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ALTERNATIVE DEFENSES AGAINST HERBIVORES IN *INGA* (FABACEAE: MIMOSOIDEAE) OVER AN ELEVATIONAL GRADIENT¹

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Abstract. *Inga densiflora* and *Inga punctata* have foliar nectaries that promote protection against herbivores by ants. Nectar-drinking ants were found to be less active at higher elevations than at lower elevations in Costa Rica, and ant defense less effective in upland populations of these trees. Herbivore damage to leaves was greater at higher elevations than at low elevation, although the abundance of lepidopteran larvae was not different. This study tested the hypothesis that lack of ant defense in *Inga* at high elevations is compensated for by alternative defenses. Upland *I. densiflora* and *I. punctata* had higher concentrations of phenolics in their leaves than their lowland counterparts. Extrafloral nectaries were found to be present and actively secreting nectar on plants at high as well as at low elevations. Adult wasp and fly parasitoid presence at nectar sources was greater at high elevations in the absence of ants, and parasitization of caterpillars reared from upland *Inga* was significantly higher than in those reared from lowland *Inga*. Thus, upland caterpillars on *Inga* are more vulnerable than those at low elevations to predators and parasitoids attracted to nectar, because at high elevations less of the nectar is taken by ants. The antiherbivore properties of upland *Inga* represent a novel complex of facultative defenses in the absence of protection by ants.

Key words: ants; caterpillars; Costa Rica; defense; elevational gradient; extrafloral nectaries; herbivores; parasitoids; phenolics; tannins; tropical trees.

INTRODUCTION

The protection of plants by ants has been demonstrated in numerous recent studies (Bentley 1977b, Buckley 1982); mutualistic ants are attracted to plants in a number of ways. Ants gather nectar from extrafloral nectaries (Bentley 1976, Koptur 1979, Schemske 1980, Stephenson 1982), harvest food bodies (Janzen 1967, Risch et al. 1977), reside in the plant body (Gomez 1977, Huxley 1978, 1980), and even visit honeydew-producing insects, analogues of extrafloral nectaries (Way 1963, Messina 1981, Fritz 1983). It has been assumed that plant features allowing ant-mutualisms have a fitness cost (O'Dowd 1979, Keeler 1981), and that plants may lose these traits either through natural selection when they no longer benefit the plants (Bentley 1977a, Rickson 1977), or through Mullerian "decay" whereby random mutations destroy a character unless maintained by natural selection (Muller 1949). Support for the costliness of ant-adaptations is shown in those plant features presumably adapted for mutualistic relationships with ants that lose prominence when the range of the plants extends into areas where ants do not exist (e.g., certain high-elevation and island populations of *Cecropia peltata* [Janzen 1969, Rickson 1977], high-elevation populations of *Bixa orellana* [Bentley 1977a], and Hawaiian populations of *Ipomoea indica* [K. Keeler, *personal communication*]). In addition, some plants produce

certain food items, harvested by ants, only when ants are present (e.g., food bodies of *Piper cenocladum* [Risch and Rickson 1981]).

Some examples suggest that trade-offs exist between ant defense and other kinds of defense against herbivores. The compensation may be chemical or mechanical. Rehr et al. (1973) found that species of *Acacia* protected by ants have much lower levels of cyanogenic glycosides than non-ant acacias. Bentley (1977a) observed that sepal nectaries of *Bixa orellana*, which at low elevations promote ant-protection against ovule and seed predators, do not exist at high elevations. Instead, the upland sepals are thick and leathery, providing greater physical protection from herbivores than the more papery lowland sepals.

The same plant features that attract ants can attract other organisms of potential benefit to the plants: extrafloral nectaries may also promote biotic protection by attracting parasitoids (Gilbert 1975, Atsatt and O'Dowd 1976, Smiley 1978a, b, Price et al. 1980, Hespeneide, *in press*). Certain kinds of extrafloral nectaries may have evolved for feeding and thereby encouraging protection by parasitoids (Gilbert and Smiley 1978); other plants with extrafloral nectaries, adapted for protection by ants, may be preadapted for mutualism with parasitoids.

To investigate whether compensation by other defenses exists in the absence of ant defense, I studied antiherbivore defenses of *Inga* spp. over an elevational gradient. *Inga densiflora* Benth. and *I. punctata* Willd. are protected by a variety of ants that visit their foliar nectaries at low elevations in Costa Rica (Koptur 1984a). The same species of *Inga* occur over a wide

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elevational range (sea level to 1400–1800 m) and through a series of tropical forest communities (León 1966, Croat 1978, S. Koptur, *personal observation*). In general, ant abundance declines as elevation increases in the tropics (Janzen 1973, Bentley 1977a), and preliminary observation suggested that this was so at my study sites. Field observations were conducted to answer the following questions. (1) Are *Inga* foliar nectaries functional at high elevations? (2) What is the abundance and activity of ants and other nectary visitors over the elevational range? (3) How does herbivore abundance compare on a given *Inga* species over the elevational range? (4) What are damage rates to leaves at different elevations? (5) How are these trees protected against herbivores in areas where there can be little or no ant protection?

In this study I document relevant aspects of the natural history of *Inga densiflora* and *I. punctata*, and also of mechanical and chemical properties of their leaves, in order to examine several hypotheses concerning the ecology and evolution of antiherbivore defenses. I report here on herbivore abundance and damage levels on *Inga* at different sites, differences in leaf phenolics in upland *Inga* populations, changes in the insect fauna at extrafloral nectaries over the elevational range, and the implications of these changes for plant protection.

INGA NATURAL HISTORY

Inga is a large (≈ 400 spp.) neotropical genus of mimoid legume trees, of which 25–30 species occur in Costa Rica (León 1966, Holdridge and Poveda 1975). *I. densiflora* and *I. punctata* are medium-sized trees, ranging from lower mid elevation wet forests (600 m elevation) to montane wet forests (1500–1800 m) in Costa Rica. They are commonly used as shade trees in coffee and cacao plantations and are therefore often found in disturbed areas, but are primarily mature forest species.

