Experimental Evidence for Defense of Inga (Mimosoideae) Saplings by Ants

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EXPERIMENTAL EVIDENCE FOR DEFENSE OF
INGA (MIMOSOIDEAE) SAPLINGS BY ANTS[1]

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Abstract. *Inga densiflora* and *I. punctata* have foliar nectaries that are visited by a variety of ants. Extrafloral nectar secretion on new leaves is continuous throughout the day and night; ant activity on both old and new leaves is also continuous. Experiments compared the effectiveness of five species of ants in removing caterpillars and three other types of insect herbivores from leaves. All ant species tested could remove insect herbivores to some extent; of these ants, *Pheidole biconstricta* was the most effective.

Leaves from which ants were excluded suffered substantially greater damage than control leaves. Ant-defense is a generalized and effective defense operating in the protection of *Inga* saplings against herbivores, but the extent of protection may vary according to what species of ants visit the nectaries— a consequence of facultative mutualism.

Key words: antiherbivore defense; ants; Costa Rica; extrafloral nectaries; facultative mutualism; herbivores; Inga; *mutualism; nectar secretion; tropical trees.*

INTRODUCTION

A number of plants bearing extrafloral nectaries have been shown to be protected by ants that gather the nectar (reviewed by Bentley 1977b; Buckley 1982). These ant-plant relationships may be obligate mutualisms (e.g., *Acacia cornigera* and *Pseudomyrmex* ants; Janzen 1966, 1967), but most protective interactions between ants and plants are facultative and nonsymbiotic (Boucher et al. 1982). Not only can many plants exist fairly well without their ant mutualists, but any number of ant-partners can be involved in the interaction (oligophily to polyphily, sensu Boucher et al. 1982). Neither the broad-scale nor local distribution of ant species is uniform; there exists a mosaic of ants with which plants can interact (Leston 1973). The relative benefit to plants resulting from different visitors to nectaries may provide insight into the evolution of facultative mutualisms.

This study investigated the function of extrafloral nectar secretion in two species of the large neotropical genus *Inga, I. densiflora* Benth., and *I. punctata* Willd. in premontane moist forest of Costa Rica. *Inga* is a neotropical genus with ~400 species, many bearing extrafloral nectaries, including all those that occur in Costa Rica (León 1966). *Inga* have parapinnate leaves, with foliar nectaries generally located between each pair of opposite leaflets. Foliar nectaries secrete nectar starting at the first unfolding of a new leaf and ceasing when the leaf is fully hardened and mature. All *Inga* also have floral nectaries (Salas 1974, Koptur 1983). Both *Inga densiflora* and *I. punctata* are canopy (sometimes subcanopy) trees, with wide-spreading crowns. Leaves of these trees serve as food for a wide variety

of herbivores, from large vertebrates such as howler monkeys (Milton 1978) and sloths (Montgomery and Sunquist 1978) to invertebrates like snails, and a variety of insects (katydids, beetles, sucking insects, leaf miners, and externally feeding caterpillars). I chose *Inga* not only because there have been few ecological studies of extrafloral nectaries in tree species of the mature tropical wet forest, but because many species of ants interact with the same species of *Inga,* allowing a comparison of their potential benefit to the plants. In this paper I report on (1) the production of foliar nectar by *Inga* and its use by different species of ants, (2) the nectar secretion patterns and ant activity over time, (3) the protective role of ants against phytophagous insects, and (4) the effectiveness of different ant species against a variety of insect herbivores.

METHODS

This work was conducted from June 1979 to June 1980 in premontane moist forest near Turrialba, Costa Rica (elevation 620–660 m). One study area was in undisturbed forest, and the other was in forest remnants, both on the grounds of the Centro Agronomico Tropical de Investigacion y Enseñanza (C.A.T.I.E.). Annual rainfall was 1.9 m in 1979. January through March were the driest months.

