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Interspecific interactions among common insects of the salt myrtle, Baccharis halimifolia L. (Asteraceae)

Laura F. Altfeld
University of South Florida

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Interspecific interactions among common insects of the salt myrtle, *Baccharis halimifolia*
L. (Asteraceae)

by

Laura F. Altfeld

A dissertation submitted in partial fulfillment
of the requirements for the degree of
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Department of Biology
College of Arts and Sciences
University of South Florida

Major Professor: Peter Stiling, Ph.D.
Susan Bell, Ph.D.
Henry Mushinsky, Ph.D.
Anthony Rossi, Ph.D.

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Interspecific interactions among common insects of the salt myrtle, *Baccharis halimifolia*

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ABSTRACT

Baccharis halimifolia is host to many species of insect herbivore, including myrmecophilous aphids. P*revious* studies with *B. halimifolia* have revealed strong effects of competition by an early-feeding beetle, *Trirhabda bacharidis,* and nitrogen enrichment. The effects of ant mutualists, however, have not been evaluated for their potential influence on interspecific interactions among insects on the host plant. I have employed a series of experiments aimed at answering the following general questions. (1) How does the density of aphid-tending ants affect common insects on the host plant? (2) What are the relative effects of (a) competition from *T. bacharidis*, (b) nutrient enrichment, and (c) ant presence on common insects of the host plant? (3) How do the effects of exotic ants differ from those of native ants?

The density of aphid-tending ants had positive effects on myrmecophilous aphids and aphid predators. However, given a choice between tended and untended aphid populations, aphid predators preferred to forage in the absence of ants. The density of

aphid-tending ants also increased predation on leaf miners although this did not necessarily translate into reduced densities of leaf miners.

Competition by early-season feeding of *T. bacharidis* negatively affected later-feeding herbivores but the effects of competition were unaffected by nutrient enrichment. Nutrient enrichment had positive effects on some herbivores, often only in the absence of early season herbivory. *Trirhabda bacharidis* larvae showed evidence of nitrogen and phosphorus limitation and suffered no predation by aphid-tending ants. Ant presence increased host plant survivorship from stemborer damage in 2004.

Ant species identity was an important factor determining the densities of myrmecophiles and non-myrmecophiles on the host plant in addition to affecting the responses of herbivores to increases in host plant quality. Aphids were more abundant in the presence of the exotic *Linepithema humile* (Hymenoptera: Dolichoderinae) versus the native *Camponotus floridanus* (Hymenoptera: Formicinae). Aphid predators also had higher densities in the presence of *L. humile* versus *C. floridanus*. Only *L. humile* acted as predator on leaf mines although predation did not always translate into reduced seasonal abundances for both species of leaf miner.

CHAPTER 1

THEORY, BACKGROUND AND OBJECTIVES

The meta-subject for this dissertation is interspecific interactions among common

insects that share the host plant, *Baccharis halimifolia* L. (Asteraceae), in Florida. I

chose this general topic because of my interests in how multiple species interact when

sharing a resource and what factors influence the population densities of those species.

This dissertation draws upon ecological theories for competition, nutrients (so called

bottom-up factors), myrmecophily, and exotic species as these theories pertain to plant-

insect herbivore interactions. The inference space for conclusions drawn from this body

of work is small, an island, a single host plant, relative to the infinite possibilities for

interspecific interactions among insects on this host plant, let alone the possibilities for

plant-insect interactions in general. That notwithstanding, the following series of

experiments add to increasing evidence in support of community-wide effects of exotic

species, conditional importance of bottom-up factors, and asymmetric competition while

at the same time challenging ecologists to question generalities about ant mutualisms and

how both the presence of an ant-aphid mutualism and the identity of the ant mutualist can

differentially affect mrymecophilous and non-mrymecophilous insects that share a host

plant.

