Plant Ecology **166:** 189–198, 2003.

Seed predators are undeterred by nectar-feeding ants on *Chamaecrista nictitans* (Caesalpineaceae)

Scott Ruhren[1,2]
[1]*Department of Ecology, Evolution, and Natural Resources 1 College Farm Road, Rutgers, The State University of New Jersey, New Brunswick, NJ 08901-1582, USA;* [2]*Current address: Department of Biological Sciences, Ranger Hall, University of Rhode Island, Kingston, RI 02881-0816, USA (e-mail: ruhren@etal.uri.edu; phone: 401-874-2626; fax: 401-874-5974)*

Received 22 January 2001; accepted in revised form 18 January 2002

Key words: Ant-plant interactions, Herbivory, Seed predation, *Sennius cruentatus*

Abstract

There are many examples of mutualistic interactions between ants and plants bearing extrafloral nectaries (EFN). The annual legume *Chamaecrista nictitans* (Caesalpineaceae) secretes nectar from EFN, specialized structures that attract ants, spiders, and other arthropods. The effects of manipulated *C. nictitans* patch size and location on plant-ant interactions were tested. Defense from herbivores was not detected; plants with ants did not set significantly more fruit or seed than plants with ants excluded. On the contrary, in one year, plants without ants set more fruit and seed than *C. nictitans* with ants. The cause of this was not determined. Furthermore, insect herbivore damage was low during three years of observations. *Sennius cruentatus* (Bruchidae), a specialist seed predator beetle, escaped ant defense despite the presence of numerous ants. Beetle progeny are protected during development by living inside maturing *C. nictitans* fruit and preventing fruits from dehiscing before emerging as adults. Although ants reduced percent of infestation in 1995, the total number of *S. cruentatus* per plant was not affected by ants in years of infestation. Overall, larger experimental *C. nictitans* patches attracted more ants, parasitoid wasps, and percent infestation by *S. cruentatus* while insect herbivores declined with increasing patch size. Location of patches within fields, however, did not affect numbers of arthropod visitors. Similar to manipulated populations, very little insect herbivory occurred in four reference populations. In contrast to the experimental populations, no *S. cruentatus* were recovered in reference populations of *C. nictitans*. Herbivory by insects may not always depress seed set by *C. nictitans* or may not exceed a threshold level. Thus, herbivory-reduction by ants may not have been detectable in these results. Seed predation may be more influential on *C. nictitans* reproduction.

Introduction

Host plant patch size may have numerous consequences such as influencing herbivore behavior and impacts (e.g., Harper (1977) and Crawley (1983), Bach (1988), McCauley (1991), Fritz (1992)). Larger host patches often are chosen more frequently (Root 1973; Crawley 1983; McCauley 1991; Morris and Kareiva 1991), and as host plant density increases, herbivore emigration often declines (Morris and Kareiva 1991). Furthermore, the tendency of many herbivores to aggregate is typically a combined effect of host plant traits, plant detectabilty, increase in food plant number and herbivore mobility (Crawley 1983). Though less discussed, plant quality and susceptibility may also influence the number and behavior of seed predators and their parasitoids (Segarra-Carmona and Barbosa 1992) and arthropod predators that function as plant defense mechanisms (Crawley 1983). Therefore, plant patch size may influence the responses of mutualists such as plant-defending ants as well as seed predators and herbivores.

Arthropod plant defenders such as ants, or less commonly spiders, may effectively enhance plant physical and chemical defenses, increasing overall resistance to herbivores and improving plant fitness (Fritz 1992; Ruhren and Handel 1999). For example, extrafloral nectaries (EFN), easily accessible nectar sources, may attract ants (Koptur 1979; Keeler 1981; Beattie 1985; Barton 1986; Koptur and Lawton 1988). Subsequently, these ants may provide the plant with protection from herbivores and seed predators (Koptur 1979; Huxley 1986). In many terrestrial communities, EFN mediate general yet very effective plant defense mechanisms and ants tend to increase numerically around EFN-bearing plants (Koptur (1979, 1984); Keeler 1981). Consequently, a correlated increase in plant defense is expected.

Yet, numerical increases in ants may not be correlated with benefits conveyed to the plants. Outcomes of facultative mutualisms and other plant-insect interactions are often unpredictable, dependent on both space and time (Cushman and Whitham 1989; Bronstein (1994a, 1994b)). Therefore, EFN-arthropod interactions may be unique for each plant within each community. Often, mutualisms persist only if benefits exceed the costs of maintaining the relationships (Bronstein 1994a). Furthermore, many perceived mutualisms provide variable benefits or lead to inconsistent outcomes (Barton 1986; Kelly 1986; Cushman and Addicott 1991). Because natural interspecific interactions are taking place within a fluctuating environment there is no guarantee that outcomes will be uniform (Thompson 1988). Responses of arthropod visitors are variable and impacts of both herbivores (Bach 1986; Grez and González 1995) and ants (Cushman and Whitham 1989) on plants may differ.

Using *Chamaecrista nictitans* (L.) Moench (Caesalpineaceae) (= *Cassia nictitans* and *C. procumbens*), a native annual legume bearing EFN, the relationships between plants, ants, and other arthropods were examined. Little has been reported about the visitors to EFN of *C. nictitans* and this species was chosen to test the conditional outcomes of nectar-mediated plant-ant-herbivore interactions. Barton (1986) concluded that ants visiting EFN of the congener *C. fasciculata* Greene increased reproductive success but ant and herbivore densities varied with population. Based on pod number and size, Boecklen (1984) determined that EFN did not enhance the survival of *C. fasciculata* and concluded that dense plant populations reduced ant densities on individual plants. However, no correlated effects on actual seed production were recorded, nor were density treatments tested directly.

