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Facultative Mutualism between Imported Fire Ants (*Solenopsis invicta*) and a Legume (*Senna occidentalis*)

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FACULTATIVE MUTUALISM BETWEEN IMPORTED FIRE ANTS  
(*SOLENOPTIS INVICTA*) AND A LEGUME (*SENNA OCCIDENTALIS*)

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**ABSTRACT**—Extrafloral nectaries of *Senna occidentalis* attract imported fire ants which protect the plant against two species of herbivores, the cloudless sulphur butterfly (*Phoebis senna*) and the sleepy orange butterfly (*Eurema nicippe*). Ant-defended plants had increased growth as measured by plant height and number of leaves, and increased reproductive effort as measured by numbers of pods, numbers of seeds, and weight of pods, compared to ant-excluded plants (using Tanglefoot barriers). Survival of herbivore eggs and larvae was reduced in the presence of ants suggesting that ants provide plants with protection from larval herbivory thus increasing the amount of primary production which in turn allows greater reproductive output.

**RESUMEN**—Los nectarios extraflorales de *Senna occidentalis* atraen a las hormigas de fuego importadas lo cual protege a la planta contra dos especies de herbívoros, la mariposa gigante azufurada (*Phoebis senna*) y la mariposa soñolienta anaranjada (*Eurema nicippe*). Las plantas defendidas por las hormigas aumentaron su crecimiento, el cual se midió por la altura de la planta y el número de hojas, y su esfuerzo reproductivo el cual se midió por el número de vainas, número de semillas, y peso de las vainas, comparado con las plantas sin hormigas (usando barreras “Tanglefoot”). La sobrevivencia de los huevos y larvas de los herbívoros disminuyó con la presencia de las hormigas, sugiriendo que las hormigas proporcionan a las plantas la protección de herbivoría larval, aumentando así la cantidad de producción primaria la cual en turno permite mayor capacidad reproductiva.

Extrafloral nectaries are found in many plant families, predominantly in tropical species (Bentley, 1977a), but also occur among temperate species (Tilman, 1978; Inouye and Taylor, 1979; Keeler, 1981). Nectar production for extrafloral nectaries represents a metabolic cost to plants because of the nectar's high sugar and amino acid content. A number of studies have suggested that extrafloral nectaries, despite their caloric and nitrogen cost, confer a benefit to plants through attraction of ants and subsequent reduction in herbivory due to defense by ants (Koptur, 1979; Stephenson, 1982; Costa et al., 1992). Likewise, plant protection via parasitoid attraction also may be facilitated by extrafloral nectaries (Pemberton and Lee, 1996).

The majority of studies that have documented significant ant protection and fitness enhancement of plants with extrafloral nectaries indicate that ants interfere with or attack insects that are feeding directly on reproductive tissues, thus improving reproductive output

(Bentley, 1977b; Stephenson, 1982; Rico-Gray and Thien, 1989; Del-Claro et al., 1996). In many studies, nectar production by extrafloral nectaries was found to be highest during or restricted to the time of plant reproduction (Bentley, 1977b; Tilman, 1978; Koptur, 1979).

Most of the documented ant-plant mutualisms are characterized by extrafloral nectary visitation and subsequent plant protection by several, occasionally as many as 12, ant species (Bentley, 1977b; Keeler, 1977; Barton, 1986; Rico-Gray and Thien, 1989). In some systems, plant protection is realized only at high ant densities (Boecklen, 1984; Rashbrook et al., 1992) or not at all (O'Dowd and Catchpole, 1983). Ant efficiency in reducing herbivory often increases with the size of the ant species (Rico-Gray and Thien, 1989). Also soil nutritional status may be a factor in determining food rewards and ultimately the ability of an ant-protected plant to exhibit measures of enhanced fitness because of flower and fruit

abortion under poor soil quality (Oliveira, 1997).

Mutualism systems in which a plant species gains a fitness advantage by ant protection from folivores should have a high density of ant visitors and extrafloral nectaries that are active throughout the growing season of the plant. Here we report on experiments designed to test for potential facultative mutualism between the imported fire ant (*Solenopsis invicta*) and an annual legume, the coffee senna (*Senna occidentalis*). Ants can defend plants against herbivores and seed predators. Their defense can result in reduced damage through reduction in herbivore oviposition, feeding activity, and survival. We monitored herbivore oviposition, hatching success, and larval survival, and plant fitness correlates in both the presence and absence of ants to investigate the ant-plant relationship.