Connell (1983) defined competition among species as "…the term used when each species of a pair has a negative effect on the other". The extent to which species compete with each other is a topic of continued interest, particularly in terms of the influence competition may have in structuring communities. Contemporary ecological theory is divided in support of the role competition plays in determining the abundances and identities of species within a community. Up until the late 20th century, competition was considered the primary structuring force in communities. Ecological theory had long since been under the strong influence of processes that were born out of studies done on plant communities, such as the role of competition among plants during succession.

Hutchinson's (1959) classical competition model suggested that competition is the primary structuring force in communities. Later, this model was amended by Hairston et al. (1960) who established a top-down trophic scheme stressing that, while competition was important among plants and predators, herbivores do not compete because of the top-down pressure from predators. Janzen (1973) considered competition among herbivores to be important on an evolutionary time scale but suggested that, on an ecological time scale, the importance of competition, particularly for insect herbivores, is dependent upon the predilection of herbivore species for particular plant parts and the host plant's response to herbivory. Weins (1977) also challenged the Hutchinson model by suggesting that because resources are not always in short supply, competition is not a primary structuring force for herbivore communities, i.e. competition is only important during the times when resources are in short supply relative to demand. In 1983, two independent literature reviews (one by Connell and one by Schoener) were published that concluded a less pervasive role for interspecific competition among herbivores,

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advocating the more frequently observed and relevant role of intraspecific competition in affecting population densities. Sih et al.'s (1985) review concluded that competition was no more important than predation in structuring communities. The theory of competition had become much maligned as the primary factor structuring communities owing to a significant lack of evidence and confusion about what validly qualified as evidence of true competition among species. Competition is currently considered to be one of *several* potentially important factors shaping communities. Among insect herbivores, the presence of competition among species has been documented in all types of feeding guilds (Denno et al. 1995) and has been shown to be important for host plants, herbivores and predators in several systems (Hudson and Stiling 1997, Denno et al. 2000, Moon and Stiling 2002).

The community of insect herbivores on *Baccharis halimifolia* (Asteraceae) provides an example of a system that can be substantially influenced by competition. The salt myrtle has a broad range in the U.S. and has been reported to support 133 phytophagous insect species, 11 of which are specialists (Palmer 1987). Among these is an early-season foliage-feeding beetle, *Trirhabda bacharidis* (Coleoptera: Chrysomelidae), that reduces the densities of leaf miners and a stem galling fly which occur on the plant later in the year (Hudson and Stiling 1997). The negative effects of *T. bacharidis* were described by Hudson and Stiling as an example of exploitative competition of leaves and growing tips by the specialist beetle.

Several insect herbivores on *B. halimifolia* have been shown to be positively affected by the bottom-up effect of increases in host plant quality (Moon and Stiling 2004). In fact, it is common for insect herbivores to respond positively, in terms of

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growth and/or fecundity, to increases in host plant quality because herbivores are typically limited by the nitrogen content of their food relative to their demand for nitrogen (Waring and Cobb 1992, Kyto et al. 1996). In addition to the importance of nitrogen, phosphorus is also a limiting nutrient for some herbivores, particularly those with rapid growth rates (Waring and Cobb 1992, Sterner and Elser 2002). The relative importance of such bottom-up factors for herbivores may change depending on heterogeneity in other variables such as environmental stress, plant chemistry, omnivory, competition or predation (Menge and Sutherland 1976, Hunter and Price 1992, Polis and Strong 1996, Forkner and Hunter 2000, Moon and Stiling 2002).

Insect herbivores on the host plant *B. halimifolia* contend with competition by an early-season feeding herbivore, nitrogen limitation and ant predation by exotic aphid-tending ants (Hudson and Stiling 1997, Moon and Stiling 2004, Altfeld and Stiling 2006). The goals of this research are to examine the relative roles of these factors when they occur in concert.