Many arthropod species visit *C. nictitans* (Ruhren 1998) and the congener *C. fasciculata*. For example, Barton (1986) recorded more than 50 species of insects in addition to the ants and herbivores that visited *C. fasciculata*. In Iowa and Florida, 9 ant species visited *C. fasciculata* (Kelly 1986; Barton 1986). Previously, it was reported that jumping spiders (Araneae: Salticidae) collected nectar from *C. nictitans*, and increased fruit and seed production but were unable to reduce seed predation (Ruhren and Handel 1999). This indicated that, as with the congener *C. fasciculata*, a possibility exists for a diverse array of plant-arthropod interactions and changes in fitness for *C. nictitans*.

The major objectives of these experiments were: 1) to describe the ants and herbivores visiting variable-sized patches of *C. nictitans*; and 2) to evaluate ant effects on herbivores and seed predators of *C. nictitans*. Ultimately this study tested two hypotheses: 1) *C. nictitans* patch size will influence ant defense, seed predation and herbivory; and 2) plant fitness will be correlated with the amount of ant defense, seed predation, and herbivory.

Methods

Study organism

C. nictitans (wild sensitive plant) is a low-growing (10–50 cm) annual legume with petiolar EFN (Gleason and Cronquist 1995) visited by ants and many other arthropods. EFN are produced on each petiole near the flowers and fruit, where they secrete nectar from the time of first leaf expansion to senescence (Ruhren 1998). Each *C. nictitans* plant may bear up to 30 inflorescences (1–5 flowers per inflorescence) with 1–12 seeds produced per fruit (Lee 1989). The fruit are compressed pods that dehisce explosively as the two valves dry and coil tightly (Gleason and Cronquist 1995). Fruit and seed production by this self-compatible legume is limited by resources, not pollinators or seed predators (Lee and Bazzaz 1982; Lee 1989). Using an annual plant allows for evaluation of fitness determined as total seed production per generation. Like *C. fasciculata* (Boecklen 1984), *C. nictitans* grows in diverse habitats of the eastern United States including disturbed areas, open woodlands, and fields-all with well-drained soil (Lee 1989; Gleason and Cronquist 1995). Populations in New Jersey typically occur in grassy edges, frequently in disturbed habitats such as roadsides and utility rights-of-way. All plants used in this study were started in the glasshouse at Rutgers University from field-collected seed.

Investigation of plant-animal interactions

Field work was initiated in three fields dominated by perennial herbs (ex. *Solidago* sp., *Aster* sp., *Daucus carota* L., *Achillea millefolium* L.) and scattered woody plants (ex. *Juniperus virginiana* L., *Acer rubrum* L., *Cornus florida* L., *Rosa multiflora* Thunb., *Lonicera japonica* Thunb.) at Hutcheson Memorial Forest (HMF). This site is located near East Millstone, (Somerset County), New Jersey, USA (40°30′ N, 74°34′ W). *C. nictitans* has been collected sporadically from HMF during the past 30 years but has not been commonly sighted recently.

To test the effect of plant patch size on arthropod activity, interactions, and plant fitness, *C. nictitans* seedlings were planted in 3 fields at HMF in May of 1995–1997 (Figure 1). One plot was placed in each field and each plot was divided into an array of patches. Each plot was approximately 15 × 20 m and was approximately 100 m from the next plot. For the plant patch size experiments each patch was separated by 3 m from adjacent patches. After heavy herbivory by *Odocoileus virginianus* Zimmermann (white-tailed deer) and to a lesser degree by *Microtus pennsylvanicus* Ord. (meadow voles) and *Sylvilagus floridanus* J. Allen (cottontail rabbits), in 1995 in plots B and C, these plots were enclosed within a 2 m high fence. In 1996 and 1997 plot A was also enclosed and each patch in plots A, B, and C was protected with a 30 cm tall cylinder of galvanized hardware cloth (1.2 cm mesh) to reduce small mammal herbivory. Comparisons were made within and between these plots for three years.

The numbers of *C. nictitans* were manipulated in these field plots using an artificial array of plants. The surrounding vegetation was undamaged. In 1995, patches of 2, 4, 8, and 16 plants were planted initially. However, many of these plants were removed by mammalian herbivores. Afterwards, treatments of 1, 3, 6, and 9 plants were replanted. In 1996, patches of 2, 10 and 30 plants were planted, and 2 and 30 plant patches were planted in 1997. Within a patch, all *C. nictitans* were planted within 6 cm of the next nearest neighbor, exceeding *C. nictitans* densities seen naturally. This spacing ensured that foliage would intermingle and create a single thicket of multiple individuals. Twenty-two patches were planted per plot in 1995 (n = 198), thirty per field in 1996 (n = 1,296), and forty patches in 1997 (n = 1,920).