**METHODS AND MATERIALS—Study Site and Organisms—***Senna occidentalis* (Fabaceae) is a pioneer invader species with a pantropic and subtropic distribution including the southeastern United States to central Texas. In our east Texas (Nacogdoches Co.) study area, the plant is found in old fields, pastures, and as a weed within cultivated row crops. The plant reaches a maximum height of 2 m usually with several ascending branches from a central stem. Leaves are pinnately compound, spirally arranged, with four to six paired leaflets. In eastern Texas germination occurs in May; most rapid growth occurs in August through September with production of seed pods 8 to 12 cm long.

A petiolar gland extrafloral nectary is borne on the pulvinus in the axil of each leaf. These glands produce a clear exudate throughout the life of the leaf. Using microcapillary tubes, exudate from multiple plants (minimum of 3) was collected at two times during the 1997 growing season. A test of this exudate via refractometer indicated a sugar concentration in excess of 40% on both occasions. Single plants did not yield sufficient volume of exudate for individual measurements. Ants, principally imported fire ants, are attracted to and imbibe from these petiolar extrafloral nectaries throughout the growing season.

The imported fire ant was introduced to the United States, probably from Argentina, through the port of Mobile, Alabama, in the 1930s. The species spread rapidly and by the 1960s was common throughout the southeastern United States. These ants are voracious predators on other insects and occur in particularly high densities, up to 500 colonies per ha in old fields, roadsides, or pasture hab-

itats (Porter et al., 1991). Lanza (1988) has demonstrated that *S. invicta* readily collects nectar from plants and does not always discriminate among nectars based on composition or caloric content (Lanza et al., 1993).

**Experiments—**Ant exclusion experiments were conducted on a blueberry farm near Nacogdoches, Texas in 1995, 1996, and 1997. The farm has naturally occurring populations of *S. occidentalis* and imported fire ants. *Senna occidentalis* was seeded into 7.58 l black plastic pots filled with a 1:5 mixture of potting soil and local sandy loam soil. Plants were thinned to one per pot after germination and subsequently paired by height and number of leaves. Individuals of each pair were randomly assigned to either experimental (ants excluded) or control (ant accessible) groups in a matched pairs design. Sample size was 13 pairs in 1995, 20 in 1996, and 19 in 1997. Ants were excluded from experimental plants by applying a coating of Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan) around the base of the stem. Plants were raised in full sun, watered daily via a drip irrigation system, and monitored for treatment effects until the first fall frost. Upon plant death, seed pods were collected, air dried for 10 days, and number of pods and seeds and weight of pods were determined for each plant.

In the 1997 experiment treatment for ant exclusion was altered. Boecklen (1984), working with *Cassia fasciculata*, pointed out that experiments using Tanglefoot test the null hypothesis that Tanglefoot has no effect. Thus, in order to avoid possible treatment effects associated with Tanglefoot as an ant excluder, we treated all plants with a Tanglefoot coating around the stem. Control plants were then made accessible to ants by covering the Tanglefoot with dirt.

An additional ant exclusion experiment was conducted in 1995. Field specimens of *S. occidentalis*, growing at the study site, were selected for study on 22 August. Plants by this date had achieved heights in excess of 1 m and had developed seed pods. Five pairs of plants were matched for height and treated as above for experimental and control plants. Seed pods were collected after the first fall frost on 11 November and treated as previously described.

Throughout the 3 years of experiments, all observations of insect associates of *S. occidentalis* were recorded. These associates included ant protectors, insect herbivores and their predators, and occasional visitors to the petiolar nectaries.

During the 1996 experiment a daily record was kept of insect herbivores, mainly butterfly larvae, by visually inspecting the upper leaf surfaces of all plants. In 1997 a more intensive search for insect herbivores was initiated in an attempt to trace the history and fate of these herbivores. During this period all leaf and stem surfaces of all plants were ex-

amined daily. Location of eggs, larvae, and size of larvae of the two principal butterfly herbivores were recorded for 13 pairs of plants.

**Data Analysis**—Prior to experimentation, paired plants were compared for similar height, number of leaves, and percent herbivory. Nonparametric Wilcoxon signed-rank tests yielded no significant differences between control and experimental plants for these parameters. Differences in mean pod number, weight, and number of seeds from ant exclusion experiments were analyzed as differences in matched pairs of experimental and control plants. Data were tested for normality using either a Shapiro-Wilk test or Kolmogorov-Smirnov test (Steel et al., 1997). If found to be normally distributed, these data were subjected to a paired *t*-test. Non-normal data were analyzed with a Wilcoxon signed-rank test (Zar, 1996). Differences in height and number of leaves across the growing season between experimental and control plants were tested using a Repeated Measures ANOVA.