The observations and experiments performed on extrafloral nectaries of *Inga* and ants were done on large saplings of *Inga densiflora* and *Inga punctata* (2–4 m in height) growing in forests. As extrafloral nectar is produced only on new and developing leaves, the phenology of new leaf production was monitored. On 20 marked trees of each species, the percentage of new leaves was estimated visually each month over the period of the study.

Herbivorous caterpillar abundance was monitored on 10 tagged saplings of each species. Each month, the foliage of each sapling was examined thoroughly for

Lepidoptera larvae and eggs, and those found were removed from the trees (along with the leaflet they were on) and reared for identification. For most species the larval development times were longer than 1 mo, so that almost all caterpillars hatched from eggs deposited on trees in the time between examinations were found. Between 500 and 1000 leaves of each species were examined each month; herbivore abundance was then expressed as the number of larvae per 100 leaves.

To determine the diurnal pattern of extrafloral nectar secretion by *Inga densiflora* and *Inga punctata,* I marked a sample of 35 new leaves on five saplings of each species. I removed ants from these branches and banded the branches bearing these leaves with Tanglefoot resin (a sticky substance which does not allow ants to pass). I removed what nectar had accumulated, and covered the leaves with brown paper Pollen-tector (Carpenter Paper Company, Des Moines, Iowa) bags to prevent flying visitors from removing nectar. I then collected all the nectar from nectaries on 30 of these leaves every 2 h using micropipettes. I estimated nectar volumes from spots made on strips of chromatography paper using the spot size/volume conversions developed by Baker (1979). Sugar concentrations were measured in nectar from the other 5 leaves using a pocket refractometer (Bellingham and Stanley) which measures percent sugar on a mass/mass basis (Bolten et al. 1979). Ant activity was assessed by counting the number of ants present on 30 new leaves and 30 old leaves on the same saplings at the time of sampling. Ants were counted prior to nectar sampling to minimize the effects of disturbance.

The protective role of ants was tested in ant-exclusion experiments. On a number of saplings (seven of *I. densiflora;* six of *I. punctata*), I tagged all of the new leaves with thin aluminum bands around the petioles or rachises. Ants and caterpillars were seen to traverse the bands freely, and the bands did not cause the leaves to abscise or rot. I excluded ants from approximately half of these leaves on each tree by manually removing the ants, clipping overhanging leaves and branches, and banding the branches bearing these leaves with Tanglefoot resin. The other leaves served as control leaves, and received the same treatment (ants removed, overhanging foliage clipped) except that Tanglefoot resin was not applied to their branches. I assessed the amount of damage present initially using a scale of 0–8 (representing 12.5% increments in damage) to score each leaflet. The leaves were checked regularly for 25 d to ensure that ants were indeed being excluded from experimental leaves. Occasional corrective measures were necessary, but ants could never have been on experimental branches for >3 d. After 25 d, the new leaves had fully expanded, and I assessed damage to each leaflet again. Increases in damage were compared for control and experimental leaves.

In order to determine the efficacy of different kinds of ants in removing herbivores, a series of placement experiments was performed using five different kinds of herbivores and several different kinds of ants on each species of *Inga.* The herbivores were of five types, chosen to span the array of insect herbivores on *Inga:* (1) small caterpillars (2nd-3rd instar), (2) large caterpillars (5th-6th instar), (3) katydid nymphs, (4) beetles, (5) leafhoppers. On a sapling occupied by one species of ant, I placed single herbivores on the upper surface of the foliage and conducted 5-min observations noting discovery and removal actions by ants. Each herbivore type was tested 10–15 times per ant species. Herbivores placed on foliage were not all *Inga* herbivores; they were collected from other plants as well, and grouped according to size and type. Controls were trials on the same plants in which no encounter took place between ants and herbivores, thus providing a measure of how frequently the various herbivores would leave the foliage if unmolested, and also a measure of how often ants actually encountered herbivores.

RESULTS

New leaf production and caterpillar herbivore abundance

New leaf production on both species of *Inga* is continuous at a relatively low rate (Fig. 1). Most trees therefore have some new leaves at all times of the year, with extrafloral nectar being produced. Vouchers of *Inga* spp. studied are deposited in the University of California herbarium, the herbarium of the Museo Nacional de Costa Rica, and the Missouri Botanical Garden.