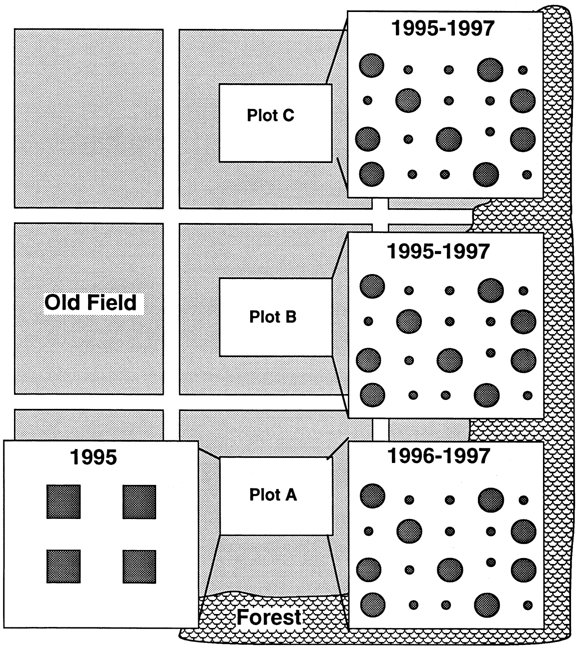

Figure 1. Relative placement of *Chamaecrista nictitans* field experiments in old fields at Hutcheson Memorial Forest from 1995–1997. In 1995, Plot A was arranged with four subplots of single plants in 5 × 5 arrays to test for seedling survival. Plots A in 1996 and 1997 and B and C from 1995–1997 were arranged to test for the effect of plant patch size on *C. nictitans*-insect interactions. Each plot was approximately 15 × 20 m and 100 m from the next plot. Plot placement and arrangement of patches within plots are not drawn to scale.

A separate experiment in plot A was designed to test for effects of EFN and herbivores on *C. nictitans* seedling survival in 1995 (Figure 1) because seedlings secrete nectar with the first leaf expansion (Ruhren 1998). Within each of the four subplots, single *C. nictitans* seedlings were planted 50 cm apart in an evenly spaced 5 × 5 array (n = 100). All treatments and observations of the seedling survival experiment were conducted similarly to the patch size experiment.

Each year, plants were watered during dry periods. Within all experiments, Tanglefoot® (The Tanglefoot Company, Grand Rapids, Michigan), was applied to the base of the stems of a random subset of patches at the time of planting and as needed during the growing season. This sticky compound excluded crawling arthropods, allowing for comparison of patches with or without ants. Because *C. nictitans* has a single stem and an upright stature, coating all stems within a patch at the soil surface effectively excluded crawling insects. These barriers proved effective and did not damage the study plants (Boecklen 1984; Ruhren 1998). To further prevent access by ants, vegetation in contact with patches was clipped.

Each year plants were monitored approximately every other day from 0800–1600 for four months. All visitors to *C. nictitans* were identified. Data included daily organism counts, and the time, duration, and outcome of interactions between ants and herbivores. Each patch was observed for 5 minutes. When reaching the end of the set, monitoring resumed with the first patch until the end of the day. Patches were monitored from the date of planting in June until onset of senescence in September when nectar production ceased and fruit maturation began. All fruit and seed were collected as they matured prior to dehiscence and were analyzed by treatment.

Reference populations

Four reference populations of *C. nictitans* were observed at sites in New Jersey to determine natural rates of insect visitation and herbivory. Then, 50 fruit were randomly sampled and examined from each population and the seeds were collected. The first reference population, Jockey Hollow (JH), is approximately 30 km north from HMF in Morristown, (Morris County). This population was in a grassy edge of a mixed hardwood forest. Fruits and seeds of *C. nictitans* were collected from JH in 1995 and checked for herbivores and other insects from 1995–1997. The second and third reference populations, also in grassy edges of mixed hardwood forests, were in North Brunswick (NB), (Middlesex County), and Cheesequake (CH), (Middlesex County), approximately 10 km and 22 km southeast from HMF, respectively. Fruit were collected from these populations and examined for damage in 1995 and plants were observed in 1995 and 1996. Also, in 1995, *C. nictitans* fruit were collected from a fourth roadside population, Plainfield (PF), approximately 18 km northeast from HMF, to evaluate amounts of seed predation and to use as a seed source.

Data analysis

C. nictitans fruit and seed set were analyzed with a mixed model ANOVA with plot as a fixed effect. Patch size and ant exclusion were treated as random sources of variation. Student-Newman-Keuls (SNK) *post hoc* means comparisons were run within years and among patches and plots (Sokal and Rohlf 1969). Mean fruit and seed production per treatment were compared. Data from 1996 and 1997 were analyzed separately because of altered experimental design. The seedling survival experiment from 1995 was analyzed for effects of ants on survival and reproduction of *C. nictitans* and for effect of herbivores.

For 1996 and 1997, cummulative per-plant insect herbivore counts for the season were compared for ant (presence or absence) and patch size effects, using an analysis of covariance (ANCOVA) with presence/absence of ants as a main source of variation and patch size as a covariate (Sokal and Rohlf 1969). Then, the number of insect herbivores per plant for each season were analyzed separately-with or without ants. Also, the number of ants per-plant for the 1996 and 1997 seasons were compared for patch size effects using an ANOVA. SNK means comparisons were utilized to compare mean ant and herbivore numbers per plant.

Sennius cruentatus Horn (Coleoptera: Bruchidae) (= *Bruchus cruentatus* Horn, *B. nigrinus* Horn, *B. nictitans* Motschoulsky, *B. depressus* Fall, and *Sennius nigrinus* Horn) (Bottimer 1968), a specialist seed predator beetle native to North America, were detected in *C. nictitans* pods in 1995 and 1997. For this reason, all fruit were inspected each year and analyzed for the effects of ants and patch characteristics on percent of infestation by *S. cruentatus* and total number of beetles per fruit and plants. Percent infestation of *C. nictitans* with or without ants was compared with a Chi-square goodness of fit test and the relationship between *S. cruentatus* and number of *C. nictitans* fruit per plant was analyzed with a linear regression technique (Sokal and Rohlf 1969).