Leaves of *Inga densiflora* and *I. punctata* have foliar nectaries between each pair of opposite leaflets (2–3 pair in *I. punctata*, 4–8 pair in *I. densiflora*). These nectaries begin secretion as the leaf unfolds and continue to do so until the leaf is fully expanded and mature; most plants have some new leaves (and therefore some active nectaries) at all times (Koptur 1984a). Many species of ants, while visiting the foliar nectaries of *Inga*, provide protection of both young and mature leaves against a variety of insect herbivores by predation or by disturbing the herbivores until they leave. Some ants are better able to remove herbivores than others, but all common species tested removed at least small caterpillars (Koptur 1984a). Leaves on branches from which ants were excluded sustained greater damage than control leaves (Koptur 1984a).

Inga leaves are eaten by a wide variety of animals, including howler monkeys (Glander 1978, Milton 1978), sloths (Montgomery and Sunquist 1978), Or-

thoptera, Coleoptera, Hemiptera, Hymenoptera, snails, and caterpillars of Lepidoptera (S. Koptur, *personal observation*). This study focused on caterpillars, as they were the most numerous and most damaging of all herbivores found on *Inga* saplings in the study areas. Lepidopteran larvae from 16 families were found eating *Inga* and were reared to adulthood in the course of this study (Koptur 1982). The same species of herbivore rarely occurred over the entire elevational range of an *Inga* species, but frequently congeners had similar impact on the same species of *Inga* growing at different elevations. Major defoliators were caterpillars of the butterfly genus *Dismorphia* (Pieridae) (*D. amphione* Cramer in lowlands, *D. crisia lubina* Cramer in uplands; 22% of lepidopterans discovered and reared), and the skipper genus *Telemiades* (Hesperiidae) (*T. antiope* Plotz at lower elevations, *T. centrutes gallius* Mab. at higher elevations; 5%). Of secondary importance were moths of the families Notodontidae (*Hemiceras* nr. *sigula* Guenee, *Disphragis* nr. *handleyi* Schaus., *Rosema deolis* Cram.; 7%), Megalopigidae (*Plodia* sp.; 8%), Oecophoridae (*Stenoma ptychta* Walsingham, *S. prosora* Walsingham; 36% but total leaf damage slight), and Gelechiidae (*Charistica iriantha* Meyrick; 1%).

MATERIALS AND METHODS

The fieldwork was conducted at four sites in two different parts of Costa Rica. The site at the lowest elevation (600 m) was located at Turrialba, in two wooded areas in the grounds of the Centro Agronomico de Investigacion y Enseñanza. The other three sites were in three forest types near Monteverde (Puntarenas Province): one in Lower Montane Wet Forest (Holdridge 1967) remnants on farms in and around the community of Monteverde, elevation 1300–1380 m; the second in Lower Montane Wet Forest/Rain Forest Transition, elevation 1400–1520 m, in a large tract of privately owned forest contiguous with the Monteverde reserve; and the third in Lower Montane Rain Forest (“cloud forest”), elevation 1550–1650 m, in the Monteverde Cloud Forest Reserve. Elevational differences among the three Monteverde sites influence differences in rainfall (which increases with elevation) and temperature (which decreases with elevation), but differences in exposure may be of even greater importance in this regard. The higher sites were near the Continental Divide and were more exposed, experiencing greater winds and more rainfall because of airflow and cloud accumulation over the mountaintops. The Turrialba site has been described in Holdridge et al. (1971). The lowest, middle, and highest Monteverde sites were described by Feinsinger (1976), Powell (1979), and Lawton and Dryer (1980), respectively.

I used baiting experiments to determine the abundance of ants and parasitoids visiting nectaries at each site. Honey baits were placed on transects on the ground (as this is standard procedure) and on plants (since

these are more important to a study of foliar nectaries). For ground baiting, 20 white cards (3 × 4 cm) each dotted with one large drop of honey were placed 1 m apart on transects through the woods and monitored every 2 min for 1 h; I recorded the time of discovery by insects, identified the insects present each time, and noted whether or not recruitment by ants had taken place. (Recruitment was considered to occur when > 10 ants came to a food source subsequent to its initial discovery.) Plant baiting was carried out on 10 plants with foliar nectaries (mostly *Inga* spp.) and 10 plants without nectaries along a transect through the forest. Three leaves of each plant were dotted with honey at a height ≈ 1 m above the ground, and the baits were monitored every 10 min for 2.5 h, as discovery took longer for plant baits than for ground baits. Baiting experiments were performed in the daylight during clear weather and were repeated four times at each site: two wet-season dates (July and October), and two dry-season dates (January and March).

I surveyed *Inga* plants at each site for the presence of ants. Nectar secretion was examined in bagged leaves. Parasitoids were collected from nectaries and baits, and levels of parasitization were determined by rearing caterpillar herbivores.

To compare herbivore species diversity and abundance on *Inga* at different elevations, caterpillars and eggs were counted, removed, and reared once each month for a year from 10 tagged saplings, 1.8–3 m in height, of each *Inga* species at every site at which the species occurred. These were all forest individuals growing away from trails. Because the number of leaves sampled varied among trees and visits (range: 500–1000 leaves examined for each species at each site at which it occurred), data were expressed as the number of caterpillars per hundred leaves. Caterpillars were reared in plastic bags in the laboratory at ≈ 27°C. Parasitoid larvae emerging from caterpillars were allowed to pupate, then were transferred to vials in which the adults emerged.

At each site, new leaves were tagged and cumulative damage assessed on intact leaves of 10 other individuals of the same species. Damage was assessed using a scale of 0–8 to score each leaflet of the compound leaf (i.e., 12.5% increments). The presence of herbivores on these trees was recorded without removing the animals to provide a picture of undisturbed damage rates.

