

SPATIAL VARIATION IN THE EFFECT OF ANTS ON AN EXTRAFLORAL NECTARY PLANT¹

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Abstract. I investigated variation in the effect of ants at extrafloral nectaries on plant reproductive success among three populations of *Cassia fasciculata* (Leguminosae) in northern Florida. Results show that the possession of extrafloral nectaries can lead to increased reproduction. Density of ants and removal of experimentally placed *Drosophila* larvae were far higher on *C. fasciculata* than on nonnectariferous background plants. Ants preyed on eggs and small larvae of lepidopteran herbivores. *C. fasciculata* plants from which ants were excluded had more larvae of the major seed pod predator *Phoebis sennae* (Pieridae; Lepidoptera), suffered higher pod predation (at one site), and had lower reproductive output (at two sites) than did control plants to which ants had access. Effects of extrafloral nectaries on reproduction of *C. fasciculata* varied among the three populations, due apparently to differences in density of ants and potential herbivores. At the site with the lowest density of ants and herbivores, pod set was not significantly different between control and ant exclusion groups. Where they were more numerous, ants had a small but significant positive effect. Only where the abundance of both ants and potential herbivores was high did ants visiting extrafloral nectaries strongly increase the reproductive success of individuals of *C. fasciculata*. The species of ants present and differences among herbivore species in susceptibility to ant attack may have also influenced the effect of extrafloral nectaries at any one site. Although the average effect of extrafloral nectaries throughout a plant species may be positive, the strength of this effect was found to vary widely among local populations.

Key words: ant exclusion; *Cassia fasciculata*; extrafloral nectaries; gelechiid larva; herbivory; mutualism; *Phoebis sennae*; plant reproduction; predation; variation.

INTRODUCTION

Many recent field studies have demonstrated that ants visiting extrafloral nectaries can increase plant fitness by deterring leaf herbivores (Koptur 1979, Stephenson 1982), flower herbivores (Deuth 1977, Schemske 1980, Horvitz and Schemske 1984), and seed predators (Inouye and Taylor 1979, Pickett and Clark 1979, Keeler 1981a). Aimed at testing whether or not the adaptive significance of extrafloral nectaries lies in their attraction of ants, these studies deal primarily with the typical or average effect of extrafloral nectaries on plant reproduction (but see Horvitz and Schemske 1984).

For at least two reasons, however, the effect of possessing extrafloral nectaries on plant fitness should vary over space. First, the density of ants available to plants may differ from place to place (e.g., Sanders 1970, Doncaster 1981, Levings 1983). In some sites few ants will visit plants regardless of the presence of extrafloral nectaries, and the ecological effect of extrafloral nectaries will be insignificant (see Bentley 1976). Second, independent of this variation, the density of potential herbivores may vary widely over space (e.g., Root 1973, White 1974). In sites where plants possess few herbivores, extrafloral nectaries would again have little effect on plant reproduction. Possession of extrafloral nectaries, therefore, should increase plant reproductive

success strongly only where both ant density and the abundance of potential herbivores is high.

In 1982 I investigated variation in the effect of possessing extrafloral nectaries on the reproductive output of *Cassia fasciculata* (Leguminosae) in northern Florida. Here I report the potential effect of extrafloral nectaries by answering three questions. First, does the presence of extrafloral nectaries increase ant visitation over that of nonnectariferous background vegetation? Second, can these ants deter potential herbivores on the plants? Third, can the presence of these ants lead to reproductive output higher than that of conspecifics from which ants are excluded? Then I document spatial variation in density of ants and potential herbivores, and investigate whether, due to this variation, the intensity of benefit from ant visitation varies over space.

NATURAL HISTORY

The plant

Cassia fasciculata Michx., partridge pea, is an annual herbaceous legume found throughout most of the eastern United States (Pullen 1963, Isley 1975). In Florida the plant occurs in a wide range of habitats, including open oak woodland, saw palmetto-oak prairie, longleaf pine-turkey oak sandhill, openings in white sand scrub, and most commonly on roadsides and in old fields.

Seeds of *C. fasciculata* germinate in May. Leaves are 3–6 cm long and consist of 6–20 pairs of linear leaflets. Protruding from each leaf petiole is a cup-shaped extrafloral nectary ≈ 1.5 mm in diameter and 0.5 mm tall, which in my study sites secreted nectar at an average

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TABLE 1. Ant species visiting the extrafloral nectaries of *Cassia fasciculata* control plants. Values are means per plant over all censuses ($n = 40$ control plants per site).

Ant species	Site 1	Site 2	Site 3
% total no. ants visiting at site			
Dolichoderinae			
<i>Conomyrma edeni</i>	0.22	3.28	NP*
<i>Iridomyrmex pruinosus</i>	81.63	75.60	5.94
Formicinae			
<i>Camponotus socius</i>	5.94	0.21	8.17
<i>Formica pallidefulva</i>	NP	NP	8.78
<i>Paratrechina parvula</i>	NP	0.17	10.22
Myrmicinae			
<i>Crematogaster clara</i>	1.20	0.21	31.24
<i>Crematogaster minutissima</i>	NP	NP	0.28
<i>Monomorium viridum</i>	NP	NP	0.60
<i>Pheidole metallescens</i>	0.18	1.27	23.35
<i>Pheidole morrisi</i>	1.44	16.13	2.04
<i>Solenopsis geminata</i>	9.39	4.31	6.48
Pseudomyrmecinae			
<i>Pseudomyrmex delicatulus</i>	NP	0.08	2.67
Total number of species	7	9	11
Total number of ant individuals	2923	2066	1148

* NP = not present.

rate (mass sucrose equivalents per hour ± 1 SD) of $11.05 \pm 6.59 \mu\text{g/h}$. Racemes, holding up to eight flowers, emerge from leaf axils during the July-through-September flowering period. Flowers bloom for one day, produce no nectar, and are self-compatible, although they require insect visitation for effective pollen transfer (Hobson 1972). Pollination is effected primarily by bees in the families Apidae, Anthophoridae, and Halictidae (Robertson 1890, Thorp and Estes 1975, Parrish and Bazzaz 1979; A. M. Barton, *personal observation*). Seed pods 3–10 cm long and 1–2 cm wide mature from August through October. These pods dehisce elastically, usually by the middle of October. A typical plant at the time of dehiscence is ≈ 50 cm tall and possesses ≈ 500 leaves and 100 pods.