Results

Investigation of plant-animal interactions

Although ants visited *C. nictitans* from planting date to senescence, survival at the seedling stage in 1995 was not affected by the presence of ants (ANOVA, $P > 0.05$). Ninety-eight percent of all seedlings survived and 62% of these survivors produced fruit. Of these plants, fruiting was approximately equal for plants with (46%) or without (54%) ant protection. Within the seedling survival plots in 1995, mean fruit [with

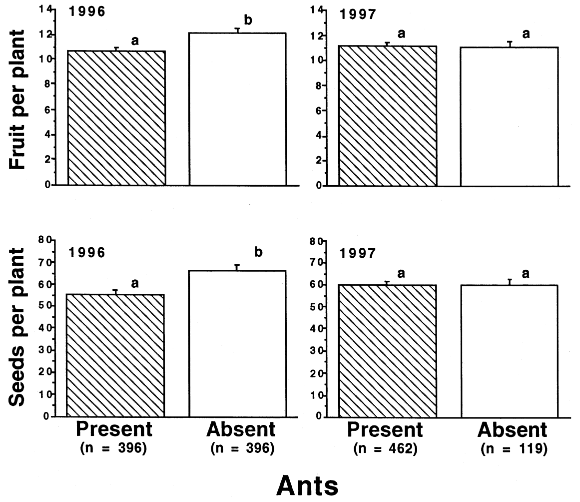

Figure 2. Comparison of mean (± SE) fruit and seed production by *Chamaecrista nictitans* averaged across plots and patch sizes as a function of presence or absence of ants in 1996 and 1997. Differences in sample sizes are attributed to experimental design and mortality. Bars marked with different letters are significantly different (SNK test, $P < 0.05$).

ants: 2.9 (3.8 S.D.); without ants: 2.6 (3.2 S.D.)] and seed production per plant [with ants: 13.7 (18.4 S.D.); without ants: 9.8 (13.3 S.D.)] were not significantly affected by the presence or absence of ants (ANOVA, $P > 0.05$).

Survivorship of *C. nictitans* was low in 1995 for plots B (32%) and C (15%) with mortality attributed to mammal herbivory. After fencing plots and enclosing individual patches with hardware cloth, survivorship increased in 1996 (A: 83%; B: 60%; C: 47%) and 1997 (A: 97%; B: 88%; C: 93%). Some herbivory by *M. pennsylvanicus* still occurred after animals burrowed beneath the hardware cloth. The following comparisons of fruit and seed production and arthropod visitations to *C. nictitans* were made on surviving plants for all three years.

Fruit and seed production were significantly greater on *C. nictitans* without ants in 1996 (ANOVA, fruit: 1 df, $F = 7.1$, $P = 0.008$; seeds: 1 df, $F = 10.9$, $P = 0.001$), but neither fruit nor seed production was significantly affected by the presence or absence of ants in 1997 (ANOVA, P > 0.05) (Figure 2).

C. nictitans supported a diverse arthropod community; ants, parasitoid wasps, halictid bees and jumping spiders fed on nectar from EFN. The most common ant on *C. nictitans* was *Crematogaster lineolata* Say. Other workers observed in descending frequency were *Dolichoderus plagiatus* Mayr, *Formica pallidefulva nitidiventris* Emery, *F. schaufussi* Mayr, *Tapinoma sessile* Say, *Monomorium minimum* Buckley, and *Solenopsis molesta* Say. All ant species fed on *C. nictitans* EFN nectar and are listed as opportunistic nectar-feeders by Smith (1947). Insect herbivory was low to non-detectable at HMF for three years and all reference populations at JH in 1995–1997, and NB and CH in 1995 and 1996. The most common insect herbivores on *C. nictitans* at HMF were Dictyopharidae, Aleyrodoidea and other Homoptera, and small Coleoptera. Insect herbivores were not observed feeding at EFN. Ant predation on herbivores was not observed. However, ant foraging behavior interfered occasionally with plant visitors. For example, when herbivores, parasitoid wasps, and pollinators encountered ants, they either left the plant or relocated on the plant or within the patch of *C. nictitans*. Three clusters of unidentified eggs on the underside of leaflets were removed from *C. nictitans* within 24 h of observation—most likely by ants—in 1996 and 1997.

S. cruentatus were detected in *C. nictitans* pods in 1995 and 1997 but were not present in 1996. *C. nictitans* seeds were consumed within infested fruit. The local distribution of *S. cruentatus* varied among years (Figure 3). Adults were recovered from fruit from plot A in 1995 and in plots B and C in 1997 (Figure 3). In 1995, 51% of *C. nictitans* with fruit in field A (n = 61), the seedling survival plots, had at least one *S. cruentatus* per plant (Figure 3). Ants reduced infestation of plants by 21% compared to ant-free plants in 1995 ($X^2 = 4.84$, 1 df, $P < 0.05$). However, there was no significant ant effect on numbers of *S. cruentatus* per plant in either year (ANOVA, $P > 0.05$). Infestation declined in 1997 to 9% of 581 fruiting *C. nictitans* survivors. Furthermore, 79% of plants with *S. cruentatus* were visited by ants and 75% of infested patches were large patches in 1997. However, within infested patches, there was a significant patch size effect (ANOVA, 1 df, $F = 5.01$, $P = 0.034$). A SNK test revealed that the number of beetles per plant was significantly greater in small patches [3.0 (2.8 S.D.)] than in patches of 30 plants [1.5 (0.81)]. Also, the number of *S. cruentatus* recovered per plant increased with number of fruit per plant (Figure 4). No *S. cruentatus* were detected in fruit from JH, NB, CH and PF.