Toughness of leaf tissue was measured with a rod-shaped puncturing device (as in Feeny 1970) on 20 leaves of each species of each size-class. Punctures were always made at the same spot on a leaflet in the same position for each leaf sampled. The puncture rod diameter was 1.2 mm (area = 1.1 mm²). Pubescence was quantified by counting the number of hairs within an area of 0.5 cm² on 20 leaflets each of four different sizes (ages). Size-class categories of leaflets were: one-

quarter size, one-half size, three-quarter size (still expanding), and full size (mature).

To determine secondary compounds present, I performed a series of screening tests (Fong et al. 1971) on fresh leaves in the field. Cyanogenic glycosides were tested using picrate papers and Na₂CO₃. I tested for the presence of alkaloids with Dragendorff's test. Saponins were tested by shaking macerated leaf tissue in water. Phenols were detected with the *p*-nitraniline test.

For further study of phenolic constituents, leaf samples were collected and dried in an oven at ≈ 40°. Samples were extracted in 1% HCl in methanol (1 mL/0.1 g, solvent to dry mass of leaf tissue) for 12 h in darkness. The Folin-Denis method was used to measure overall phenol content (Ribereau-Gayon 1972). Different *Inga* species have different phenols (as shown by thin-layer chromatography; S. Koptur, *personal observation*), and different phenols produce different intensities with the Folin reagent (Ribereau-Gayon 1972). Comparisons were therefore made only within a species, under the assumption of only quantitative variation within a species, as the Folin-Denis test is not accurate for comparisons between species. For each species, an extract derived from a composite sample of new and old leaves from five plants was used to generate a standard curve relating absorption to concentration of the extract; absorption values were related to the mass of phenols in the extract by weighing the dried sample before and after extraction. (Concentration values therefore may have included small amounts of compounds other than phenols.) The Folin reading for a leaf sample could then be equated to the mass of phenol in the sample. The Biorad test was used to estimate protein content of five samples of fully expanded new leaves and five samples of mature leaves of the two species. For each analysis there were three replicates.

Palatability of foliage of different ages and phenol levels was investigated in feeding preference tests using four of the major lepidopteran herbivore species. Each experiment was repeated 20–35 times for each species in each comparison. Mature and new leaves from the same individuals of *I. densiflora* (growing at 1500 m) were compared in the first series of experiments. The second set of experiments compared mature foliage from *I. densiflora* high in phenols with mature foliage from another individual much lower in phenols. In the late afternoon, six fresh, undamaged leaflets from each of the two trees, all approximately the same size, were placed in a plastic box (12 × 20 × 8 cm) and mixed. One fourth-instar caterpillar was placed in the box, and allowed to feed until the next morning (12 h). The caterpillar was then removed and the total area eaten of each leaf type was compared. If the caterpillar did not feed at all, the trial was not included in the results. A score of "no preference" indicated no significant difference between leaf types in the amount eaten.

TABLE 1. Comparisons of *Inga* trees at different elevations with respect to presence of active extrafloral nectaries and presence of attendant ants.

Elevation	<i>Inga densiflora</i>			<i>Inga punctata</i>		
	<i>n</i>	With active nectaries	With ants	<i>n</i>	With active nectaries	With ants
			Number of trees†			
600 m	21	21	20*	16	16	16*
1300 m	25	21	11*
1500 m	25	20	4*
1650 m	25	23	1*
Contingency chi-square‡		5.3 (<i>P</i> = .07)	47.9 (<i>P</i> < .0001)		1.3 (<i>P</i> = .25)	11.23 (<i>P</i> = .0008)

* Significant differences among elevations.

† Trees without new leaves were not included in the sample; trees with new leaves but no extrafloral nectar secretion were counted as having inactive extrafloral nectaries. Blanks in the table occur where one *Inga* species was absent at a site.

‡ For presence/absence of nectaries (or ants) at different elevations.

The potential role of phenols as digestibility-reducing substances was investigated with the most abundant herbivore, the pierid butterfly *Dismorphia crisia lubina*, at the higher elevation site (1500 m). Eggs and first-instar larvae were found in the field and brought into the laboratory where they were reared on new (high phenol) and mature (low phenol) leaves of the same individual of *I. densiflora* from 1500 m. The number of days spent from egg hatching to pupation was tallied for each individual. Measurements of dry mass and of body and wing length were made on oven-dried (1 h at 40°) adults.

RESULTS

Active nectaries and ant attendance

Virtually all individuals of both *Inga* spp. had active extrafloral nectaries on their young foliage at 600 m

(Table 1). Activity of foliar nectaries remained high at high elevations; the morphological structures were present on every individual examined, and only a few individuals did not secrete foliar nectar (not a statistically significant difference, as shown by contingency table analysis: Table 1).

Ant attendance, however, declined significantly with increasing elevation (Table 1). Ants were rarely found on *Inga* at the highest site.

Baiting experiments

Discovery of ground baits and plant baits by ants was greater at low than at high elevations (Table 2). Discovery of ground baits by ants also differed significantly on different dates. Temporal differences may reflect a seasonal difference in ant abundance and/or activity. The rank order of number of baits discovered

TABLE 2. Discovery of ground and plant baits by ants, and recruitment to baits, at different elevations. Data are number of baits (out of 20) discovered or recruited to in 60 min (ground baits) or 150 min (plant baits).