Daily larvae counts for 1996 were compared by randomized complete block design ANOVA after square root transformation. Daily counts of herbivore egg and larval survival in 1997 were analyzed using a randomized complete block design (each pair of plants was a block) with two fixed main effects (date and treatment). Egg and larval number was square root-transformed and an arcsine-square root transformation was applied to percent survival data.

To examine within-plant differences in egg or larval numbers, we selected a 2-week period during our study (27 July to 10 August). The upper three leaves were considered to be the top of the plant and remaining leaves were designated bottom leaves. Egg and larval number were compared between top and bottom portions of the plant. Mean egg and larval number on exposed surfaces versus undersides of leaves also were compared across the entire plant using a randomized complete block ANOVA.

Chi-Square test of association was used to identify species-specific oviposition patterns on the plant. Pearson's correlation was used to quantify the relationship between number of eggs and percent herbivory.

**RESULTS—Ant Species on *S. occidentalis***—Plants typically were colonized by imported fire ants after the first petiolar nectaries appeared with the fourth leaves. Once occupancy was established, it was usually continuous throughout the growing season although ant numbers tended to fluctuate. Imported fire ants were active on the plants, drinking at nectaries and patrolling leaves and stems 24 h per day. Numbers of imported fire ants occupying plants var-

ied from fewer than 10 to greater than 100. Ants frequently established satellite mounds in soil at the base of control plants. In wet weather these mounds would increase in height around the plant base and culminate in dirt tunnels surrounding and going upward on the stem. These tunnels extended as high as 10 cm and often ended in dome-shaped coverings over the extrafloral nectary. Ants remained active on the plants beneath the dirt covering.

It was rare for other ant species to occupy a plant simultaneously with imported fire ants. The little black ant (*Monomorium minimum*) was the only ant species to occupy plants for long periods while imported fire ants were at peak activity. Little black ants were found commonly on only three of the control plants. It has been suggested that these ants are successful in cohabitation with imported fire ants because of their worker ants' ability to emit a repellent liquid during encounters with imported fire ants (Baroni Urbani and Kownowski, 1974). In October when activity and plant occupancy by imported fire ants declined, presumably due to cooler fall temperatures, control plants no longer inhabited by imported fire ants were occupied by carpenter ants (*Camponotus pennsylvanicus*). We experienced no stem breakage using Tanglefoot as reported by Barton (1986); however, an unidentified species of red ant was found occasionally in 1995 and 1997, somehow being able to bypass the Tanglefoot barrier.

**Insect Herbivores on *S. occidentalis***—The primary insect herbivores on the plants were the larvae of *Eurema nicippe* (sleepy orange butterfly) and *Phoebis senna* (cloudless sulfur butterfly). *Eurema nicippe* larvae were the more common, appearing at least five times more frequently than *P. senna*. In 1997, mean number of larvae larger than 10 mm per plant per day was 2.74 ( $\pm 0.18$  SE) for *E. nicippe* versus 0.19 ( $\pm 0.03$ ) for *P. senna*. *E. nicippe* larvae appeared earlier than *P. senna*, were strictly folivores, and often were able to completely defoliate experimental plants (Fig. 1). Larvae reached a maximum length of ca. 25 mm and occasionally were able to pupate on control plants. *Phoebis senna* larvae fed primarily on leaves but also were observed feeding on flowers and developing seed pods. These larvae reach a maximum length of ca. 40 mm and, at that size, leave the plant via a silk line and pupate elsewhere (Barton, 1986).





FIG. 1—Photograph of a defoliated experimental *S. occidentalis* (right) and an intact control plant (left).

The two butterfly species exhibited different ovipositional preferences ( $\chi^2 = 121.6$ ,  $df = 1$ ,  $P < 0.001$ ) with 82.2% of *E. nicippe* eggs laid on lower portions of plants as compared to 71.9% of *P. senna* eggs which were laid on the top three leaves of plants. *Phoebis senna* larvae were more commonly observed feeding on top

leaves and flowers, perhaps due to their nearby hatching location. Eggs and small larvae of both species were more common on the under surfaces of leaves ( $P < 0.0001$ ; greater than 78.5% of small larvae and eggs on underside of leaves); however, larger caterpillars were most abundant on the upper visible leaf sur-