The most common lepidopteran larvae found eating *Inga* were the butterfly *Dismorphia amphione praxinoe* Doubleday (Pieridae); the skipper *Telemiades antiope* Plötz (Hesperiidae); and the moth *Charistica irianthana* Meyrick (Gelechiidae). Vouchers of herbivores are in the author's collection, the Museo Nacional de Costa Rica, and the British Museum. Overall caterpillar herbivore abundance on both species of *Inga* over time is also shown in Fig. 1. Caterpillar numbers are low in October and November (the end of the wet season), and greater on both species during the dry season. Although trees were not monitored carefully through the wet season, observations during May through September 1979 showed caterpillars to be present in low numbers through these months.

Extrafloral nectar secretion and ant activity

Extrafloral nectar secretion is continuous day and night in both *Inga densiflora* and *I. punctata* (Fig. 2). Mean total leaf nectar volumes are slightly higher for *I. densiflora,* but each leaf of this species has 5–7 pairs of leaflets, and 5–7 nectaries; *I. punctata* leaves have only 2–3 pairs of leaflets, and 2–3 nectaries.

Extrafloral nectar sugar concentrations range from 28.5–40.2% in *I. densiflora,* and 30.8–47.2% in *I. punctata* over 24 h. Sugar concentrations were slightly
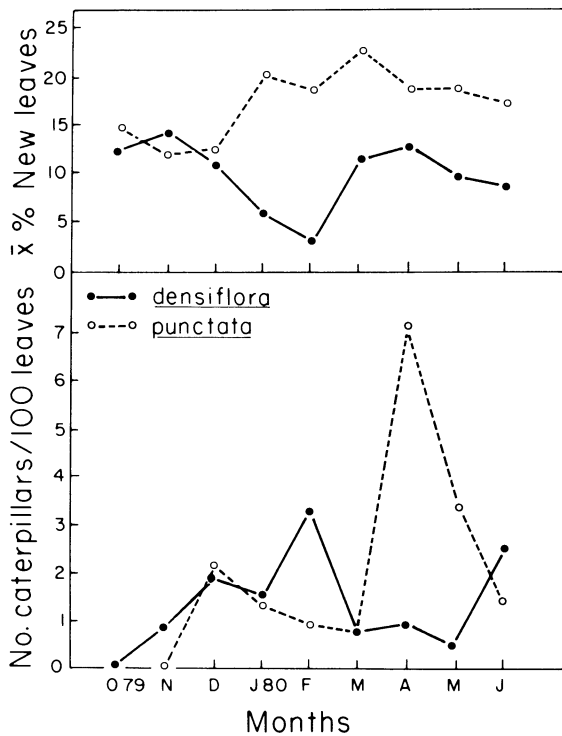
FIG. 1. New leaf production and caterpillar abundance on *Inga densiflora* and *I. punctata*. The number of new leaves as a percentage of all leaves was estimated visually on 20 marked trees monthly over the period of the study. Herbivore abundance is expressed as the number of larvae per 100 leaves. On 10 tagged saplings of each species, 500–1000 leaves were searched for eggs and larvae every month.

TABLE 1. Ants visiting nectaries of *Inga densiflora* (D) and *I. punctata* (P). Sizes are approximate as only 2–3 individuals were measured for each species. Ant abundance: + + + = common, + + = occasional, + = rare.