Insects

I investigated all of the major herbivores that use *Cassia fasciculata* near Gainesville, Florida. First, the larvae of *Polyhymno luteostrigella*, a tiny gelechiid moth, occur on the plant from July to October. Solitary black eggs are oviposited by adult female moths on leaf surfaces. After hatching, each larva ties together several opposite leaflets with silk. Within this protected space, it removes tissue from the leaf surface, leaving behind skeletonized leaflets. After attaining a size of ≈ 4 –6 mm, larvae pupate and then emerge from within the larval feeding space.

A second herbivore is the caterpillar *Phoebis sennae*, the cloudless sulphur butterfly (Pieridae; Lepidoptera). From July to October, adult females deposit solitary

eggs, primarily on new leaves. Larvae are usually found on growing tips, flowers, and pods, although they feed on all plant parts. Final-instar larvae (35–45 mm long) leave the plant via a silk line or the stem and pupate on other vegetation.

The numbers of two other lepidopteran herbivores, *Anticarsia gemmatalis* (Noctuidae) and an unidentified geometrid, were combined because they were relatively uncommon on *C. fasciculata*. *A. gemmatalis*, the velvetbean caterpillar, is a major pest of soybeans and occurs on several native legumes; it has not, however, been recorded as feeding on *C. fasciculata* (Moscardi 1979) and may move accidentally onto the plant from surrounding vegetation (F. Slansky, Jr., *personal communication*).

A fourth group consists of several species of grasshoppers from the superfamilies Acrididoideae and Tetragonioideae. These are found on the plants throughout the growing season.

Herbivores comprise only a small part of the insect fauna I found on *C. fasciculata*. More than 50 species of insects that were neither herbivores nor seed predators of this plant visited the extrafloral nectaries. Ants were the most abundant visitors (for species composition, see Table 1). Other insects (e.g., wasps, flies, beetles) also commonly visited plants. Some of these may be mutualists of the plant because they may parasitize or prey upon herbivores, whereas others probably simply usurp nectar.

METHODS

Study sites

To sample from the wide range of ecological conditions where *Cassia fasciculata* occurs in northern Florida, I chose three sites that differed in plant species composition and soil characteristics.

Site 1, in Levy County 40 km west of Gainesville, was in a typical 15–20 yr old sandhill association (see Laessle 1942, Veno 1976), with a canopy dominated by *Pinus palustris* and *Quercus laevis*. Common understory plants, in addition to *C. fasciculata*, were *Ceratiola ericoides*, *Rhus copallina*, and *Eupatorium compositifolium*. I sampled *C. fasciculata* on each side of a little-used road ≈ 1 m into the adjacent woods. These plants received a high level of sunlight and grew in sandy soil containing little litter.

Site 2 was located along the edges of a power-line right-of-way that cuts through mature pine and oak woods in San Felasco State Park, 13 km north of Gainesville. *Quercus hemisphaerica*, *Pinus taeda*, and *Carya* spp. dominated the canopy vegetation. In the power-line cut, the most abundant plant species were *Rhus copallina*, *Q. hemisphaerica*, *Eupatorium compositifolium*, and *Cassia fasciculata*. I sampled plants on each ecotone between the power-line cut and the woods. Although litter accumulation was substantial in the woods, soil on the ecotone was bare and sandy.

Conditions were less sunny than at site 1 due to partial shading from canopy trees.

Site 3 was in a 30-ha tract of mature sandhill vegetation bordering the Department of Plant Industry on Southwest 34th Street in Gainesville. As at site 1, the canopy was dominated by *Pinus palustris* and *Quercus laevis*. Because they had not been burned for many years, however, the forest understory and floor were diverse and dense compared to those of site 1. Common plants were *Rhus copallina*, *Quercus hemisphaerica*, *Indigofera hirsuta*, and *Cassia fasciculata*. I used *C. fasciculata* individuals ≈ 2 m on each side of the perimeter of a circular, artificial opening ≈ 40 m in diameter and 40 m within the woods. Conditions were shadier, moister, and less sandy than at the other two sites.

Ant exclusion

During the 1st wk in June 1982, I tagged 40 randomly chosen control plants and 40 exclusion plants at each site. I prevented ants from crawling up the stems of exclusion plants by applying Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan, USA) to the bases of the stems at least every 2 wk. The area within 1 m of every tagged *C. fasciculata* individual was kept clear of vegetation taller than 10 cm; this served to block access to plants by ants from surrounding vegetation and to standardize plant density among sites and between control and exclusion treatments. The ant exclusion probably did not alter access to the plants by potential herbivores; among the common herbivores, only grasshoppers gained access to the plants from the ground, and generally they accomplished this by jumping.

Several of the exclusion plants snapped at the points of Tanglefoot application, during a severe storm on 20 July. I terminated the experiment, and on 24–28 July applied Tanglefoot over masking tape on new exclusion plants. Only the data from the second experiment (final four censuses) were used in comparisons of control and exclusion plants. However, for among-site comparisons of ants and herbivory, results from both experiments (all seven censuses) were used.

To compensate for the reduction of sample size caused by the death of tagged plants, I replaced dead control plants immediately with the nearest *C. fasciculata* individual of similar size. Since many weeks of ant exclusion may be required to affect plant reproduction, I did not replace dead exclusion plants.

Ant censuses

I censused all tagged plants for ants in the morning (0800–1100) and afternoon (1300–1600) of a sunny day once every 3 wk from the beginning of June to the middle of October (seven censuses in all). I also sampled ants twice at night. At each plant I recorded the number of ants of each species present upon my arrival. To see whether extrafloral nectaries increased ant den-

sity over that expected on nonnectariferous vegetation, I also sampled ants on 100 similar-sized plants without extrafloral nectaries (e.g., *Indigofera hirsuta*, *Eupatorium compositifolium*) on two days at each site in early September, when ant and herbivore abundance was very high.