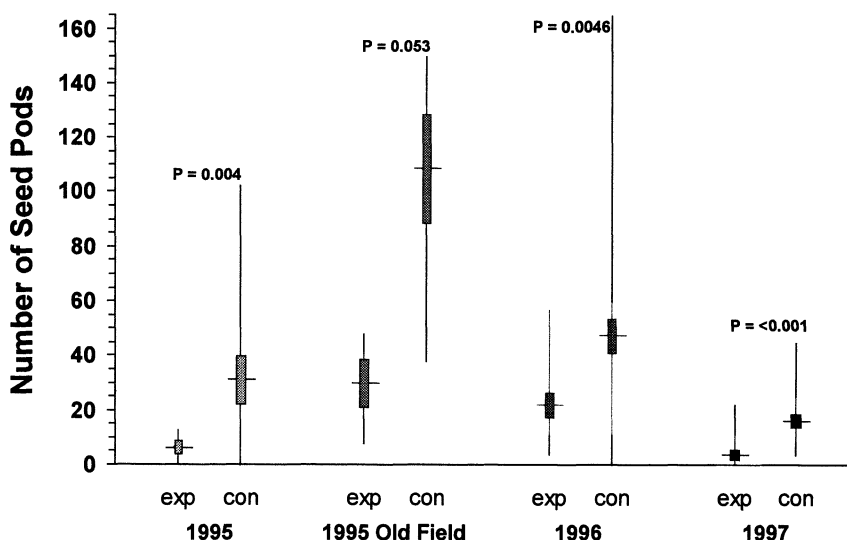


FIG. 2—Number of seed pods for control (con) and experimental (exp) plants during each experiment. Box plot indicates mean  $\pm$  SE and range.  $P$  values were determined using a Wilcoxon signed-rank test.

face ( $P < 0.0001$ , 78.6% upper versus 18.5% lower with 1.9% found on the stem).

Plant-sucking Homopterans were common insect herbivores, though found in small numbers. Leafhoppers (Cicadellidae) were found, usually singly, on both experimental and control plants. They were seldom found on plants after August. Stinkbugs (*Euschistus*) were found on both experimental and control plants into September.

**Effects of Ant Exclusion on Plant Reproductive Parameters and Growth**—Three measures of plant fitness (number of seed pods, weight of seed pods, and number of seeds) were determined for the 1995–1997 experiments (Figs. 2–4). In all cases, except number of seed pods in the 1995 old field experiment, control plants had significantly ( $P < 0.05$ ) greater allocation to reproduction, although control plants had increased variability in these measures, possibly due to varying levels of ant activity (ranging from fewer than 10 to more than 100 ants per plant). In all but the 1995 old field experiment, significantly fewer seed pods were produced on experimental plants (Fig. 2). In all four experiments significantly lower pod weights and significantly fewer seeds were produced on the experimental plants (Figs. 3 and 4).

In all three years, a number of experimental plants experienced complete and repeated de-

foliation by lepidopteran larvae with all experimental plants experiencing a substantial reduction in leaf surface as measured qualitatively as percent herbivory (1997; Table 2). This defoliation resulted in significantly reduced growth (height) in experimental plants as the season progressed (Fig. 5, treatment effect:  $F_{1,36} = 40.57$ ,  $P = 0.0001$ ; treatment  $\times$  time:  $F_{6,31} = 8.39$ ,  $P = 0.0001$ ). Number of leaves was significantly reduced also on experimental plants ( $F_{1,36} = 5.85$ ,  $P = 0.021$ ).

**Lepidopteran Egg and Larval Success**—During the study only eight ant attacks on lepidopteran larvae were observed, all occurring on larvae of *E. nicippe* within a 10 to 25 mm size range. Seven of the attacks were by *S. invicta* and the last by *M. minimum*. No ants were observed removing eggs.

During 1996 upper leaf surfaces and stems of all potted plants were examined daily for lepidopteran larvae greater than 5 mm in length. Daily larval numbers were compared between experimental and control plants, with significantly fewer larvae being found on controls ( $F_{1,887} = 6.98$ ,  $P = 0.008$ ).

In 1997 a daily inspection of all leaf surfaces of potted plants was initiated to record oviposition site and to trace the fate of all eggs and resulting small larvae. Larval survival was measured in three size classes: 1 to 3 mm, 4 to 9 mm, greater than 10 mm.