Ant species	Worker size (mm)	*Inga* sp.	Abundance
Dolichoderinae			
Monacis bispinosa	6	P	+ +
Formicinae			
Camponotus substitutus	5	D, P	+ + +
C. (Myrmobrachys) sp. 1	...	P	+
C. (M.) sp. 3	4	P	+ +
Myrmelachista sp. 1	6	D, P	+
Paratrechina sp. 1	2.5	D	+
Ponerinae			
Ectatomma sp. nov. (R. Snelling, *personal communication*)	9.5	D	+ +
Myrmecinae			
Crematogaster limata palans	3	P	+ +
C. nigropilosa	4	P	+
C. stolli	3	P	+
Pheidole biconstricta	3.5	D, P	+ +
P. radoszkowskii	2.5	P	+
Procryptocerus sp. 1	5.5	P	+
Solenopsis sp. 1	2	D	+

higher during the late morning and early afternoon. Evaporation undoubtedly occurred during sunny, warm days. Afternoon showers occurred briefly on study days, and may explain the slight decrease in sugar concentration in the later afternoon (nectaries were bagged, and therefore protected from the rain, but the air was more humid after the rain).

There is more than one species of ant associated with each species of *Inga* (Table 1). Usually there is only one species of ant on a given sapling or tree. On large trees, there may be different species of ants on different parts of the tree. The species of ant visiting nectaries and traversing the foliage of a given *Inga* tree appears to correspond with which ant nest is nearest to or in the tree. Occasionally an ant nest may be in the branches of the tree itself (e.g., *Monacis bispinosa*), or in dead twigs; there are, however, no special domatia formed by plant tissue as shelter for the ants. The species of ants chosen for experiments were those that were most commonly found associated with *I. densiflora* and *I. punctata*.

Ants were present on both new leaves (with actively secreting nectaries) and old leaves of both species day and night, from 5–22 ants on 30 new leaves, and from 4–16 ants on 30 old leaves, at each sampling time. There was an increase in activity at midday and also around midnight for ants on *I. densiflora*. Ant activity was slightly higher on new leaves at most times, but old leaves at some times had more ants than new leaves.

Ant-exclusion experiments

The mean change in leaflet damage score was calculated for leaflets of control and of experimental leaves for each species (Table 2). Because the data are not normally distributed (many values of 0 and 1), a nonparametric test was used. The Wilcoxon test for a 2 × *c* contingency table (Ridit Analysis: Bross 1958) examined the null hypothesis that mean damage increase is equal in control and experimental leaves; the null hypothesis was rejected for both species. For *Inga densiflora*, a mean increase in damage was <12% for the control and roughly 37% for leaves with ants excluded. For *I. punctata*, mean increase in damage was ≈13% for the control and ≈20% for leaves with ants excluded. *Inga densiflora* controls (with ants) show a somewhat lower damage increase than *I. punctata* controls. Damage increase to ant-excluded *I. densiflora* is substantially greater than increases in ant-excluded *I. punctata*.