Plant patch size had a significant positive effect on the number of ants and a negative effect on the number of herbivores per plant in both 1996 and 1997 (Figure 5). In 1996, the presence of ants did not have

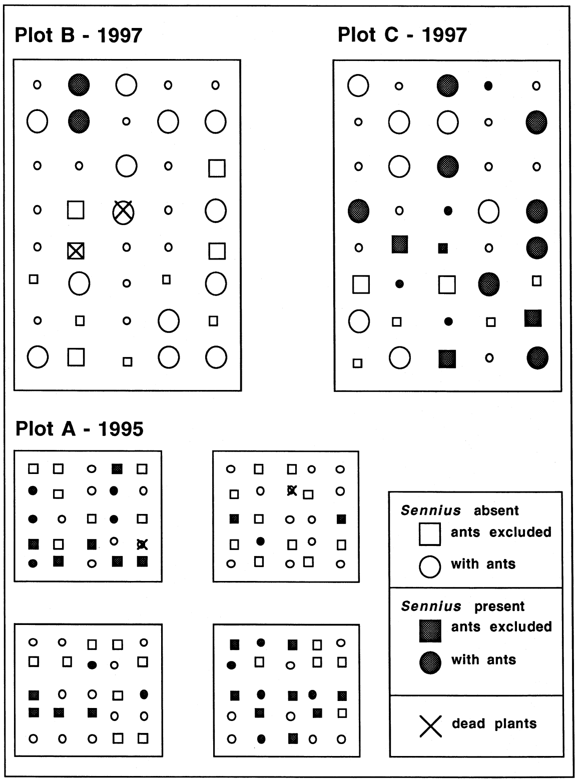

Figure 3. Location of patches of *Chamaecrista nictitans* infested with *Sennius cruentatus* (Bruchidae) in 1995 and 1997. Plot placement is not accurate; see Figure 1 for correct placement. Size of symbols (circles and squares) indicates relative patch size-1 plant per symbol in Plot A in 1995, 2 and 30 plants per symbol in Plots B and C in 1997. Plot A was arranged like Plots B and C in 1996 and 1997. No *S. cruentatus* were detected in Plot A in 1997 nor in any patch in 1996.

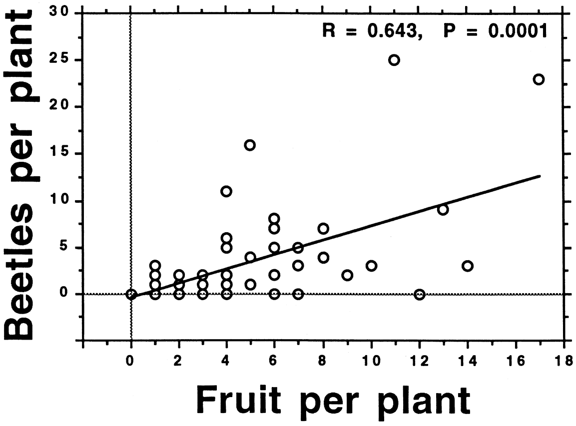

Figure 4. Relationship between number of *Sennius cruentatus* and number of fruit per *Chamaecrista nictitans* in 1997. *S. cruentatus* were not discovered in the patch size experiment in 1995 or in any *C. nictitans* in 1996.

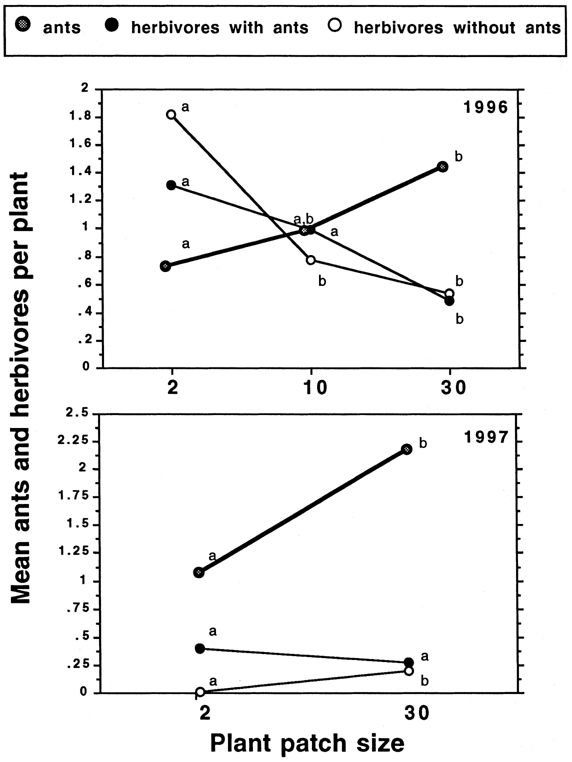

Figure 5. Mean total number of ants and insect herbivores per plant as a function of *Chamaecrista nictitans* patch size and presence and absence of ants in 1996 and 1997. Points within a line marked with different letters are significantly different (SNK test, $P < 0.05$).

a significant effect on the number of herbivores per *C. nictitans* (ANCOVA, $P > 0.05$). In 1997, the presence of ants had an overall significant effect on the number of herbivores per plant (ANCOVA, 1 df; $F = 6.03$; $P = 0.015$) (Figure 5) and when analyzed separately (without ants) herbivores increased significantly per plant (ANOVA, 1 df; $F = 17.15$; $P = 0.0003$) (Figure 5). Herbivores declined in 1997 from 1996 (Figure 5).