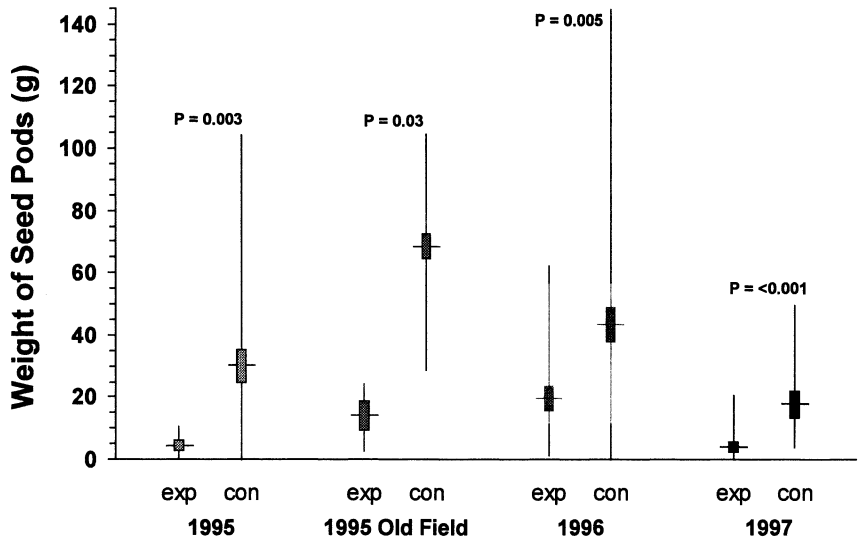


FIG. 3—Weight of seed pods for control (con) and experimental (exp) plants during each experiment. Box plot indicates mean  $\pm$  SE and range. *P* values were determined using a Wilcoxon signed-rank test.

Egg number differed significantly between experimental and control plants ( $F_{1, 1,081} = 15.67$ ,  $P < 0.0001$ ; Table 1); however, total oviposition was higher on control plants. Oviposition varied significantly across the weeks of the experiment ( $F_{6, 1,081} = 4.89$ ,  $P < 0.0001$ ). Because eggs were more numerous on ant-infested plants, butterflies did not appear to

avoid oviposition on plants on the basis of ant presence. By week 3, substantial herbivory (60% of leaf surface for experimental versus 31% for control) reduced the available surface area of experimental plants (Table 2), therefore egg numbers may also have been higher on control plants due to the greater availability of ovipositional surface. Egg number was sig-

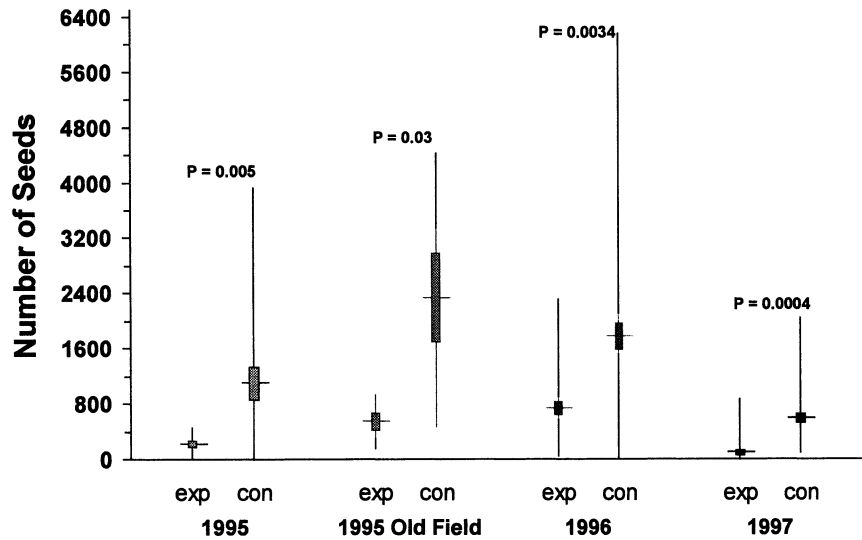


FIG. 4—Number of seeds for control (con) and experimental (exp) plants during each experiment. Box plot indicates mean  $\pm$  SE and range. *P* values were determined using a Wilcoxon signed-rank test.

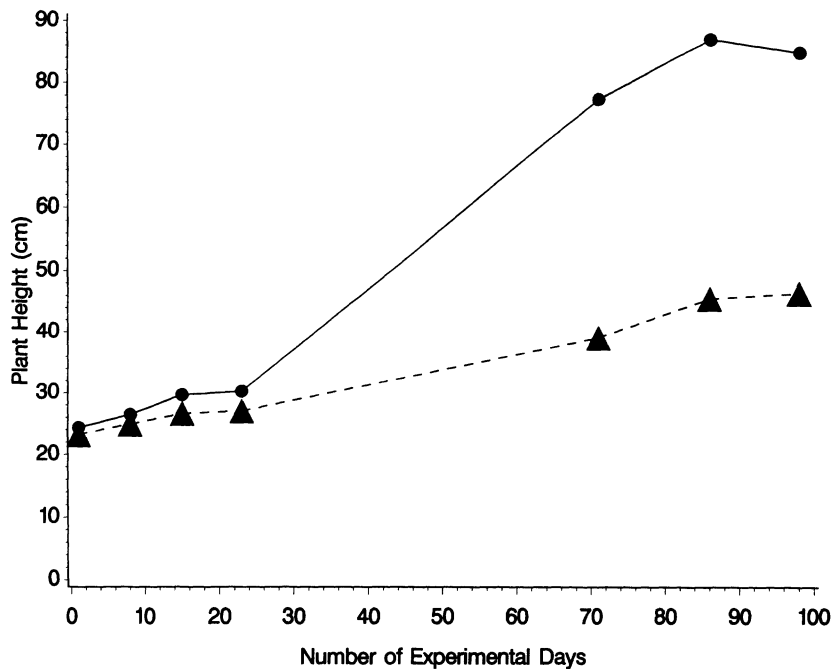


FIG. 5—Mean plant height (cm) for control (circles) and experimental (triangles) plants across the experiment from 13 July to 25 October 1997.