Date	Discovery						Recruitment					
	600 m	1300 m	1500 m	1650 m	Total	LRChi†	600 m	1300 m	1500 m	1650 m	Total	LRChi
	Ground baits											
Jul 1979‡	20	14	10	11	55	19.69***	11	9	5	3	28	9.14*
Oct–Nov 1979	20	12	4	9	45	35.19***	12	7	4	6	29	7.51
Jan–Feb 1980	18	4	10	4	36	29.34***	10	1	8	2	21	16.52***
Mar 1980	18	2	9	6	35	31.68***	14	2	3	2	21	24.75***
Total	76	32	33	30	171	88.36***	47	19	20	13	99	38.77***
LRChi	5.76	23.31***	5.45	6.35	13.32**		1.83	13.34**	3.64	3.66	3.33	
	Plant baits											
Jul 1979‡	20	7	1	0	28	69.75***	18	5	0	0	23	60.49***
Oct–Nov 1979	19	0	0	0	19	79.77***	18	0	0	0	18	72.30***
Jan–Feb 1980	17	0	0	0	17	65.85***	15	0	0	0	15	54.72***
Mar 1980	19	2	0	0	21	71.16***	17	1	0	0	18	60.46***
Total	75	9	1	0	85	266.04***	68	6	0	0	74	235.80***
LRChi	4.62	17.37***	2.81	...	4.30		2.23	12.19**	2.29	

† Likelihood-ratio chi-square and associated significance level: * *P* < .05; ** *P* < .01; *** *P* < .001.

‡ Except June 1980 for 600 m site.

TABLE 3. Mean time to discovery of ground baits by ants at different sites ($\bar{X} \pm SD$; $n = 20$ baits at each site).

Date	Elevation (site)			
	600 m	1300 m	1500 m	1650 m
	Time to discovery (min)			
Jul 1979*	9.9 ± 6.3	27.7 ± 23.5	41.8 ± 23.5	37.9 ± 22.7
Oct–Nov 1979	11.8 ± 11.7	35.5 ± 24.2	53.9 ± 15.1	44.5 ± 21.7
Jan–Feb 1980	15.2 ± 17.6	51.3 ± 20.2	34.9 ± 25.8	54.5 ± 15.5
Mar 1980	16.1 ± 17.7	54.7 ± 15.9	41.9 ± 24.0	52.2 ± 16.5

* Except June 1980 for 600 m site.

changed among the upland sites during the two dry-season experiments, but baits at the 600 m site were always discovered much more frequently. For neither ground nor plant baits at 600 m, 1500 m, or 1650 m did rate of discovery differ according to date, but at 1300 m it did for both bait types, apparently due to wet season/dry season differences (July and October vs. January and March). At high elevations, discovery of plant baits by ants was substantially less frequent than discovery of ground baits.

Recruitment of ants to both ground and plant baits was greater at low than at high elevations (Table 2). On all dates for plant baits, and on all except October 1979 for ground baits, the sites differed significantly from each other in recruitment; again, the 600 m site had the greatest activity. Only at the 1300 m site did recruitment differ with date, exhibiting the same wet/dry seasonal pattern found for discovery of ground baits.

Finally, the mean time to discovery of ground baits by ants (Table 3) was much shorter at the 600 m site than at the other sites, again suggesting that nectar-drinking ants were most active at this elevation. By

assigning undiscovered baits a score of 61 min to discovery, I obtained a conservative estimate of the mean difference and variation among sites (in most trials some baits were not discovered).

The rate of discovery of ground baits by parasitoid Diptera and Hymenoptera differed significantly at different sites, but the trend was the reverse of that for ants (Table 4). Overall visitation to ground baits by parasitoids was low compared to visitation to plant baits. The number of parasitoids at plant baits differed significantly at different sites (Table 4), and this difference was found on each sampling date. Parasitoid discovery of plant baits differed significantly with date over all elevations, but not at each of the individual sites analyzed separately.

Caterpillar herbivore abundance

Caterpillar abundance did not differ significantly by elevation for either *I. densiflora* (Fig. 1) or *I. punctata* (Fig. 2) (Wilcoxon signed rank test): month-to-month variation was great, but overall means for the study period did not differ significantly (Figs. 1 and 2). Peaks of abundance occurred in April, late in the dry season.

TABLE 4. Discovery of (A) ground and (B) plant baits by parasitoids at different elevations; $n = 20$ baits in each case.

A) Ground baits						
Date	600 m	1300 m	1500 m	1650 m	Total	LRChi†
	No. baits discovered in 60 min					
Jul 1979‡	0	0	4	6	10	15.83**
Oct–Nov 1979	0	0	3	1	4	6.91
Jan–Feb 1980	0	1	2	3	6	4.77
Mar 1980	0	1	2	3	6	4.77
Total	0	2	11	13	26	26.58***
LRChi	...	2.82	1.13	4.81	3.07	
B) Plant baits						
Date	600 m	1300 m	1500 m	1650 m	Total	LRChi
	No. baits discovered in 150 min					
Jul 1979‡	0	1	6	10	17	22.66***
Oct–Nov 1979	1	0	6	1	8	11.70**
Jan–Feb 1980	0	0	8	2	10	20.36***
Mar 1980	1	8	12	12	33	19.74***
Total	2	9	32	25	68	49.01***
LRChi	2.82	21.41***	4.97	23.78***	27.54***	

† Likelihood-ratio chi-square and associated significance level: ** $P < .01$; *** $P < .001$.

‡ Except June 1980 for 600 m site.

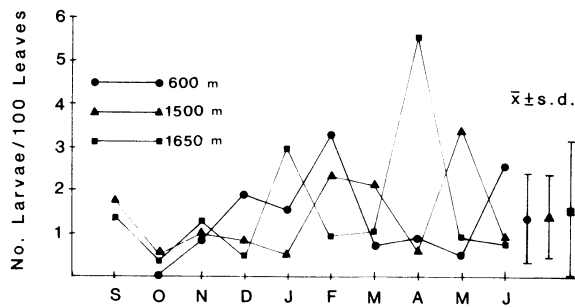


FIG. 1. Number of caterpillar herbivores per 100 *I. densiflora* leaves. Sample sizes: at 600 m, 324 leaves; at 1500 m, 1278 leaves; at 1650 m, 633 leaves (on 10 saplings). Overall $\bar{X} \pm \text{SD}$: 600 m, 1.36 ± 1.06 caterpillars; 1500 m, 1.43 ± 0.98 caterpillars; 1650 m, 1.60 ± 1.56 caterpillars.