Direct effects of ants on herbivores

Whether or not ants could deter herbivores on *C. fasciculata* was examined in two ways. First, I observed natural interactions between the ants and herbivores. Second, I compared removal rates by ants of *Drosophila* larvae on control plants, exclusion plants, and similar-sized plants of species without extrafloral nectaries. At sites 2 and 3, in the middle of September, five larvae each were placed at the nodes of 20 plants in each of the above three groups. Larvae were observed for 45 min, and all removals recorded.

Determining herbivore levels, herbivory, and reproductive success

Every 3 wk, for each plant I determined plant size, the number of herbivores, and the amount of leaf herbivory. Plant size was estimated as the number of leaves on each plant. I counted the number each of grasshoppers, *Phoebis sennae*, *Anticarsia gemmatilis*, and the unidentified geometrid on each plant. To account for differences in plant size, I also calculated the abundance of these herbivores per 100 leaves. Because *Polyhymno luteostrigella* was very abundant and difficult to count, I subsampled it on the top 10 fully expanded leaves of 10 randomly selected branches per plant. The same herbivore individual probably was never counted on successive censuses; developmental time for the lepidoptera was < 3 wk, and grasshoppers rarely spent more than a few hours on the same plant. To estimate leaf herbivory, I examined these same 100 leaves on each plant; for each 10 leaves the percentage of area removed was estimated visually. This choice of leaves has the advantage of avoiding old leaves, which lose leaflets independently of herbivores, and unfolded leaves, for which damage is difficult to assess accurately. Because *P. luteostrigella* seemed to prefer new, fully expanded leaves, however, its abundance and leaf herbivory may be overestimated by my method.

At the beginning of pod dehiscence, I estimated plant reproductive output and pod predation. Reproductive output was estimated in two ways. First, I counted the number of undamaged pods on each plant. Second, to approximate viable reproductive output more closely, I included partially eaten pods: from the total number of pods on each plant, I subtracted the sum of the fractions of damage to all pods. I will refer to this measure as "total pod set." I also counted the number of seeds per pod in 20 undamaged pods of each plant. I estimated pod predation by calculating for each plant the percentage of pods damaged by predators. Inclusion of the fractions of damage to each pod did not

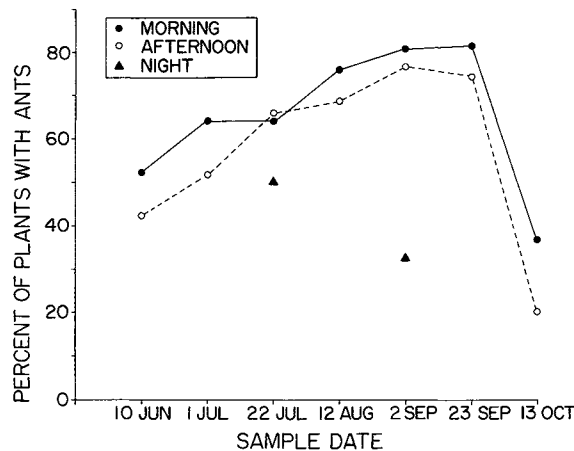


FIG. 1. The percentage of *Cassia fasciculata* control plants with ants, as a function of date and time of day, for the three sites combined. The sample size was 117 plants for each date.

change the results, and thus this analysis is not presented here.

Data analysis

Because most of the data sets were heteroscedastic, nonnormally distributed, or both (even after several transformations), in many cases I used nonparametric statistics (Siegel 1956). Differences among the three sites were tested with three pairwise comparisons. Such nonorthogonal multiple comparisons increase the chance of making a Type I error. In these cases, I used Dunn-Sidak probabilities to calculate the appropriate alpha value for rejection of the null hypotheses (Ury 1976, Sokal and Rohlf 1981). All analyses were carried out using the 1981 BMDP Statistical Software Package (Dixon and Brown 1981).

RESULTS

Ant visitation to plants

The proportion of *Cassia fasciculata* control plants occupied by ants greatly surpassed that for nonnectariferous background vegetation. In both censuses in which comparisons were made (one in September and one in October at all sites), usually <10% of the background plants were occupied by ants, compared to >75% of control *Cassia* (differences significant at $P < .001$ at each site for each date; χ^2 tests).

As a group, ants were diverse and abundant visitors to the extrafloral nectaries of *C. fasciculata*. I recorded 12 ant species in four families, all species native to northern Florida (Table 1). The number of ants on a plant at any time ranged from 0 to 51. On all control plants, ants averaged 3.71 individuals per plant and occupied 61.4% of the plants.

Ant visitation to the nectaries varied over time. Ants began feeding at the nectaries ≈ 2 wk after plant emergence, when plants possessed ≈ 5 –10 leaves. The percentage of plants with ants increased from $\approx 50\%$ in

June to $\approx 75\%$ from August through September, and then declined abruptly to <30% at the time of pod dehiscence in October (Fig. 1). These changes corresponded only roughly to the temporal changes in herbivore abundance (see below and Fig. 2). Ant visitation to plants was generally higher in the morning than in the afternoon, and both the number of ant individuals and species were higher during the day than at night (Fig. 1). Diurnal variation in ant activity did not appear to correspond to changes in herbivore behavior.

The ant exclusion was clearly effective. While a few ants were consistently found on exclusion plants, the percentage of exclusion plants with ants was $< 1/10$ that of the control plants ($P < .001$ for censuses both on 23–30 August and 13–20 September; χ^2 test).

Direct effects of ants on herbivores

Most ant species found on *C. fasciculata* were not aggressive to large herbivores or to me. No ants attacked lepidopteran larvae >10 mm in length or grasshoppers of any size. On several occasions, however, I observed ants removing eggs and small larvae of *Phoebis sennae*, and on one occasion saw them remove a larva of *Polyhymno luteostrigella*.

For both sites tested, Mann-Whitney U tests revealed that the mean number of *Drosophila* larvae disappearing (out of five placed on each plant) from control plants was significantly greater than from exclusion plants or from nonnectariferous neighbors (Table 2). Removal of *Drosophila* did not differ between the latter two groups at either site ($P > .05$). Most ant species readily removed the larvae. *Iridomyrmex pruinosus* and *Camponotus socius*, however, ignored *Drosophila*, and although they tried with great persistence, *Pheidole metallescens* individuals were not large enough to transport the larvae.