nificantly negatively correlated with herbivory regardless of treatment ( $r = 0.262$ ,  $P = 0.0001$ ). Egg hatching success was significantly greater on the experimental plants ( $F_{1, 847} = 24.26$ ,  $P = 0.001$ ; Table 1) with weekly means ranging from 48.1% to 81.4%.

Survival of larvae from the newly hatched size class (1 to 3 mm) to the 4 to 9 mm size class was significantly reduced with ant presence ( $F_{1, 525} = 14.20$ ,  $P = 0.0002$ ; Table 1). Ant activity increased over the first few weeks of the study as colonies established themselves near plants. Survival of small larvae peaked on control plants in the first week of the experiment (65.2%) when ants were least active.

Survival of larvae from the 4 to 9 mm size class to those larger than 10 mm increased sig-

nificantly with ant exclusion ( $F_{1, 395} = 6.86$ ,  $P = 0.009$ ; Table 1). The average daily number of large larvae (>20 mm) per plant typically was greater on experimental plants (control:  $1.21 \pm 0.10$ , experimental:  $2.04 \pm 0.14$ ; Table 3); however, numbers dwindled on experimental plants during periods of peak herbivory (Tables 2 and 3).

**DISCUSSION**—The imported fire ant was effective in deterring herbivores on our control plants; however, not all studies that have documented reduction in herbivory in the presence of ants have been able to demonstrate increased seed set. Kelly (1986) showed that ant pressure increased the probability of plant survival to reproduction and the amount of

TABLE 1—Egg number and larval survival rates by size class (mean  $\pm$  SE).

|              | Number of eggs<br><i>E. nicippe</i> | Number of eggs<br><i>P. senna</i> | Egg survival<br>% | Larval survival<br>1 to 3 mm to<br>4 to 9 mm (%) | Larval survival<br>4 to 9 mm to<br>>10 mm (%) |
|--------------|-------------------------------------|-----------------------------------|-------------------|--|---|
| Control      | 4.33 $\pm$ 0.30                     | 0.59 $\pm$ 0.07                   | 55.15 $\pm$ 1.58  | 54.04 $\pm$ 2.56                                 | 70.43 $\pm$ 2.99                              |
| Experimental | 3.34 $\pm$ 0.24                     | 0.73 $\pm$ 0.08                   | 65.97 $\pm$ 1.65  | 70.34 $\pm$ 2.28                                 | 83.70 $\pm$ 2.03                              |



TABLE 2—Total egg number by week (mean  $\pm$  SE) and percent herbivory (mean  $\pm$  SE) for each treatment.

| Week | Mean number of eggs |                 | Percent herbivory |                  |
|------|---------------------|-----------------|-------------------|------------------|
|      | Control             | Experimental    | Control           | Experimental     |
| 1    | 4.26 $\pm$ 0.40     | 4.83 $\pm$ 0.44 | 4.20 $\pm$ 0.72   | 5.14 $\pm$ 0.83  |
| 2    | 7.48 $\pm$ 0.40     | 7.31 $\pm$ 0.56 | 7.33 $\pm$ 1.08   | 13.09 $\pm$ 1.50 |
| 3    | 5.92 $\pm$ 0.59     | 2.49 $\pm$ 0.41 | 31.00 $\pm$ 3.84  | 60.39 $\pm$ 3.96 |
| 4    | 4.05 $\pm$ 0.60     | 1.14 $\pm$ 0.21 | 38.99 $\pm$ 3.64  | 80.82 $\pm$ 2.65 |
| 5    | 5.31 $\pm$ 0.80     | 5.61 $\pm$ 0.74 | 44.81 $\pm$ 4.24  | 82.75 $\pm$ 2.81 |
| 6    | 5.83 $\pm$ 0.68     | 4.82 $\pm$ 0.51 | 44.82 $\pm$ 3.20  | 71.29 $\pm$ 2.76 |
| 7    | 2.14 $\pm$ 0.22     | 2.83 $\pm$ 0.30 | 47.86 $\pm$ 3.25  | 74.44 $\pm$ 2.78 |