Leaf damage

For *I. densiflora*, leaf damage percentages varied among all elevational sites (ANOVA, $F = 281.6$, $df = 2$, $n = 2117$, $P < .0001$) (Fig. 3). Leaves at 1500 m sustained the most damage, followed closely by leaves at 1650 m; leaves at 600 m had the least damage. Mean leaf damage percentages after 6 mo did not differ significantly between 600 m and 1300 m elevations for *Inga punctata* (Fig. 4; two-tailed t test of arcsine-transformed percentages [Sokal and Rohlf 1969:607]: $t = 1.71$, $df = 1158$, $.10 > P > .05$).

Mechanical properties

For both *Inga densiflora* and *I. punctata* mature and new leaves differed significantly in toughness ($F = 717.17$, $df = 1$, and $F = 219.48$, $df = 1$, respectively, $P < .0001$, for each; two-way analysis of variance), but leaves of the same age from different elevations did not differ significantly in toughness (total $df = 79$, $P > .05$) (Table 5). Pubescence of *I. densiflora* leaves differed with age ($F = 1847.08$, $df = 3$, $P < .0001$) and elevation ($F = 57.02$, $df = 1$, $P < .001$); the interaction between age and elevation was significant ($F = 3.09$, $df = 3$, total $df = 89$, $P < .05$). Averaged over all sizes (ages) leaves were somewhat hairier at 1500 m than at 600 m (Table 5). For *I. punctata*, pubescence also differed with both age ($F = 496.02$, $df = 3$, $P < .0001$) and elevation ($F = 10.36$, $df = 1$, $P < .002$), and the interaction between age and elevation was also significant ($F = 3.89$, $df = 3$, total $df = 79$, $P < .025$). Averaged over sizes, leaves were less hairy at 1300 m than at 600 m. The hairs on both species are soft and unbranched.

Chemical properties

Screening tests for cyanogenic glycosides, alkaloids, and saponins were all negative. All *Inga* species tested (including *I. brenesii*, *I. densiflora*, *I. longispica*, *I. mertoniana*, and *I. punctata*) gave a strong positive response with *p*-nitraniline, indicating the presence of phenolic compounds.

Total phenol levels of new and mature leaves of low-elevation *I. densiflora* were not significantly different; at higher elevations, new leaves had higher total phenol concentrations than mature leaves (Table 6). Furthermore, both mature and new upland leaves had significantly more phenols than their low-elevation counterparts (Table 6). Phenol levels differed with age ($F = 74.2$, $P < .0001$, $df = 1$) and elevation ($F = 40.49$, $P < .0001$, $df = 1$), and the interaction between elevation and age was significant ($F = 14.01$, $P < .001$, $df = 1$; total $df = 103$). Similar trends were seen in leaves of *I. punctata* (Table 6); phenol levels differed with age ($F = 3.99$, $P < .05$, $df = 1$) and elevation ($F = 54.45$, $P < .0001$, $df = 1$), but there was no significant interaction ($F = 1.81$, $P > .05$, $df = 1$; total $df = 99$).

Protein contents of new leaves of *I. densiflora* were substantially greater than those of mature leaves (protein as percentage of dry mass ranged from 2.4 to 4.1% in new leaves, $\bar{X} = 2.9 \pm 0.7\%$ [SD]; and from 1.0 to 2.0% in mature leaves, $\bar{X} = 1.4 \pm 0.4\%$); these differences are significant (Mann-Whitney $U = 25$, $P = .01$, two-tailed test, $n = \text{five trees}$). Protein content of new *I. punctata* leaves ranged from 2.5 to 4.7% ($\bar{X} = 3.6 \pm 1.2\%$), and for mature leaves ranged from 2.2 to 4.3% ($\bar{X} = 2.8 \pm 1.0\%$); these differences are not significant (Mann-Whitney $U = 19$, $P > .10$).

In feeding preference tests with high-elevation new leaves vs. high-elevation old leaves from the same trees, there were different responses by the four caterpillar herbivore species tested (results analyzed using the sign test). Two species (*Dismorphia* and *Plodia*) showed no preference; another preferred old leaves (*Telemiades*; $P < .001$), and the other preferred new leaves (*Rosema*; $P = .02$). Also, mature leaves high in phenols were

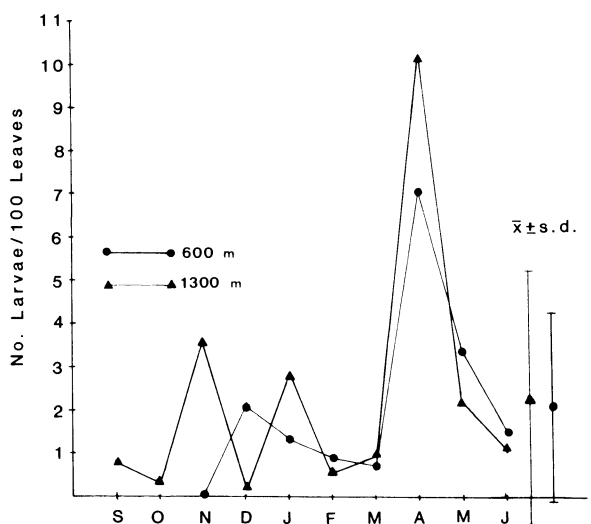


FIG. 2. Number of caterpillar herbivores per 100 *I. punctata* leaves. Sample sizes: at 600 m, 484 leaves; at 1300 m, 1441 leaves (on 10 saplings). Overall $\bar{X} \pm \text{SD}$: 600 m, 1.91 ± 2.23 caterpillars; 1300 m, 2.30 ± 3.02 caterpillars.