Based on bite patterns and hoof prints, it was determined that *O. virginianus* initially removed most of *C. nictitans* in 1995. Subsequent herbivory in 1995 was attributed to *M. pennsylvanicus* and to a lesser degree *S. floridanus*, also based on bite patterns. Despite replacing plants, repeated mammalian herbivory and severe drought conditions eliminated any further herbivory or *C. nictitans* fitness analyses. Fruit and seed production were not analyzed from these patch size experiments, but seeds were collected and inspected for *S. cruentatus* infestation. Little insect herbivory was detected on *C. nictitans* from JH in 1995–1997, NB and CH in 1995 and 1996 and PF in 1995.

Discussion

Ants did not enhance the fitness of *C. nictitans*. Although increased patch size resulted in an increased number of ants, there were no correlated increases in fruit and seed production or resistance to insect herbivores. Ants may not act as predators of these herbivores or failure to detect positive effects of ants on *C. nictitans* may be because of herbivore defensive behavior and ability to escape. For three years, the insect herbivores observed on *C. nictitans* were mobile feeders capable of quick escapes. This, combined with inadequate aggressive action of the resident ant species on *C. nictitans*, would influence the results (Cushman and Addicott 1991). Furthermore, positive ant effects may not be detected when conditions are unfavorable for the plants (i.e., drought field conditions) (Kelly 1986) or when there is low herbivore pressure (Cushman and Whitham 1989). Stress levels of *C. nictitans* were not manipulated and no herbivore outbreaks were apparent in three years of observations. Finally, reduced fruit and seed production with ants one year may be because of interference with pollinators; this was not observed.

Although ants engage in mutualistic relationships with many species of plants (Keeler 1981; Beattie 1985; Huxley 1986; Cushman and Addicott 1991; Koptur 1992), other studies have reported the absence of EFN-mediated ant benefits for host plants. Tempel (1983) and Rashbrook et al. (1991) described a lack of mutualistic relationships between nectar-feeding ants and *Pteridium aquilinum* (L.) Kuhn. O'Dowd and Catchpole (1983) did not see protection of *Helichrysum* spp. Even negative effects have been attributed to ants associated with EFN. For example, Buckley (1983) and DelClaro and Oliveira (1993) reported that ants continued to guard membracid bugs, while they simultaneously fed on the host plants' EFN.

Furthermore, the role of ants may change subtly over time; one-time defenders may later interfere with pollinators and parasitoids (O'Dowd and Catchpole 1983). Ants on *Vicia sativa* L. repelled the parasites of lepidoptera larvae leading to an increase in seed-eating (Koptur and Lawton 1988). Parasitoid wasps often visited EFN on *C. nictitans*, yet did not interact directly with ants or herbivores at HMF. Such interactions could be instigated by introducing ants, wasps, and herbivores onto *C. nictitans* in a controlled setting

Increased *C. nictitans* patch size resulted in more ants per plant and more parasitoid wasps, but fewer insect herbivores per *C. nictitans*. However, the numerical response by ants in larger plant patches did not result in enhanced protection. Ant defense could decrease as foraging ants spend most of their time collecting nectar from EFN without defending plants or interfering with herbivore behavior (Cushman and Whitham 1989). Thus, nectar could distract ants from potentially mutualistic behavior. Furthermore, patches of *C. nictitans* may have lacked the stimulus that triggers defensive behavior in the guild of foraging ants.

Declining herbivore numbers in larger *C. nictitans* patches countered the results reported in Root (1973) and Crawley (1983), Bach (1988), McCauley (1991). A direct relationship between the increase in ants to the decrease in herbivores could not be determined and encounters witnessed between foraging ants and herbivores on *C. nictitans* were rare, short-term, and not apparently antagonistic. Most importantly, *C. nictitans* reproduction did not increase with decreased insect herbivores.

Many plants interact with coevolved herbivores and seed predators (e.g., Center and Johnson (1974) and Johnson and Slobodchikoff (1979), Crawley (1983), Price (1984)). Bruchidae in general (Johnson 1981) and *S. cruentatus* in particular are examples of this phenomenon. *S. cruentatus* are strongly sclerotized black beetles collected previously from *C. nictitans* (Cushman 1911; Johnson and Kingsolver 1973), as well as *C. fasciculata* and *Parkinsonia* sp., throughout its range in the eastern half of the United States south to Mexico (Johnson and Kingsolver 1973). Because most Bruchidae depend almost entirely on seeds for development and approximately 80% of the species in the United States attack the Leguminosae (Arnett 1973), it is not surprising that many bruchid species exhibit host-specific oviposition behavior (Johnson and Slobodchikoff 1979; Siemens et al. 1991). Because *S. cruentatus* adults were not observed on *C. nictitans*, no interactions between *S. cruentatus* and ants were recorded.

Occasionally, ants interfered with oviposition by *S. cruentatus*, as seen in the reduced percentage of infested, ant-visited *C. nictitans* in 1995. However, ants did not significantly affect the total number of beetles per plant in infestation years. Perhaps female *S. cruentatus* were occasionally discouraged by ants but when oviposition could take place, more eggs were deposited per plant. The positive relationship between number of *C. nictitans* fruit and *S. cruentatus* per plant may indicate the effects of localized oviposition preferences for larger, more fecund plants. Although large host patches may be more detectable within the surrounding vegetation, a greater total number of *S. cruentatus* per small *C. nictitans* patch may indicate saturation of suitable oviposition sites by gravid females. Apparently, this specialist seed predator is capable of bypassing ants–not unusual for many specialist herbivores on ant-patrolled plants (Koptur 1992).