leaf area; however seed set was not affected. Our herbivory rates were comparable to her study (maximum of 70% herbivory for experimental and 40% for controls); however, we did observe significant increases in seed set. All reproductive measures increased in the presence of ants (with the exception of pod set in the field experiment in 1995) which paralleled the findings of Stephenson (1982) and Bentley (1977b). Pod set in *Cassia* has been correlated with the number of leaves (Barton, 1986); therefore reductions in leaf herbivory should be manifested in increased reproduction. Our inability to detect differences in the 1995 field experiment was due probably to its late initiation date (22 August). *Cassia* fruits which have already formed are capable of photosynthesis and require fewer carbon resources from the rest of the plant (Kelly, 1986).

Plants can benefit from ant defense through reductions in herbivory via less oviposition, removal of herbivore eggs, or consumption of herbivore larvae by ants. Ovipositing butterflies did not discriminate between ant-guarded and unprotected plants; however, some studies have described ovipositional avoidance (Inou-

ye and Taylor, 1979; Freitas and Oliveira, 1996; Oliveira, 1997). Number of eggs laid decreased with reduced leaf surface area resulting in higher numbers on plants with low previous herbivory (ant-guarded). Egg survival declined in the presence of ants and survival of small and large caterpillars was also negatively impacted. Larval mortality rates are comparable to the 48% mortality with ants versus 23% without ants observed in *Heliconius ismenius* on ant-defended *Passiflora* (Smiley, 1986). Larval mortality was size-dependent as in Freitas and Oliveira (1996) with larger larvae experiencing higher survival rates (Table 1).

Ant-defended *S. occidentalis* had increased growth as measured by plant height and number of leaves and increased reproductive effort, in numbers of pods, seeds, and weight of pods. Herbivore survival was reduced in the presence of ants. Bronstein (1994) described ant protection mutualisms as having conditional outcomes depending on the biotic environment; ant species and density may strongly affect the outcome of the relationship. Although control plants responded with faster growth and larger seed set, they exhibited greater variation in these traits perhaps due to variable ant activity. Although smaller native ant species were found near the plants and occupied three of the study plants, imported fire ants were the predominant species found on all control plants. Rico-Gray and Thien (1989) documented decreased effectiveness in smaller ant species. Variation in ant effectiveness also can be due to low nectar quality (Rashbrook et al., 1992), microspatial variation in plant densities (Boecklen, 1984), and herbivore susceptibility to ant defense (Barton, 1986).

Our described mutualism utilizes an intro-

TABLE 3—Number of large caterpillars ( $>10$  mm) per plant per day (mean  $\pm$  SE) by experimental week (13 July to 31 August).

| Week | Control         | Experimental    |
|------|-----------------|-----------------|
| 1    | 0.37 $\pm$ 0.10 | 0.43 $\pm$ 0.08 |
| 2    | 2.57 $\pm$ 0.39 | 4.96 $\pm$ 0.50 |
| 3    | 2.63 $\pm$ 0.38 | 6.19 $\pm$ 0.55 |
| 4    | 1.52 $\pm$ 0.30 | 1.17 $\pm$ 0.19 |
| 5    | 0.52 $\pm$ 0.16 | 0.48 $\pm$ 0.13 |
| 6    | 0.63 $\pm$ 0.12 | 0.75 $\pm$ 0.13 |
| 7    | 0.48 $\pm$ 0.10 | 0.94 $\pm$ 0.14 |

duced species of ant which is attracted by the extrafloral nectaries on *S. occidentalis* and is highly effective at reducing herbivory. Although native species are found near the plants, they rarely occupy plants simultaneously with imported fire ants. The presence of extrafloral nectaries on this plant suggests that ant protection has existed for generations prior to the appearance of imported fire ants. The larger size of individual imported fire ants and their large colony sizes may result in more effective herbivore protection than offered by native species. Further studies of this plant in the absence and presence of native and introduced ant species may be able to elucidate the conditional outcomes of this mutualism.