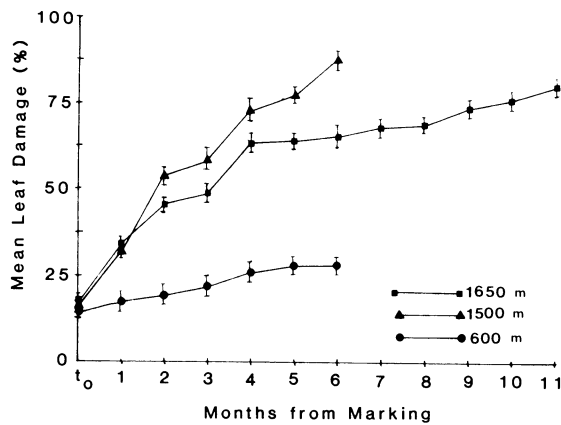


FIG. 3. Cumulative damage levels on marked leaves of *I. densiflora*. Error bars are ± 1 SE. Sample sizes: at 600 m, 456 leaves; at 1500 m, 832 leaves; at 1650 m, 829 leaves.

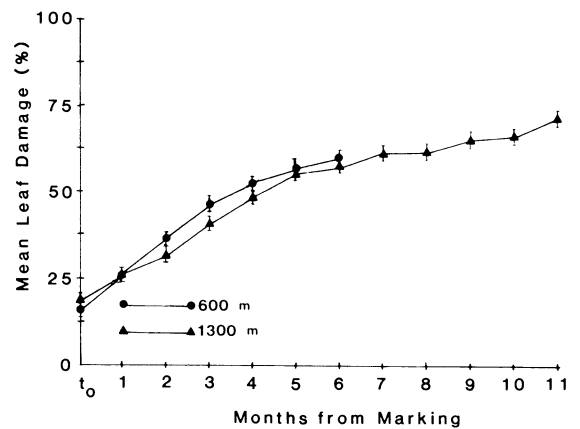


FIG. 4. Cumulative damage levels on marked leaves of *I. punctata*. Error bars are ± 1 SE. Sample sizes: at 600 m, 498 leaves; at 1300 m, 660 leaves.

compared with mature leaves low in phenols, and no preference was found in either *Dismorphia* or *Plodia*.

Developmental time of *Dismorphia* caterpillars did not differ on diets of upland new or mature leaves: mean time from hatching to pupation was 42.3 ± 2.4 d on new leaves ($n = 30$) and 43.5 ± 5.9 d on old leaves ($n = 21$) (Student's *t* test, $P > .05$). Most larvae went through five instars, but a greater proportion of the individuals reared on old leaves (16 out of 27) than of those reared on new leaves (12 out of 47) went through six instars (chi-square = 5.09, $P < .025$). I considered male and female adults separately, and although mean dry mass, forewing length, and body length were slightly greater for individuals reared on new leaves, no differences were significant ($P > .05$, ANOVA).

Parasitoids

Parasitization of caterpillars on *Inga* increased significantly with elevation over all *Inga* species and all caterpillar families combined (Likelihood-Ratio chi-square = 16.4, $P < .01$; Table 7). Within *I. densiflora*, *I. punctata*, or each of the three other species, the dif-

ferences among elevations were not significant; only on *I. mertoniana* were the elevational differences significant. Within major defoliator families, the Pieridae and Oecophoridae had significantly higher levels of parasitization at high than at low elevations.

Both Hymenoptera and Diptera parasitoids were reared from Lepidoptera larvae and eggs on *Inga* (Koptur 1982). The same parasitoid species was frequently reared from a variety of hosts; for each of seven parasitoid species, rearing occurred from two or more different families of Lepidoptera. Some of the same parasitoids (two of the six Braconidae species, for example) reared from herbivores were collected at *Inga* nectaries (Koptur 1982). A large proportion (roughly half) of the parasitoids collected at *Inga* nectaries are known to have lepidopteran hosts (Koptur 1982).

DISCUSSION

Most *Inga* individuals growing at high elevations have active extrafloral nectaries. However, nectar-drinking ants visit nectaries less at upland sites than at lowland sites, and ant recruitment to nectar resources is much lower once they have been discovered.

TABLE 5. Physical properties of *Inga* leaves at different elevations: leaf toughness (pressure required to puncture tissue) for new and mature leaves, and leaf pubescence (measured on the adaxial surface) for four size (age) classes of leaflets. $n = 20$ leaves for each measure (1 leaflet per leaf); data are means ± 1 SD.

Species	Elevation (m)	Leaf toughness (kPa)		Leaf pubescence (no. hairs/0.5 cm ²)			
		New leaves	Mature leaves	¼ size	½ size	¾ size	Mature leaves
<i>I. densiflora</i>	600	658.56 ± 98.78	2740.51 ± 484.98	262.7 ± 13.66	222.6 ± 8.54	16.50 ± 8.50	10.60 ± 9.42
	1500	637.88 ± 110.99	2646.81 ± 740.31	266.0 ± 12.45	230.6 ± 13.75	19.10 ± 9.18	9.90 ± 10.76
<i>I. punctata</i>	600	1044.32 ± 137.38	2804.17 ± 483.47	487.5 ± 9.41	338.2 ± 10.22	256.4 ± 7.37	109.5 ± 8.20
	1300	1092.55 ± 193.82	3140.62 ± 947.14	501.4 ± 10.15	341.2 ± 12.93	254.2 ± 8.91	114.2 ± 8.06

TABLE 6. Results of Folin-Denis tests for total phenols in *Inga* foliage. $n = 30$ samples total from five trees combined for each leaf type.

Species	Elevation (m)	Phenol concentration (% of dry mass)*	
		New leaves ($\bar{X} \pm SD$)	Mature leaves ($\bar{X} \pm SD$)
<i>I. densiflora</i>	600	5.05 \pm 1.6 ^a	5.12 \pm 1.49 ^a
	1500	20.62 \pm 6.72 ^b	8.73 \pm 5.14 ^c
<i>I. punctata</i>	600	2.55 \pm 0.84 ^d	2.70 \pm 0.68 ^d
	1300	6.25 \pm 0.75 ^c	5.75 \pm 1.69 ^f

* Different superscript letters mark significantly different means ($P < .05$), based on ANOVA followed by t tests.