By specializing on seeds, developing bruchids have a rich source of nitrogen and frequently a protected nursery (e.g., Price (1984)). Johnson (1981) suggests that legume pod dehiscence helps reduce seed predation by scattering seeds and reducing oviposition. This mechanism has been bypassed by *S. cruentatus*; all *C. nictitans* pods containing *S. cruentatus* were glued shut with silk strands spun by the larvae. Thus, infested *C. nictitans* fruit do not explosively dehisce, allowing *S. cruentatus* to pupate safely among seed fragments (Center and Johnson 1973). *S. cruentatus* may further avoid predation because of their superficial resemblance to seeds—hard, compressed, shiny, and black–as well as playing dead when pods are forced open.

Aside from seed predation, *C. nictitans* may endure a low level of insect herbivory with no measurable effect on reproduction. Harper (1977) and Rosenthal and Kotanen (1994), Foggo (1996) suggest that plant tolerance and response to herbivory are variable within and among species. Furthermore, many plants maintain reproductive productivity by increasing rates of photosynthesis in the remaining leaves as long as herbivory does not exceed a threshold (Harper 1977; Hulme 1996). Such mechanisms were not examined for *C. nictitans* nor were the chemical defenses of *C. nictitans* foliage and seeds. Perhaps a combination of tolerance and repellence factors would help explain the lack of insect herbivory in the manipulated and reference populations of *C. nictitans*.

Ants on *C. nictitans* may not deter foliar herbivores and it is apparent that they are incapable of defending *C. nictitans* from mammal herbivores that are too large and seed predators like *S. cruentatus* that are too stealthy. Moreover, *C. nictitans* may not be affected by modest insect herbivore levels, and the low insect herbivore pressure may have prevented the detection of ant defense. Confounding this is the unpredictable behavior of ants through time, season and location (O'Dowd and Catchpole 1983). Moreover, ant effects on herbivores may be detected only above a certain threshold (Cushman and Whitham 1989), such as during insect population outbreaks higher than that witnessed in three years of observations. Finally, the presence of either herbivores and ants does not always lead to predictable responses in plant reproductive output. Facultative plant-ant mutualisms, encouraged by the presence of EFN, may be important under special conditions, but variation in ecological interactions through time and lack of benefits may occur more frequently than expected.

Acknowledgements

This research was partially funded by a grant from the William L. Hutcheson Memorial Forest and the Anne B. and James H. Leathem Scholarship Fund. The author thanks T.D. Lee and C.B. Fenster for providing growing instructions, life history, and reproduction information for *C. nictitans*. I am grateful to S. Endres, L. Florek, S.J. Meiners, and M.E. Yurlina for assisting in various aspects of the field work and K. Stevens for glasshouse assistance. D. Smith, Systematic Entomology Laboratory, Agricultural Research Service, US Department of Agriculture, verified ant identifications and C.D. Johnson identified *S. cruentatus* and shared fascinating bruchid life history information. S.N. Handel, K.C. Ruhren and two anonymous reviewers kindly read early versions of this report.

References

Arnett R.H. 1973. The Beetles of The United States. American Entomological Institute, Michigan.

Bach C.E. 1986. A comparison of the responses of two tropical specialist herbivores to host plant patch size. Oecologia 68: 580–584.

Bach C.E. 1988. Effects of host plant patch size on herbivore density: underlying mechanisms. Ecology 69: 1103–1117.

Barton A.M. 1986. Spatial variation in the effect of ants on an extrafloral nectary plant. Ecology 67: 495–504.

Beattie A.J. 1985. The Evolutionary Ecology of Ant-Plant Interactions. Cambridge University Press, New York.

Boecklen W.J. 1984. The role of extrafloral nectaries in the herbivore defense of *Cassia fasciculata.*. Ecological Entomology 9: 243–249.

Bottimer L.J. 1968. Notes on bruchidae of America north of Mexico with a list of world genera. The Canadian Entomologist 100: 1009–1049.

Bronstein J.L. 1994a. Conditional outcomes in mutualistic interactions. Trends in Ecology and Evolution 9: 214–217.

Bronstein J.L. 1994b. Our current understanding of mutualism. The Quarterly Review of Biology 69: 31–51.

Buckley R. 1983. Interaction between ants and membracid bugs decreases growth and seed set of host plants bearing extrafloral nectaries. Oecologia 58: 132–136.

Center T.D. and Johnson C.D. 1973. Comparative life histories of *Sennius* (Coleoptera: Bruchidae). Environmental Entomology 2: 669–672.

Center T.D. and Johnson C.D. 1974. Coevolution of some seed beetles (Coleoptera: Bruchidae) and their hosts. Ecology 55: 1096–1103.

Crawley M.J. 1983. Herbivory: The Dynamics of Animal-Plant Interactions. University of California Press, Berkeley.

Cushman J.H. and Addicott J.F. 1991. Conditional interactions in ant-plant-herbivore mutualisms. In: Huxley C.R. and Cutler D.F. (eds), Ant-Plant Interactions. Oxford Science Publishers, New York, pp. 92–103.

Cushman J.H. and Whitham T.G. 1989. Conditional mutualism in a membracid-ant association: temporal, age-specific, and density-dependent effects. Ecology 70: 1040–1047.

Cushman R.A. 1911. Notes on the host plants and parasites of some North American Bruchidae. Journal of Economic Entomology 4: 489–510.