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#### LITERATURE CITED

- BARONI URBANI, C., AND P. B. KANNOWSKI. 1974. Patterns in the red imported fire ant settlement of a Louisiana pasture: some demographic parameters, interspecific competition and food sharing. *Environmental Entomology* 3:755–760.
- BARTON, A. M. 1986. Spatial variation in the effect of ants on an extrafloral nectary plant. *Ecology* 67:495–504.
- BENTLEY, B. L. 1977a. Extrafloral nectaries and protection by pugnacious bodyguards. *Annual Review of Ecology and Systematics* 8:407–427.
- BENTLEY, B. L. 1977b. The protective function of ants visiting the extrafloral nectaries of *Bixa orellana* (Bixaceae). *Journal of Ecology* 65:27–38.
- BOECKLEN, W. J. 1984. The role of extrafloral nectaries in the herbivore defense of *Cassia fasciculata*. *Ecological Entomology* 9:243–249.
- BRONSTEIN, J. L. 1994. Conditional outcomes in mutualistic interactions. *Trends in Ecology and Evolution* 9:214–217.
- COSTA, F. M. C. B., A. T. OLIVEIRA-FILHO, AND P. S. OLIVEIRA. 1992. The role of extra-floral nectaries in *Qualea grandiflora* (Vochysiaceae) in limiting herbivory: an experiment of ant protection in cerrado vegetation. *Ecological Entomology* 17:362–365.
- DEL-CLARO, K., V. BERTO, AND W. RÉU. 1996. Effect of herbivore deterrence by ants on the fruit set of an extrafloral nectary plant, *Qualea grandiflora* (Vochysiaceae). *Journal of Tropical Ecology* 12:887–892.
- FREITAS, A. V. L., AND P. S. OLIVEIRA. 1996. Ants as selective agents on herbivore biology: effects on the behaviour of a non-mymecophilous butterfly. *Journal of Animal Ecology* 65:205–210.
- INOUE, D. W., AND O. R. TAYLOR, JR. 1979. A temperate region plant-ant-seed predator system: consequences of extra floral nectar secretion by *Helianthella quinquenervis*. *Ecology* 60:1–7.
- KEELER, K. H. 1977. The extrafloral nectaries of *Ipomea carnea* (Convolvulaceae). *American Journal of Botany* 64:1182–1188.
- KEELER, K. H. 1981. Function of *Mentzelia nuda* (Loasaceae) postfloral nectaries in seed defense. *American Journal of Botany* 68:295–299.
- KELLY, C. A. 1986. Extrafloral nectaries: ants, herbivores and fecundity in *Cassia fasciculata*. *Oecologia* 69:600–605.
- KOPTUR, S. 1979. Facultative mutualism between weedy vetches bearing extrafloral nectaries and weedy ants in California. *American Journal of Botany* 66:1016–1020.
- LANZA, J. 1988. Ant preferences for *Passiflora* nectar mimics that contain amino acids. *Biotropica* 20:341–344.
- LANZA, J., E. L. VARGO, S. PULIM, AND Y. Z. CHANG. 1993. Preferences of the fire ants *Solenopsis invicta* and *S. geminata* (Hymenoptera: Formicidae) for amino acid and sugar components of extrafloral nectars. *Environmental Entomology* 22:411–417.
- O'DOWD, D. J., AND E. A. CATCHPOLE. 1983. Ants and extrafloral nectaries: no evidence for plant protection in *Helichrysum* spp.- ant interactions. *Oecologia* 59:191–200.
- OLIVEIRA, P. S. 1997. The ecological function of extrafloral nectaries: herbivore deterrence by visiting ants and reproductive output in *Caryocar brasiliense* (Caryocaraceae). *Functional Ecology* 11:323–330.
- PEMBERTON, R. W., AND J. H. LEE. 1996. The influence of extrafloral nectaries on parasitism of an insect herbivore. *American Journal of Botany* 83:1187–1194.
- PORTER, S. D., A. BHATKAR, R. MULDER, S. B. VINSON, AND D. J. CLAIR. 1991. Distribution and density of polygyne fire ants (Hymenoptera: Formicidae) in Texas. *Journal of Economic Entomology* 84:866–874.
- RASHBROOK, V. K., S. G. COMPTON, AND J. H. LAWTON. 1992. Ant-herbivore interactions: reasons for the absence of benefits to a fern with foliar nectaries. *Ecology* 73:2167–2174.
- RICO-GRAY, V., AND L. B. THIEN. 1989. Effect of different ant species on reproductive fitness of *Schomburgkia tibicinis* (Orchidaceae). *Oecologia* 81:487–489.
- SMILEY, J. 1986. Ant constancy at *Passiflora* extrafloral nectaries: effects on caterpillar survival. *Ecology* 67:516–521.
- STEEL, R. G. D., J. H. TORRIE, AND D. A. DICKEY. 1997. Principles and procedures of statistics. A biomet-

- tical approach, Third ed. McGraw-Hill Co., New York.
- STEPHENSON, A. G. 1982. The role of the extrafloral nectaries of *Catalpa speciosa* in limiting herbivory and increasing fruit production. *Ecology* 63:663–669.
- 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.
- ZAR, J. T. 1996. Biostatistical analysis, Third ed. Prentice-Hall, Upper Saddle River, New Jersey.
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