Variation among sites in ants and herbivory

As expected, the three sites differed substantially in ant visitation and herbivore pressure. I tested for heterogeneity among sites in the percentage of control plants occupied by ants with a χ^2 test of independence using loglinear models (see Dixon and Brown 1981) of the multiway frequency table of occupancy by ants (ants vs. no ants) \times site \times week \times time (morning vs. afternoon). The results show that frequency of ant oc-

TABLE 2. Number of *Drosophila* larvae, of 5 placed on each plant, disappearing within 45 min. Data are means ± 1 SD; $n = 20$ plants in each experimental group at each site.

	Ant exclusion plants	Control plants	Background vegetation
Site 2	0.45 \pm 0.61 $U = 330^{***}$	2.40 \pm 1.88 $U = 304.5^{**}$	0.80 \pm 1.06
Site 3	0.35 \pm 0.59 $U = 327.5^{***}$	1.85 \pm 1.53 $U = 299^{**}$	0.65 \pm 0.88

** $P < .01$, *** $P < .001$; Mann-Whitney U test.

TABLE 3. Differences among sites in ant visitation to *Cassia fasciculata*. * Data are for control plants for all daytime censuses (7 morning and 7 afternoon censuses of 40 plants each at each site).

Variable	Site 1	Site 2	Site 3
% of plants occupied	70.8 ^a	65.5 ^a	47.3 ^b
Ants per plant ($\bar{X} \pm 1$ SD)	5.22 ^a \pm 6.79	3.69 ^b \pm 5.71	2.05 ^c \pm 3.19

* Differences between sites were tested with pairwise χ^2 tests for the percentage of plants with ants, and with pairwise Mann-Whitney *U* tests for the number of ants per plant. Sites bearing different superscript letters are significantly different ($P < .05$, using Dunn-Sidak probabilities).

cupancy depended on site ($\chi^2 = 54.42$; $df = 2$; $P < .001$). Pairwise comparisons of the three sites revealed that the percentage of plants occupied by ants was significantly higher at site 1 and site 2 than at site 3, but site 1 and site 2 did not differ (Table 3). Additionally, all three between-site comparisons of the mean number of ants per plant revealed significant differences: site 1 > site 2 > site 3 (Table 3).

I assessed differences in herbivore pressure among sites with three measures of potential or real damage to the plants: herbivore abundance, percentage of leaf area removed by herbivores, and percentage of pods damaged by predators. To assess the site variation in herbivore pressure independently of the site variation in ant density, I used the results from ant exclusion plants.

The abundances of the two most common herbivores, *Polyhymno luteostrigella* and *Phoebis sennae*, differed significantly among sites (Table 4). The pairwise comparisons of the density of *Polyhymno luteostrigella* were all significant: site 2 > site 1 > site 3. For *Phoebis sennae* the site comparisons showed a different order: site 1 = site 3 > site 2 (Table 4). There were no significant differences for other herbivores.

The among-site variation in amount of leaf damage at the final census reflected closely the variation in *P. luteostrigella* abundance: site 2 > site 1 > site 3 (Table 4). In June, July, and August there were no significant

differences among sites, while on 2 September site 2 > site 1 = site 3 (Fig. 2). Early in the season, the level of herbivory was very low; even as late as August, herbivores had removed a mean of only 6.7% of leaf area (Fig. 2). By early September, herbivore damage had risen to 29.9%, and in the 3rd wk of September it peaked at 53.0%. These increases through time in leaf herbivory correlated closely with temporal changes in the abundance of *P. luteostrigella*.

All between-site comparisons exhibited significant differences in the percentage of pods damaged: site 1 > site 3 > site 2 (Fig. 3). This ranking of pod damage reflects the abundance of *Phoebis sennae*, the major pod predator. *P. sennae* attacked pods of all sizes and stages of maturity, eating small portions of pods as well as entire pods. The data given in Fig. 3 are measurements only of partial damage to mature pods at the end of the growing season. Actual pod predation was probably underestimated in two ways. First, pods that were entirely consumed left no physical evidence and hence could not be counted. Second, because *C. fasciculata* selectively aborts some immature pods with few seeds (Lee and Bazzaz 1982), some pods damaged early in the fruiting period were probably not included in my count.

These results reveal a clear hierarchy among the sites in terms of ant visitation and herbivore pressure (see Fig. 3). Site 1 had relatively high ant visitation and

TABLE 4. Herbivore abundance on *Cassia fasciculata* for four censuses (7 August to 15 October).†

Herbivore	Site 1		Site 2		Site 3	
	Control	Exclusion	Control	Exclusion	Control	Exclusion
<i>Polyhymno luteostrigella</i> (no. per 100 leaves)	7.11 \pm 5.23	7.76 ^b \pm 5.77	16.21 \pm 10.94	17.14 ^a \pm 10.17	4.26 \pm 3.76	4.01 ^c \pm 3.10
<i>Phoebis sennae</i> (no. per plant)	0.68 \pm 0.90	1.52 ^a \pm 2.23	0.18 \pm 0.55	0.33 ^b \pm 0.55	0.92 \pm 1.46	1.33 ^a \pm 1.27
(no. per 100 leaves)	0.07 \pm 0.10	0.35 ^a \pm 0.73	0.02 \pm 0.07	0.10 ^b \pm 0.16	0.19 \pm 0.29	0.22 ^a \pm 0.22
Other Lepidoptera (no. per plant)	0.13 \pm 0.34	0.16 \pm 0.45	0.13 \pm 0.46	0.13 \pm 0.43	0.26 \pm 0.64	0.12 \pm 0.33
(no. per 100 leaves)	0.03 \pm 0.05	0.03 \pm 0.06	0.06 \pm 0.14	0.04 \pm 0.08	0.04 \pm 0.07	0.03 \pm 0.05
Grasshoppers (no. per plant)	0.24 \pm 0.63	0.19 \pm 0.54	0.08 \pm 0.27	0.10 \pm 0.31	0.08 \pm 0.27	0.03 \pm 0.17
(no. per 100 leaves)	0.02 \pm 0.06	0.03 \pm 0.07	0.02 \pm 0.09	0.04 \pm 0.12	0.01 \pm 0.06	0.01 \pm 0.02
Number of tagged plants	38	31	40	30	39	33

† Among-site differences were tested for exclusion plants only, with pairwise Mann-Whitney *U* tests. Sites bearing different superscript letters are significantly different ($P < .05$, using Dunn-Sidak probabilities).