Ants visiting low-elevation *Inga* saplings actively prevent herbivores from feeding on leaves (Koptur 1984a). In contrast, ants provide upland *Inga* with little or no protection against herbivores. If herbivore pressure (i.e., abundance of herbivores, amount of damage they cause) is lower at upland sites, increased levels of alternative defense in the absence of ant protection would not be expected. If, however, herbivore pressure on upland *Inga* is the same or greater than on lowland counterparts, and the costs of herbivory are the same for trees at all elevations, then increased levels of alternative defenses would be selected for. The latter situation is the case for these *Inga* species. Overall herbivore abundance did not differ significantly among elevational sites for either *I. densiflora* or *I. punctata*. Late dry-season peaks in herbivore abundance may have been due to the greater number of sunny hours and the warmer temperatures, which stimulate plant growth and insect activity (Janzen 1973, Buskirk and Buskirk 1976). Damage to leaves did not differ among elevational sites for *I. punctata*; in *I. densiflora* damage levels were significantly higher at upland sites.

Leaves of upland *Inga* were neither significantly tougher nor uniformly more pubescent than their lowland counterparts. Although sclerophylly certainly functions as a defense in other plants (Rausher 1981), and increased levels of mechanical protection of foliage have been found in areas of minimal ant protection (as in *Bixa*; Bentley 1977a), *Inga* trees did not show these increases. Pubescence has a deterrent effect on some small larvae (I have seen first-instar *Plodia* held well above the young leaf tissue of *I. brenesii* by the very dense pubescence), but it may also function in thermoregulation.

Inga leaves have large quantities of phenolic compounds (5–20% dry mass). Both old and new leaves of plants at high elevations, where ants are absent, have substantially more phenols than their counterparts at low elevations, where ants are abundant. At lowland sites, *Inga* leaves receive substantial protection against herbivores from ants (Koptur 1984a). Increased levels of phenols may have resulted from selection by herbivores and may compensate for lack of ant defense at

high elevation. Phenols can influence food choice of herbivores and/or affect herbivore development (Feeny 1970, Haukioja and Niemela 1977, 1979, McKey et al. 1978, Haukioja 1979, 1980, Wrangham and Waterman 1981). High tannin contents may reduce nitrogen assimilation in animals (reviewed in Waterman et al. 1980), but tannin compounds do not always have a negative effect on protein digestibility (Fox and Macauley 1977, Bernays 1978, Bernays and Woodhead 1982). Evidence that phenols affect palatability of *Inga* foliage to caterpillar herbivores was not found in this study. In a more general investigation, Coley (1983) found no correlation between phenol and damage levels in tropical trees. Zucker (1983) reviewed the history of ecological interpretations of tannin function, questioning both the notion that tannins are “generalized” in their actions and the prevalent acceptance of an anti-herbivore function for tannins in plants.

Therefore, alternative explanations for high phenol levels in upland *Inga* populations must also be considered. The first is that phenols may be higher in response to selection by pathogens and may afford protection against microorganisms (Swain 1977, 1978, 1979, Zucker 1983). Fungi may be more prevalent or aggressive in the cool and misty cloud-forest environment (which is consistently wet, as opposed to lower elevation wet forests that sometimes dry out when it is sunny). Another explanation could involve life-history characteristics: if individual leaves live longer at higher elevations, greater concentrations of phenols may be the result of accumulation over a longer life. Observations of tagged leaves for 2½ yr at all sites (S. Koptur, *personal observation*) indicate that trees at all elevations are nondeciduous and that individual leaves live from 6 mo to >2½ yr; however, no significant differences in leaf life-span were found among elevations. A third alternative is that increased insolation at higher elevation causes leaves to produce more phenols as “sunscreen,” or some other by-product of increased radiation. This possibility can only be tested with reciprocal transplant experiments, which are now being planned.

Extrafloral nectaries of *Inga* are visited by hymenopteran and dipteran parasitoids as well as ants. Parasitoids were seen more frequently at honey baits and nectaries at upland sites, where ants are less common; ants may exclude parasitoids from *Inga* nectaries and baits at lower elevations. Aggressive behavior of ants toward parasitoids was described by Pierce and Mead (1981) in ants that tend secretory glands on lycaenid caterpillars and protect the caterpillars against parasitization by braconid wasps. Also, ants may well usurp nectary resources on plants, diminishing visitation by parasitoids. Parasitoids were more abundant at plant baits than at ground baits at my study sites; it may be that adult parasitoids are more likely to discover food resources above the ground, as they fly rather than crawl. Analyses of extrafloral nectar from several up-

TABLE 7. Parasitization of caterpillars reared from *Inga* at different elevations, (A) arranged by *Inga* species, (B) arranged by selected herbivorous caterpillar families, and (C) overall.