Ant-herbivore interactions

The results of the herbivore placement experiments to examine ant/herbivore interactions are shown in Table 3. On *Inga densiflora*, *Pheidole biconstricta* was
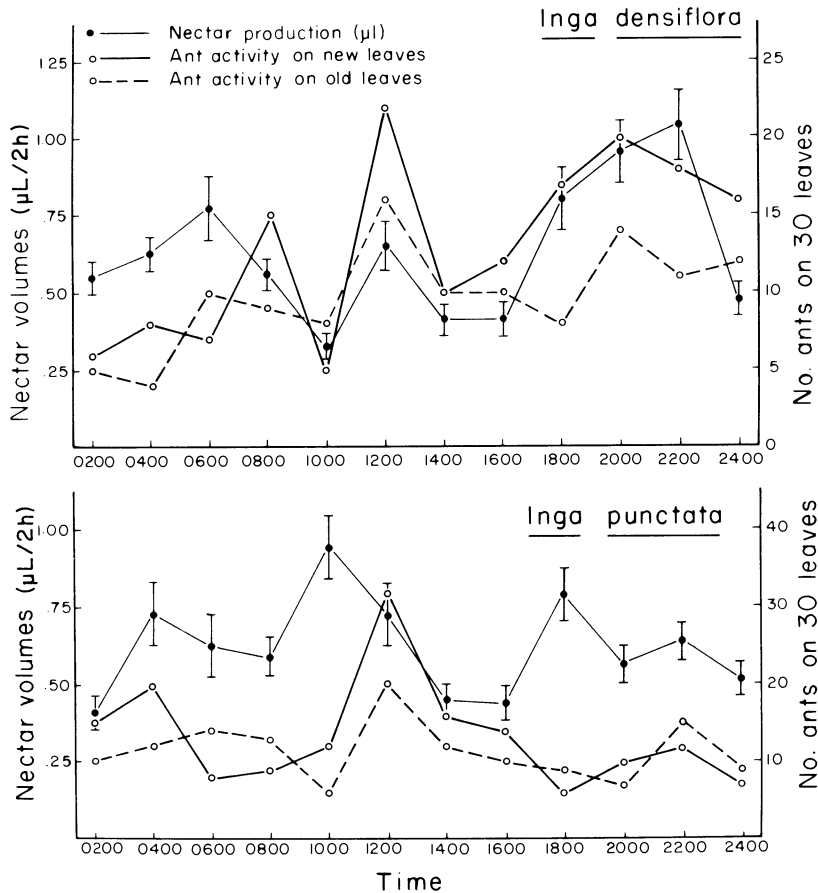
FIG. 2. Extrafloral nectar secretion and ant activity on *Inga densiflora* (above) and *I. punctata* (below). Mean nectar production (±SE) per 2-h interval was determined by combining the volumes secreted by all nectaries on a leaf for each of 30 leaves. Sugar concentration was averaged over 5 leaves at each sampling (see Results). Ant activity is the number of ants counted on 30 leaves of each type prior to measuring nectar.

the most effective in removing herbivores of all kinds tested. *Solenopsis* sp. 1 and *Camponotus substitutus* were less successful in removing large caterpillars and katydids. All of the ants more easily removed small caterpillars than large caterpillars.

TABLE 2. Results of ant-exclusion experiments: mean increases in herbivory score over a 25-d period. Herbivore damage was measured on a scale of 0–8, i.e., with 12.5% increments. n = number of leaflets.

Tree species	Control			Ants excluded			Wilcoxon test
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	
Inga densiflora	0.7	1.37	325	2.98	1.90	339	$z = 4.06$ $P <$ .0001
Inga punctata	1.04	1.86	190	1.57	2.48	192	$z = 2.21$ $P =$ .014

On *Inga punctata*, *Pheidole biconstricta* was again the most effective in removing most types of herbivores (Table 3). *Pheidole biconstricta* workers are of moderate size (3.5 mm), forage in groups, and are present in large numbers on occupied plants. *Monacis bispinosa* was the least effective against most herbivores. The workers of this species are larger (6 mm) and forage in groups (at least close to the nests, which is the only situation where I found them on *Inga*); they visited nectaries with dedication, but were less interested in insects placed on foliage. *Camponotus substitutus* and *Crematogaster limata palans* were intermediate in their ability to remove herbivores. These two species have smallish workers that forage in groups, but are often present in fewer numbers on a given plant than *P. biconstricta*.

All of these ant species were effective against at least some types of herbivores tested. Small caterpillars were frequently picked up and carried away, or bothered and/or bitten until they dropped off. The latter se-

TABLE 3. Ants vs. herbivores on *Inga* species. Numbers are the number of times an herbivore was removed by ants divided by the number of times an herbivore was encountered by ants. Controls are the number of times an herbivore left the plant after no encounter with ants divided by the number of times herbivores were not encountered by ants within 5 min.