* $P < .05$; Mann-Whitney *U* tests.

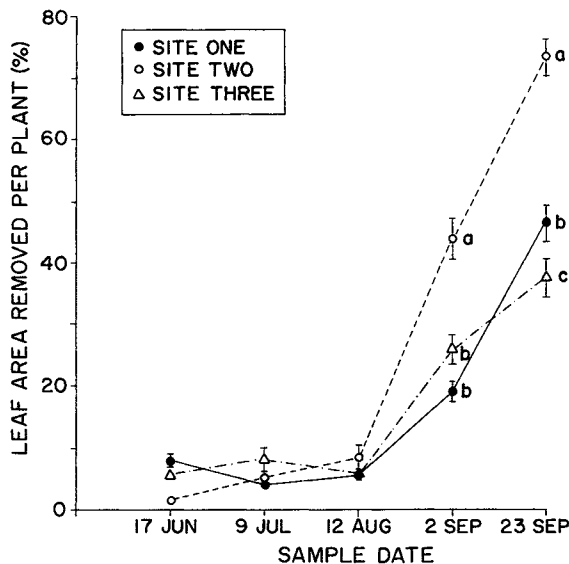


FIG. 2. The percentage of *Cassia fasciculata* leaf area removed per plant by herbivores at three sites. Data are means ± 1 SE for control and ant exclusion plants combined, since these two groups were not different at any site ($P > .05$; t tests). Differences among sites were tested for exclusion plants, with pairwise t tests. Site means for a given date that bear different lowercase letters are significantly different ($P < .05$, using Dunn-Sidak probabilities).

herbivore pressure, site 2 had intermediate ant visitation and intermediate herbivore pressure, and site 3 had low ant visitation and intermediate herbivore pressure.

The effect of ant exclusion on herbivores and plants

Among herbivores, only *Phoebis sennae* was affected by the ant exclusion. In all three sites, density (both number per plant and number per 100 leaves) was significantly increased on ant exclusion plants compared to controls (Table 4).

Control and ant exclusion plants did not differ in leaf damage at any site. Most of the leaf damage I measured was from *Polyhymno luteostrigella*. This herbivore fed only on leaves and, despite its small size, probably at least equalled the overall biomass of *Phoebis sennae* and greatly surpassed that of the other herbivore groups.

At site 1 a significantly lower percentage of pods was damaged on ant-occupied plants than on exclusion plants. At the other sites, pod damage was also reduced, but these differences were not statistically significant (Fig. 3; site 2, $P = .06$, and site 3, $P = .15$).

Similarly, only at site 1 did controls have significantly more leaves per plant, undamaged pods per plant, and total pod set per plant compared to ant exclusion treatments (Fig. 3, Table 5). Control plants at the other two sites enjoyed larger size and reproduction on average, but again these differences were not significant (site 2, $.05 < P < .07$; site 3, $.14 < P < .20$).

In contrast to the other two sites, at site 2 the number of seeds per pod was significantly higher for the control than for the exclusion group (Table 5). To incorporate this difference into an estimate of total seed-set, I multiplied the mean number of seeds per pod for a given plant by the total pod set for that plant. Using this estimate, control plants at site 2 set a significantly higher number of seeds per plant than did exclusion plants (Table 5). Because there were no differences in the number of seeds per pod between control and exclusion plants for either site 1 or site 3, similar calculations were not made for these two sites.

DISCUSSION

The effect of extrafloral nectaries on plant reproduction

The results strongly support the hypothesis that extrafloral nectaries can increase the reproductive success of *Cassia fasciculata* individuals. Secreted nectar clearly attracted ants and boosted ant visitation on *C. fasciculata* to levels much higher than for nonnectariferous background vegetation. Herbivores appeared to pose a serious threat to the reproductive success of *C. fasciculata* individuals; defenses other than ants did not shield the plants from herbivore attack. Ants on plants could remove some herbivores, and removed *Drosophila* larvae placed on these plants faster than on background vegetation (even in the site with the lowest level of ant visitation). In the exclusion experiment, *C. fasciculata* individuals with ants were attacked by fewer *Phoebis sennae* larvae (all sites) and suffered lower pod predation (site 1) than plants from which ants were excluded. Because of this lower herbivory, at both site 1 and site 2 ant-occupied plants had higher reproductive output than did exclusion plants. Other researchers have made similar conclusions about the effect of extrafloral nectaries, based on experimental results (e.g., Schemske 1980, Stephenson 1982, Horvitz and Schemske 1984; but see Tempel 1983) and correlational evidence (e.g., Bentley 1977a, Tilman 1978, Keeler 1980).

In the experiments reported here, ant foraging behavior seems to have been responsible for the increase in reproduction of *C. fasciculata* individuals. Ants were not aggressive to most herbivores, to other ant species, or to the >50 other insect species visiting the extrafloral nectaries. Ants responded only to eggs and small larvae of Lepidoptera, which were carried from the plant, presumably to the colony. Large lepidopteran larvae, which are probably difficult for ants to transport as food (see Tilman 1978), were ignored. Several other studies also have shown that ants can positively affect plant seed-set through foraging behavior alone. Schemske (1980), for example, found that *Wasmannia auropunctata* increased seed production of *Costus woodsonii* (Zingiberaceae) in Panama by preying on the larvae of a seed-eating fly (see also Inouye and

Taylor 1979, Koptur 1979, Stephenson 1982). In contrast, in some ant-plant mutualisms, ants enhance plant success as a result of aggressive territoriality ("ownership behavior"; Way 1963) toward both edible and inedible intruders. Although this behavior appears to be most marked in obligate mutualisms (e.g., ants and acacias; Janzen 1966), it has also been found in facultative mutualisms involving extrafloral nectaries (Bentley 1977a, b, Beckmann and Stucky 1981).

