomes receptive. Studies of another protandrous lobelioid, *Lobelia cardinalis*, revealed that pollen removal significantly reduced the length of the male phase and hastened the onset of the female phase relative to that of unmanipulated flowers (Devlin and Stephenson 1984). Two Organization for Tropical Studies field problems have found an effect of pollen removal (Frazee et al. 1990, Koptur et al. 1990). My investigations of *C. solanifolius* flowers demonstrated the same effect; the male phase of bagged (to exclude pollinators), unmanipulated control flowers lasted approximately 3–4 days, while that of treatment flowers from which I removed pollen lasted only 1–2 days.

The discovery of a single small larva inside the anther tubes of many of my test flowers complicated my studies. These larvae seemed to eat only the pol-

len and did not touch any other part of the flower. Surveys of *C. solanifolius* in Monteverde suggested that larval infestation was intense and widespread. In one population, I found larvae in the flowers and buds in 14 of the 16 plants; in another population, 70% of the flowers contained larvae. The presence of the larvae significantly reduced or eliminated the flowers' male phase. Uninfested flowers remained male for an average of 3.5 days, whereas infested flowers were male for an average of 1.2 days before entering the female phase. Some infested flowers skipped the male phase and opened directly as females.

Larval pollen removal seems to have a profound effect on the sex ratio of flowers in the population. Because larvae were so common in *C. solanifolius* flowers in Monteverde, I could not directly measure the sex ratio of an uninfested population. However, in populations of related species with no evidence of larval infestation, the male phase is longer than the female phase: for *L. cardinalis*, the ratio of days in the male phase to days in the female phase was 2.6:1 (Devlin and Stephenson 1984). In another *Centropogon* species, the ratio was 1.4:1 (Frazee et al. 1990). In contrast, for a population of *C. solanifolius* that included both infested and uninfested flowers, the male phase lasted for 1.8 days, and the female phase for 3.9 days. Larval infestation of the flowers may have shifted the sex ratio of the population toward a female-biased ratio, with potentially important fitness consequences for the plants.

I also documented details of the fly's life history within the flower. The larva is that of *Zygothrica neolinea* (Drosophilidae). Female flies lay single oblong eggs through the corolla onto the surface of the fully developed anther tube when the flower is still a small bud; a tiny droplet of latex on the outside of the bud often reveals the location of a recent oviposition (Fig.