Ants	2nd–3rd instar caterpillars	5th–6th instar caterpillars	Katydids	Beetles	Leafhoppers
	Herbivores on *Inga densiflora*				
Camponotus substitutus	14/15***	10/15**	6/10*	4/15	13/15***
Pheidole biconstricta	15/15***	11/15***	10/10***	12/15***	15/15***
Solenopsis sp.	14/15***	3/15	7/10*	10/15**	15/15**
Control	2/17	1/10	3/15	3/16	4/12
	Herbivores on *Inga punctata*				
Camponotus substitutus	9/10**	6/10	9/10*	2/10	8/10**
Crematogaster limata palans	9/10**	5/10	6/10	6/10	8/10**
Monacis bispinosa	5/10	4/10	3/10	8/10*	9/10***
Pheidole biconstricta	10/10***	9/10***	8/10*	7/10*	10/10***
Control	2/14	3/12	4/11	4/14	3/12

* $P < .05$, ** $P < .01$, *** $P < .005$; Fisher's Exact Probability test between ant-encounter treatment and no-ant control.

quence was common with katydids, beetles, and large caterpillars. However, on two occasions, a number of *Pheidole* ants surrounded a large caterpillar, bit and stung it, and carried it away in a group. Many beetles moved to leaflet-tips and thereby avoided encounters with ants (as ant-wanderings are generally confined to petioles and rachises of leaves, and out onto the lower three-quarters of each leaflet). Leafhoppers were especially apt to leave at the first encounter with an ant. In general, it appears that the most effective protectors are ants of small to intermediate size that forage in groups and are present in large numbers. Although not tested here the rarer solitary foragers of larger size (e.g., *Ectatomma*) are probably effective also, though their presence on these *Inga* was much less common and less predictable.

DISCUSSION

The interaction between *Inga* and ants can be summarized as follows: (1) Extrafloral nectar secretion on new leaves of *Inga* was continuous day and night. Ants were present on both new and old leaves day and night. (2) Leaves on branches from which ants were excluded experienced significantly more herbivore damage than control leaves. (3) A number of ant species were associated with each *Inga* species. All ant species tested removed a variety of insects from *Inga* leaves, but with varying effectiveness.

This suggests that ants visiting the extrafloral nectaries of *Inga densiflora* and *I. punctata* protect the trees against foliage-feeding insect herbivores. When ants are present on leaves, leaves suffer much less damage from herbivores. The species of ant present on a given tree will determine how complete and effective the protection will be. Ants can and do remove caterpillars, katydids, and other herbivores.

Ants are a generalized and effective antiherbivore defense, able to deter a variety of insect herbivores, both generalists and specialists, before damage is done.

Plant chemical defenses, though they span a wide array from generalized ("quantitative," sensu Feeny 1975) to specialized ("qualitative," Feeny 1975), may deter herbivory only after an herbivore has started feeding. Direct protection afforded by ants may be costly to maintain, but thrifty overall, if less leaf tissue is damaged.

Inga trees, as common and long-lived components of the mature forest, may experience a wide array of herbivores that they cannot escape in space and time. Generalized antiherbivore defenses, such as ant-defense, may be useful, especially in the sapling stage where substantial amounts of herbivory are more likely to result in mortality (Tilman 1978, S. Koptur, *personal observation*). Protection of plants against herbivores by ants has usually been demonstrated in plants of small stature (Bentley 1977b, Buckley 1982), but is likely important in trees as well: to become a reproductive adult, an *Inga* tree must first pass through the sapling stage, where ants can offer substantial protection against insect herbivores. *I. densiflora* and *I. punctata* have phenolic compounds (Koptur 1982) which may also function in deterring insect, and perhaps vertebrate, herbivores. I have shown here that ant defense is effective against invertebrate herbivores. Ant-protection of *Inga* foliage may be less effective against large vertebrates (monkeys, sloths). These "apparent" plants may need a high defense budget, and diverse defenses.

That new leaves of these two *Inga* species are produced at a low and constant rate may be very important in maintaining an ant-guard year-round. Because ant-guards are generalized defenses, they need not always fluctuate in accord with season, or with a particular herbivore species (but see Tilman 1978). Herbivore pressure from lepidopteran larvae is continuous year-round, although the overall level varies, and most individual herbivore species are not found year-round. Many herbivorous insects are inactive and hard to find by day, and are active and feed by night. The contin-

uous secretion of extrafloral nectar may also allow for defense against herbivores day and night (Fig. 2). Two of the three most common caterpillars eating *Inga* are "leaf sealers" (the skipper and the gelechiid); their shelters provide them with some protection from ants. The third major herbivore, the pierid butterfly *Dismorphia*, usually feeds at the leaflet edges and sits on the abaxial surface of leaves, probably minimizing contact with ants this way, because ants generally spend more time on upper leaf surfaces.