The positive effect of ants on the reproduction of *C. fasciculata* individuals probably was due solely to the deterrence of *P. sennae* larvae. Of the four groups of herbivores attacking the plant, only this population was negatively affected by ant presence. Similarly, Keeler (1980) reported that ants on *Ipomoea leptophylla* deterred only two of three herbivore species. This inconsistent guarding by ants is expected because insect species vary greatly in their susceptibility to ant predation and aggression. It is surprising, however, that ants on *C. fasciculata* measurably decreased the number of larvae of *P. sennae* but not of the smaller *Polyhymno luteostrigella*. Once inside their tied leaflets, these larvae may be protected from ant attack. There is no obvious explanation, however, why ants did not decrease larval density by preying on eggs. In contrast to *P. sennae*, which feeds on at least eight plant species, some without extrafloral nectaries (Tietz 1972), *P. luteostrigella* in Florida is known only from *C. fasciculata* (Kimball 1965). Therefore, *P. luteostrigella* may be tightly linked to *C. fasciculata* and may have evolved tactics (e.g., toxicity) to avoid predation by ants.

The decrease in *P. sennae* abundance due to ants probably translated into an increase in plant reproduction in two ways. First, removal of *P. sennae* by ants decreased the amount of pod predation on mature pods (*P. sennae* was the only abundant pod predator). Second, low *P. sennae* density might have also led to increased pod set through an increase in plant size. Because pod set is highly correlated with the number of leaves on a plant ($n = 210$, $r = 0.62$, $P < .001$), the higher pod set of ant-visited plants is partially a result of their larger size. Damage to apical meristems by *P. sennae*, which unfortunately was not measured, appeared to be severe, and could have substantially reduced growth and leaf production.

A relationship between plant size and apical meristem herbivory would explain the apparent discrepancy between the results for leaf herbivory and leaf number at site 1: ant-visited plants possessed more leaves than did exclusion plants even though there was no difference in leaf herbivory. I measured "leaf area removed" on fully-expanded leaves only, which were eaten primarily by *Polyhymno luteostrigella*. The similarity between leaf herbivory on control and treatment groups, therefore, probably resulted from the lack of an effect of ants on *P. luteostrigella*. In contrast, as argued above, the difference in leaf number probably was caused by removal of *Phoebis sennae* by ants.

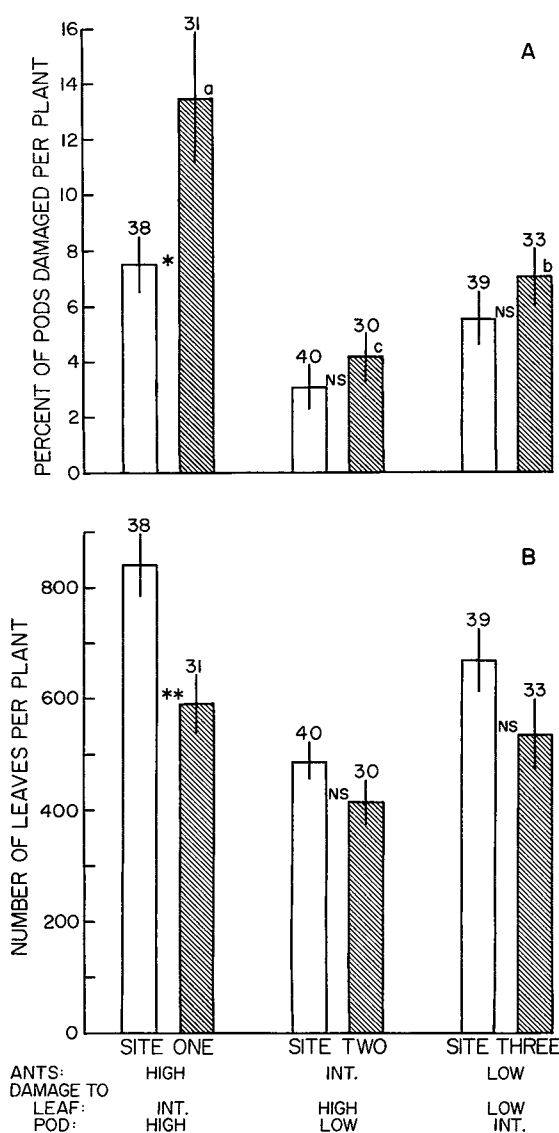


FIG. 3. (A) The percentage of mature pods showing partial damage just prior to pod dehiscence (1–7 October) and (B) the number of leaves at the final census (23–30 September) for *Cassia fasciculata*. Data are means per plant for □ control and ▨ ant exclusion plants. Sample sizes are given above vertical bars indicating ± 1 SE. Differences between control and exclusion are given between the two bars at each site (** $P < .01$; * $P < .05$; NS $P > .05$; Mann-Whitney U test). For pod predation only, differences among sites were tested for exclusion plants with pairwise Mann-Whitney U tests. Sites with bars bearing different letters at top are significantly different ($P < .05$, using Dunn-Sidak probabilities).

Differences among sites

Effects of extrafloral nectaries (due to ants) on the reproductive success of *C. fasciculata* individuals differed among sites. This variation appears to be, in part, a result of substantial variation among sites in the density of ants and potential herbivores. Where ant visitation and herbivore pressure were low (site 3), extra-

TABLE 5. Mean (± 1 SD) for each of several parameters of reproduction of *Cassia fasciculata* individuals at three sites. "Total pod set" and "number of seeds" are estimates of reproductive output, with partial damage to pods considered.

Parameter	Site 1		Site 2	
	Control	Exclusion	Control	Exclusion
No. plants sampled	38	31	40	30
No. undamaged pods per plant	135.55 \pm 151.68	* 55.58 \pm 54.29	71.75 \pm 44.82	59.77 \pm 49.15
"Total pod set" per plant	140.33 \pm 155.49	* 59.07 \pm 54.63	73.72 \pm 45.46	61.81 \pm 49.93
No. seeds per pod	10.14 \pm 2.35	10.29 \pm 2.12	11.35 \pm 1.71	* 11.05 \pm 2.21
"No. seeds" per plant†			850.64 \pm 507.01	* 688.04 \pm 591.45

* $P < .05$; Mann-Whitney U test.