	Elevation (m)				Total	LRChi‡
	600	1300	1500	1650		
A) By <i>Inga</i> species						
<i>Inga brenesii</i>						
No. reared	...	35	13	...	48	2.7
% parasitized	...	5.7	23.1	...	10.4	
<i>Inga densiflora</i>						
No. reared	13	...	120	62	195	1.69
% parasitized	15.4	...	10.8	17.8	13.3	
<i>Inga longispica</i>						
No. reared	...	17	2	29	48	2.7
% parasitized	...	5.9	0	20.7	14.6	
<i>Inga mortoniana</i>						
No. reared	...	36	74	36	146	7.17*
% parasitized	...	13.9	28.4	41.7	28.1	
<i>Inga oerstediana</i>						
No. reared	1	1	2	...	4	1.73
% parasitized	0	0	50.0	...	25.0	
<i>Inga punctata</i>						
No. reared	11	174	2	...	187	1.98
% parasitized	9.1	10.3	50.0	...	10.7	
B) By caterpillar family						
Hesperiidae						
No. reared	6	...	7	14	27	2.66
% parasitized	33.3	...	28.6	7.1	18.5	
Megalopigidae						
No. reared	...	18	33	7	58	0.11
% parasitized	...	38.9	36.4	42.9	37.9	
Notodontidae						
No. reared	2	31	14	4	51	1.4
% parasitized	0	12.9	7.1	25.0	11.8	
Oecophoridae						
No. reared	3	115	94	49	261	10.25†
% parasitized	0	2.6	11.7	14.3	8.1	
Pieridae						
No. reared	6	23	47	37	113	26.3**
% parasitized	0	0	14.9	45.9	21.2	
Saturniidae						
No. reared	...	21	2	...	23	1.83
% parasitized	...	9.5	50	...	13	
C) All <i>Inga</i> species and all caterpillar families						
No. reared	25	263	213	127	628	16.4**
% parasitized	12.0	9.9	18.3	25.2	15.9	

‡ Likelihood-ratio chi-square and associated significance levels: * $P < .05$; † $P < .025$; ** $P < .01$.

land and lowland trees of each species have revealed no substantial differences in nectar chemistry (S. Koptur, *personal observation*).

Unlike other plants with ant-related traits, *Inga* have not lost their foliar nectaries in upland areas where ants are not active. Extrafloral nectar production may serve a function by feeding adult wasp and fly parasitoids, promoting parasitization of caterpillars eating *Inga*. The fact that not every individual *Inga* at higher elevations produces nectar on its new leaves suggests that perhaps this trait is being lost in the absence of direct selective pressure by ants for its maintenance (Mullerian decay, or elimination of "molecular noise"; Regal 1977). An individual that continues to produce nectar in the absence of ants will feed parasitoids, but

the parasitization of caterpillars eating that individual will not necessarily benefit that tree directly. If the parasitized caterpillar's life is shortened, this will certainly save the individual plant from a substantial amount of damage; the later instars eat much more than the earlier instars (Scriber and Slansky 1981). However, many parasitized caterpillars on *Inga* feed well into the fifth instar, and may eat substantial amounts of foliage after being parasitized. Different parasitoids have different effects on the feeding of their caterpillar hosts; some decrease feeding rate, others increase it (Price et al. 1980). In any case, the parasitized caterpillar dies after emergence of the parasitoids, and fails to reproduce. The number of herbivores in the next generation will presumably be reduced, though

not necessarily on the tree at which the parasitoid fed, and the number of parasitoids will be increased, thus potentially benefitting the entire population of *Inga* trees. The individual producing the nectar may benefit, as may the entire population. Moran and Hamilton (1980) consider low nutritive quality as a defense against herbivores. Individual plants may suffer as well as their herbivores, but traits such as low nitrogen content, high tannins, or production of foliar nectar may be selected for if early larval stages are prolonged, increasing the likelihood of herbivore mortality via predation or parasitization before herbivores reach the later, larger instars. The individual plant possessing the trait may save some leaf area overall.

Extended developmental time can result in longer exposure of the larval stages to predators, parasitoids, and other enemies (Feeny 1976, Lawton and McNeill 1979, Price et al. 1980) and increased likelihood of discovery by enemies that feed on nectar at leaves. If caterpillars eating *Inga* at high elevations (where leaves have more phenols and temperatures are cooler) take longer to develop, they may eat more leaf area during their larval life. In fact, leaf-damage levels of *I. densiflora* (but not of *I. punctata*) were higher at high elevations, although caterpillar herbivore abundance was no higher there. Protection by ants is a generalized kind of antiherbivore defense, effective against a wide range of insect herbivores. Parasitoids visiting extrafloral nectaries and the resulting parasitization of herbivores may also be considered a generalized defense, as parasitoids of many different orders of insects (Lepidoptera, Diptera, Coleoptera) visited the nectaries of *Inga*. In addition, the same species of parasitoid was reared from a number of different families of Lepidoptera (e.g., the braconid wasp *Glyptapanteles* sp. from Pieridae, Megalopigidae, and Notodontidae).

If, on the other hand, the presence of foliar nectaries does not lower herbivory levels in upland populations, their presence at high elevations may still be maintained by gene flow between populations over the elevational gradient. *Inga* are pollinated by strong-flying hawk moths and hummingbirds capable of carrying pollen long distances (Koptur 1983), and neighborhood size in *Inga* may be quite large (Koptur 1984b); hawk moths have been found in cloud forests at Monteverde carrying pollen from lowland plant species, evidence that pollen can be moved great distances (W. A. Haber, *personal communication*). However, Endler (1973) found that the effect of gene flow in retarding the differentiation of populations over environmental gradients may be small. Alternatively, genetic correlations may exist between extrafloral nectaries and some other trait. If the other trait were selected for at higher elevations, extrafloral nectaries would be maintained indirectly. Nectar secretion may be influenced by environmental factors as well; fewer individuals may be able to secrete nectar at lower upland temperatures.

My data thus suggest that ecological and evolutionary changes have occurred in the interactions among *Inga* trees, herbivores, and protective agents at lowland and upland sites. Ants appear to provide an effective, direct antiherbivore defense: damage to *Inga* leaves in ant-protected areas is lower than in upland areas, where herbivores eat more leaf tissue before the possible chemical defense and subsequent alternative biotic defense (parasitoids) have an effect. The extreme adaptationist view that plants can be perfectly adapted to each local environment may not be realistic, and foliar nectaries may not serve to promote protection equally well wherever a plant is found; but extrafloral nectaries may play an important role in antiherbivore defense of *Inga* at all elevations, by attracting not only "pugnacious bodyguards" (Bentley 1977b), but also other, less obtrusive, benefactors.

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