DelClaro K. and Oliveira B.L. 1993. Ant-homopteran interactions: do alternative sugar sources distract tending ants? Oikos 68: 202–206.

Foggo A. 1996. Long- and short-term changes in plant growth following simulated herbivory: adaptive responses to damage? Ecological Entomology 21: 198–202.

Fritz R.S. 1992. Community structure and species interactions of phytophagous insects on resistant and susceptible host plants. In: Fritz R.S. and Simms E.L. (eds), Plant Resistance to Herbivores and Pathogens. University of Chicago Press, Chicago, pp. 240–277.

Gleason H.A. and Cronquist A. 1995. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. New York Botanical Garden, Bronx.

Grez A.A. and González R.H. 1995. Resource concentration hypothesis: effect of host plant patch size on density of herbivorous insects. Oecologia 103: 471–474.

Harper J.L. 1977. Population Biology of Plants. Academic Press, San Diego.

Hulme P.E. 1996. Herbivores and the performance of grassland plants: a comparison of arthropod, mollusc and rodent herbivory. Journal of Ecology 84: 43–51.

Huxley C.R. 1986. Evolution of benevolent ant-plant relationships. In: Juniper B. and Southwood R. (eds), Insects and the Plant Surface. Edward Auld, London, pp. 257–282.

Johnson C.D. and Kingsolver J.M. 1973. A revision of the genus *Sennius* of North and Central America (Coleoptera: Bruchidae). Technical Bulletin No. 1462. USDA, Washington, DC, USA.

Johnson C.D. and Slobodchikoff C.N. 1979. Coevolution of *Cassia* (Leguminosae) and its seed beetle predators (Bruchidae). Environmental Entomology 8: 1059–1064.

Johnson C.D. 1981. Interactions between bruchid (Coleoptera) feeding guilds and behavioral patterns of pods of the Leguminosae. Environmental Entomology 10: 249–253.

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.

Koptur S. 1984. Experimental evidence for defense of *Inga* (Mimosoideae) saplings by ants. Ecology 65: 1787–1793.

Koptur S. 1992. Extrafloral nectary-mediated interactions between insects and plants. In: Bernays E. (ed.), Insect-Plant Interactions. CRC Press, Boca Raton, pp. 81–129.

Koptur S. and Lawton J.H. 1988. Interactions among vetches bearing extrafloral nectaries, their biotic protective agents, and herbivores. Ecology 69: 278–283.

Lee T.D. 1989. Patterns of fruit and seed production in a Vermont population of *Cassia nictitans* L. (Caesalpiniaceae). Bulletin of the Torrey Botanical Club 116: 15–21.

Lee T.D. and Bazzaz F.A. 1982. Regulation of fruit and seed production in an annual legume, *Cassia fasciculata*. Ecology 63: 1363–1373.

McCauley D.E. 1991. The effect of host plant patch size variation on the population structure of a specialist herbivore insect, *Tetraopes tetraophthalmus.*. Evolution 45: 1675–1684.

Morris W.F. and Kareiva P.M. 1991. How insect herbivores find suitable host plants: the interplay between random and nonrandom movement. In: Bernays E. (ed.), Insect-Plant Interactions. CRC Press, Boca Raton, pp. 175–208.

O'Dowd D.J. and Catchpole E.A. 1983. Ants and extrafloral nectaries: no evidence for plant protection in *Helichrysum* spp.-ant interactions. Oecologia 59: 191–200.

Price P.W. 1984. Insect Ecology. 2nd edn. Wiley-Interscience, New York.

Rashbrook V.K., Compton S.G. and Lawton J.H. 1991. Bracken and ants: why is there no mutualism? In: Huxley C.R. and Cutler D.F. (eds), Ant-Plant Interactions. Oxford University Press, Oxford, pp. 230–237.

Root R.B. 1973. Organization of plant-arthropod association in simple and diverse habitats; the fauna of collards (*Brassica oleracea*). Ecological Monographs 43: 95–124.

Rosenthal J.P. and Kotanen P.M. 1994. Terrestrial plant tolerance to herbivory. Trends in Ecology and Evolution 9: 145–148.

Ruhren S. 1998. The role of extrafloral nectaries in mutualisms, herbivory, and plant defense of *Chamaecrista nictitans*. PhD Dissertation, Rutgers University, New Brunswick.

Ruhren S. and Handel S.N. 1999. Jumping spiders (Salticidae) enhance the seed production of a plant with extrafloral nectaries. Oecologia 119: 227–230.

Segarra-Carmona A.E. and Barbosa P. 1992. Host-plant patches as islands: effects of patch size, patch extinction, and seasonality of a herbaceous tropical legume (*Crotalaria pallida* Ait.) on a pod borer (*Etiella zinckenella* Treit.) and its parasitoids. Insect Science Applications 13: 709–718.

Siemens D.H., Johnson C.D. and Woodman R.L. 1991. Determinants of host range in bruchid beetles. Ecology 72: 1560–1566.

Smith M.R. 1947. A generic and subgeneric synopsis of the United States ants, based on the workers (Hymenoptera: Formicidae). The American Midland Naturalist 37: 521–647.

Sokal R.R. and Rohlf F.J. 1969. Biometry: The Principles and Practice of Statistics in Biological Research. W.H. Freeman and Company, San Francisco.

Tempel A.S. 1983. Bracken fern (*Pteridium aquilinum*) and nectar feeding ants: a nonmutualistic interaction. Ecology 64: 1411–1422.

Thompson J.N. 1988. Variation in interspecific interactions. Annual Review of Ecology and Systematics 19: 65–87.