† Calculated only for the site with significant difference in number of seeds per pod.

floral nectaries had no detectable effect on plant reproduction. Where the density of ants was higher (site 2), they caused a small but significant increase in seed-set. Only where both ant density and the abundance of herbivores were high (site 1) did ants at extrafloral nectaries strongly increase plant reproductive success.

The densities of ants and herbivores undoubtedly can be crucial to the effect of extrafloral nectaries on plant fitness at any one site. In addition, since some ant species may be incapable of capturing or deterring potential herbivores, the effect of extrafloral nectaries may rest on the identities of the visiting ants. Several studies have revealed large differences among ant species in their effectiveness at deterring herbivores (Elias and Gelband 1975, Janzen 1975, Bentley 1977a, Nickerson et al. 1977, Schemske 1980, Beckmann and Stucky 1981, Koptur 1984). Horvitz and Schemske (1984), furthermore, found that among-site variation in the composition of the ant community influenced local seed-set. In my study, site 3 differed substantially in ant fauna from sites 1 and 2, which were very similar (Table 1). The lack of a positive effect of ants at extrafloral nectaries on plant fitness at site 3, therefore, may be due to the absence of suitable ant species rather than to the low density of herbivores and ants.

The value of ants to the plants at any one site should also depend on the susceptibility of herbivores to ant attack. Extrafloral nectaries would have little effect on fitness where herbivores are unaffected by ants, regardless of the density of ants and herbivores. Thus, the potential effect of the ants at site 2 may not have been realized because of the preponderance of a non-susceptible herbivore (*P. luteostrigella*) over a susceptible herbivore (*P. sennae*).

Several researchers have now documented spatial variation in the magnitude of benefit from ant visitation to plants (Bentley 1976, Inouye and Taylor 1979, Horvitz and Schemske 1984). These studies and the results reported here suggest that the effect of extrafloral nectaries on plant reproduction should be considered on at least two levels. For the species as a whole, possessing extrafloral nectaries may on average increase reproductive success. The strength of this effect within

local populations, however, may vary widely in space. In some populations, the effect may be strongly positive, but where the densities of ants and herbivores are low or herbivores are immune to ants, extrafloral nectaries should influence reproduction very little. The effect may even be negative where ants deter other, more important enemies of herbivores, or where ants are rare and nectar-feeding adults of herbivores are attracted. In most systems, this underlying variation in insect abundance is probably not random in space (e.g., Root 1973, Levings 1983). In my study, for example, ant abundance increased from the least sunny (site 3) to the most sunny habitat (site 1), a common pattern for ants (van Pelt 1956). However, no obvious differences among the three sites explain the variation in herbivore density.

Spatial variation in benefit from ants further suggests that natural selection for extrafloral nectaries varies across space (see Keeler 1981b for a relevant model). Variation in selection pressure has been invoked to explain the absence of ant attractants in some populations of plant species typically possessing these. Janzen (1973) and Rickson (1977), for example, attribute the loss of trichilia in island populations of *Cecropia peltata* primarily to the absence of ants (see also Bentley 1977b, Inouye and Taylor 1979). My results demonstrate experimentally that selection pressures vary even in the presence of ants. Why, then, haven't some populations of *Cassia fasciculata* lost their extrafloral nectaries? Several factors, which are not mutually exclusive, could explain this phenomenon. First, gene flow could dilute the effect of directional selection in all but extremely isolated populations. Second, other predaceous and parasitic insects may be important mutualists where ants are rare. Wasps and flies, for example, often visited the extrafloral nectaries of *C. fasciculata*, and twice I observed a large sphecoid wasp remove a large *P. sennae* caterpillar. Because they were far less common and consistent visitors than ants, however, these insects probably influence the reproduction of only a small fraction of the plants at a given site. Third, the cost of producing extrafloral nectar may be so low that selection against maintaining it would be weak

TABLE 5. Continued.

Site 3	
Control	Exclusion
39	33
143.80 ± 138.78	104.88 ± 92.29
146.95 ± 139.51	108.78 ± 94.56
11.10 ± 2.28	11.08 ± 2.14

(see O'Dowd 1979). Finally, fluctuations in insect populations may alter the value of extrafloral nectaries at any one site from year to year. Selection pressure, therefore, may not be sufficiently consistent to effect evolutionary loss of nectary function, or, conversely, selection for nectaries may be exerted infrequently but the impact is great enough to maintain the trait. This final proposition suggests that although the ecological conditions selecting for extrafloral nectaries may be predictable, the location of these conditions in the landscape may change from year to year. The lack of evidence on these questions suggests that future work should examine the effect of insects other than ants, the cost as well as the benefit of producing extrafloral nectar, and both spatial and temporal variation in the effect of extrafloral nectaries.