Most plants with extrafloral nectaries do not have resident ants, and the relationship between plant and ant is neither necessarily specialized (i.e., whichever ants have a nest closest to the plant tend to visit the nectaries) nor obligate (the plants are able to survive without the ants, though presumably with diminished fitness). Though not quite as dramatic as the obligate relationships in a few myrmecophytes, recent studies have shown that facultative plant/ant relationships, which include the majority of plants with extrafloral nectaries, result in reduced damage to leaves and increased seed set over individuals with ants excluded (Koptur 1979, Stephenson 1982); nectaries borne on reproductive structures also have a direct effect on fitness, increasing seed set by ant-protection (Bentley 1977a, Inouye and Taylor 1979, Keeler 1981a). Nor should ant protection be assumed without close examination; some recent studies have shown that ants visiting nectaries on some plants provide no measurable benefits to the plants (Tempel 1983, O'Dowd and Catchpole 1983).

How might such "loose" mutualisms have evolved? Extrafloral nectaries may well have originated as chance fissures in the epidermis of some species through which phloem sap oozed and was visited by ants. Individual plants with this trait near appropriate ant species might have received some protection against herbivores when these ants visited their exudates, and thus had an increased chance of survival and reproduction. Plant-to-plant differences in the amount of nectar and other chemical defenses produced, as well as differential attentiveness and protection provided by different ant species implies that extrafloral nectary mutualisms are most likely the result of "diffuse coevolution" (Fox 1981) between plants, herbivores, and biotic protective agents. That ant protection is a viable alternative in the defensive array of plants is evidenced by the occurrence of extrafloral nectaries (and ant-protection) in many diverse plant families (Bentley 1977b, Buckley 1982) and groups (Koptur et al. 1982). I think it is likely that in situations where plants bearing nectaries have been found not to receive any benefit from ants (e.g., *Pteridium aquilinum* in New Jersey, Tempel 1983; *Helichrysum* in Australia, O'Dowd and Catchpole 1983; *Hibiscus* in Florida, B. Boeckland, *personal communication*) that the ants involved in the study may have been at the low end of the scale in "protective ability." Demonstration of lack of protection in one geographic location is not a universally applicable finding, just as demonstration of protection is not! Facultative extrafloral nectary mutualisms are likely to be different in every location they are studied, and for wide-ranging plant species this will have profound effects on plant fitness and/or alternative defenses in various areas.

Extrafloral nectaries increase ant density on plants (Bentley 1976, Koptur 1979, Keeler 1981a, b). So do ant-tended aphids, membracids, and other sap-draining "pseudo-nectaries" (Carroll and Janzen 1973, Messina 1981, Skinner and Whittaker 1981, Fritz 1983). Because it may be to a tree's advantage to control ant density, extrafloral nectaries may have been selectively favored over insect "pseudo-nectaries." Although plants cannot relocate to a spot close to a superior ant partner, the species of ants that visit the nectaries of a species may be influenced by the amounts, concentration, and composition of the extrafloral nectar presented (Baker et al. 1978). Schemske (1982) did not find meaningful correlations with ants on *Costus* species, but this possibility warrants further investigation in other systems.

The visitation of *Inga* nectaries by ants in premontane moist forest is predictable, but the degree of protection is influenced by a number of factors (especially by which species of ant has a nest closest to the tree). An analysis of the costs and benefits of this facultative mutualism (as in Keeler 1981b) will be complicated by the differential effects of various ant species on the herbivore fauna. The secretion of extrafloral nectar and its subsequent use by ants is of mutual benefit to both *Inga* and the ants. Subsequent investigation will attempt to measure the possible differential effects on plant fitness resulting from different ant visitors.

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