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LITERATURE CITED

- Beckmann, R. L., Jr., and J. M. Stucky. 1981. Extrafloral nectaries and plant guarding in *Ipomoea pandurata* (L.) G. F. W. Mey (Convolvulaceae). *American Journal of Botany* 68:72–79.
- Bentley, B. L. 1976. Plants bearing extrafloral nectaries and the associated ant community: interhabitat differences in the reduction of herbivore damage. *Ecology* 57:815–820.
- . 1977a. The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). *Journal of Ecology* 65:27–38.
- . 1977b. Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics* 8:407–427.
- Deuth, D. 1977. The function of extrafloral nectaries in *Aphelandra deppeana* Schl. and Cham. (Acanthaceae). *Brenesia* 10/11:135–145.
- Dixon, W. J., and M. B. Brown, editors. 1981. BMDP-81. Biomedical computer programs, P series. University of California Press, Berkeley, California, USA.
- Doncaster, C. P. 1981. The spatial distribution of ants' nests on Ramsey Island, South Wales. *Journal of Animal Ecology* 50:195–218.
- Elias, T. S., and H. Gelband. 1975. Nectar: its production and function in trumpet creeper. *Science* 189:289–290.
- Hobson, M. 1972. *Cassia fasciculata*. In J. W. Hardin, G. Doersken, D. Herndon, M. Hobson, and F. Thomas, editors. Pollination ecology and floral biology of four weedy genera in southern Oklahoma. *Southwestern Naturalist* 16:403–412.
- Horvitz, C. C., and D. W. Schemske. 1984. Effects of nectar-feeding ants and an ant-tended herbivore on seed production of a neotropical herb. *Ecology* 65:1369–1378.
- Inouye, D. W., and O. R. Taylor, Jr. 1979. A temperate region plant-ant-seed predator system: consequences of extrafloral nectar secretion by *Helianthella quinquenervis*. *Ecology* 60:1–7.
- Isley, D. 1975. Leguminosae of the United States: II. subfamily Caesalpinoideae. *Memoirs of the New York Botanical Garden* 25:1–228.
- Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20:249–275.
- . 1973. Dissolution of mutualism between *Cecropia* and its azteca ant. *Biotropica* 5:15–28.
- . 1975. *Pseudomyrmex nigropilosa*: A parasite of a mutualism. *Science* 188:936–937.
- Keeler, K. H. 1977. The extrafloral nectaries of *Ipomoea carnea* (Convolvulaceae). *American Journal of Botany* 64:1182–1188.
- . 1980. The extrafloral nectaries of *Ipomoea leptophylla* (Convolvulaceae). *American Journal of Botany* 67:216–222.
- . 1981a. Function of *Mentzelia nuda* (Loasaceae) postfloral nectaries in seed defense. *American Journal of Botany* 68:295–299.
- . 1981b. A model for selection for facultative non-symbiotic mutualism. *American Naturalist* 118:488–498.
- Kimball, C. P. 1965. The lepidoptera of Florida. Division of Plant Industry, Gainesville, Florida, USA.
- Koptur, S. 1979. Facultative mutualism between weedy vetches bearing extrafloral nectaries and weedy ants in California. *American Journal of Botany* 66:1016–1020.
- . 1984. Experimental evidence for defense of *Inga* (Mimosoideae) saplings by ants. *Ecology* 65:1787–1793.
- Laessle, A. M. 1942. The plant communities of the Welaka area. University of Florida Publications in Biological Science Services, Gainesville, Florida, USA.
- Lee, T. D., and F. A. Bazzaz. 1982. Regulation of fruit and seed production in an annual legume, *Cassia fasciculata*. *Ecology* 63:1363–1373.
- Levings, S. C. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecological Monographs* 53:435–455.
- Moscardi, F. 1979. Effect of soybean crop phenology on development, leaf consumption, and oviposition of *Anticarsia gemmatilis* Huber. Dissertation. University of Florida, Gainesville, Florida, USA.
- Nickerson, J. C., C. A. Rolph Kay, L. L. Buschman, and W. H. Whitcomb. 1977. The presence of *Spissistilus festinus* as a factor affecting egg predation by ants in soybeans. *Florida Entomologist* 60:193–199.
- O'Dowd, D. J. 1979. Foliar nectar production and ant activity on a neotropical tree, *Ochroma pyramidale*. *Oecologia* (Berlin) 43:233–248.

- Parrish, J. A. D., and F. A. Bazzaz. 1979. Difference in pollination niche relationships in early and late successional plant communities. *Ecology* **60**:597-610.
- Pickett, C. H., and W. D. Clark. 1979. The function of extrafloral nectaries in *Opuntia acanthocarpa* (Cactaceae). *American Journal of Botany* **66**:618-625.
- Pullen, T. M. 1963. The *Cassia fasciculata* complex in the United States. Thesis. University of Georgia, Athens, Georgia, USA.
- Rickson, R. F. 1977. Progressive loss of ant-related traits of *Cecropia peltata* on selected Caribbean islands. *American Journal of Botany* **64**:585-592.
- Robertson, C. 1890. Flowers and insects V. *Botanical Gazette* **15**:199-204.
- Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). *Ecological Monographs* **43**:95-124.
- Sanders, C. J. 1970. The distribution of carpenter ant colonies in the spruce-fir forests of northwestern Ontario. *Ecology* **51**:865-873.
- Schemske, D. W. 1980. The evolutionary significance of extrafloral nectar production by *Costus woodsonii* (Zingiberaceae): an experimental analysis of ant protection. *Journal of Ecology* **68**:959-968.
- Siegel, S. 1956. *Nonparametric statistics for the behavioral sciences*. McGraw-Hill, New York, New York, USA.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman, San Francisco, California, USA.
- Stephenson, A. G. 1982. The role of extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increasing fruit production. *Ecology* **63**:663-669.
- Tempel, A. S. 1983. Bracken fern (*Pteridium aquilinum* Kuhn) and nectar-feeding ants: a non-mutualistic interaction. *Ecology* **64**:1411-1422.
- Thorp, R. W., and J. R. Estes. 1975. Intrafloral behavior of bees on flowers of *Cassia fasciculata*. *Journal of the Kansas Entomological Society* **48**:175-184.
- Tietz, H. M. 1972. An index to the described life histories, early stages, and hosts of macrolepidoptera of the continental United States and Canada. A. C. Allyn, Sarasota, Florida, USA.
- Tilman, D. 1978. Cherries, ants, and tent caterpillars: timing of nectar production in relation to susceptibility of caterpillars to ant predation. *Ecology* **59**:686-692.
- Ury, H. K. 1976. A comparison of four procedures for multiple comparisons among means (pairwise contrasts) for arbitrary sample sizes. *Technometrics* **18**:89-97.
- van Pelt, A. F. 1956. The ecology of ants of the Welaka Reserve, Florida (Hymenoptera: Formicidae). *American Midland Naturalist* **56**:358-387.
- Veno, P. A. 1976. Successional relationships of five Florida plant communities. *Ecology* **57**:498-508.
- Way, M. J. 1963. Mutualism between ants and honeydew-producing Homoptera. *Annual Review of Entomology* **8**:307-344.
- White, T. C. R. 1974. A hypothesis to explain outbreaks of looper caterpillars with special reference to populations of *Selidosoma suavis* in a population of *Pinus radiata* in New Zealand. *Oecologia (Berlin)* **16**:279-301.