Objectives

The field experiments that will be described herein have three major objectives. First, because *B. halimifolia* commonly hosts an ant-aphid mutualism, and ant attendants may affect host use by other herbivores on the host plant, I evaluated the effects of aphid-tending ants on aphids, their predators and other herbivorous insects on the host plant. This was done by manipulating the level of ant attendance, creating naturally high and low densities of ant foragers and subsequently measuring the densities of aphids, their predators, two leaf miners, a stem borer and a gall fly over the course of a season. In

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addition, because short-term trends may help explain seasonal dynamics, the short term effects of ant removal on aphids and aphidophages were also investigated. Second, as follow-up to Hudson's and Stiling's work, I evaluated the effects of nutrient enrichment, specifically nitrogen and phosphorus, on exploitative competition by the specialist beetle *T. bacharidis*. A factorial experiment that combined N-fertilization, *T. bacharidis* larval herbivory, and ant attendance was used to tease apart the effects of each of these three important factors in affecting the densities of herbivores on the host plant. In a complementary experiment, phosphorus was evaluated for its potential as an important limiting nutrient in this system by comparing P-fertilization with NP-fertilization and ambient (non-fertilized) conditions. Lastly, I compared the effects of an exotic aphid-tending ant (*Linepithema humile*) to those of a native aphid-tending ant (*Camponotus floridanus*) on plant-insect and interspecific interactions among common insects of the host plant. The Argentine ant, *Linepithema humile* (Formicidae: Dolichoderinae), is the most commonly encountered ant attendant of the *Baccharis* aphid, *Aphis coreopsidis* (Hemiptera: Aphidinae), on Mullet Key, the site used for the experiments described above. However, some aphid populations on Mullet Key are tended by the native ant *Camponotus floridanus* (Formicidae: Formicinae). The final experiment in this dissertation describes a nested experimental design conducted to compare the effects of ant species identity, early-season herbivory and the relative effects of bottom-up and top-down factors on common insects of the host plant.

Study System

Baccharis halimifolia, also known as the groundsel tree or salt myrtle, is a native North American species that spans the east coast of the United States from Florida to

Massachusetts and along the Gulf of Mexico coast from Florida to Texas. *Baccharis halimifolia* is a dioecious perennial shrub that grows to a height of 5 m. Trees flower in late autumn at which time male and female trees can be distinguished. An excellent colonizer of disturbed or denuded habitats, *B. halimifolia* typically produces large numbers of air-dispersed seeds (Palmer 1987). Allelochemicals from *B. halimifolia* include the triterpenoid, baccharis oxide, a cardiac glycoside, and an acetone soluble resin (Anthonse et al. 1970, Kraft and Denno 1982, Krischik & Denno 1990, Hudson 1995). In addition, leaves of *B. halimifolia* increase in toughness and resin content while also decreasing in both nitrogen and water content throughout the year (Kraft & Denno 1982).

Baccharis halimifolia is associated with a large number of phytophagous insects (Palmer 1987). The most important of these is the specialist beetle *Trirhabda bacharidis* Weber (Coleoptera: Chrysomelidae). The univoltine *Trirhabda bacharidis* consumes *B. halimifolia* both in the larval stage and as an adult. Adult female beetles lay their eggs within deep grooves of *B. halimifolia* tree bark and in the late winter, stimulated by warmer temperatures and coinciding with newly budding leaves, larvae emerge to feed on foliage. Larvae pass through three instars in 35 – 40 days before pupating in the soil for an additional 20 – 26 days. Adults then emerge from the soil and return to the host to feed on foliar re-growth, remaining on the host for a further six weeks (Boldt 1989). *Trirhabda bacharidis* larvae are capable of completely defoliating a tree and their presence on the host plant has negative effects on the densities of other herbivores on the host plant later in the year (Hudson and Stiling 1997).

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The field site selected for all experiments described in this dissertation was Fort De Soto Park on Mullet Key, St. Petersburg, Florida. Mullet Key is an island that lies between the mouth of Tampa Bay and the Gulf of Mexico. In addition to *T. bacharidis*, five other herbivorous insects are common on *B. halimifolia*. These are the monophagous gall fly *Neolasioptera lathami* Gagne (Diptera: Cecidomyiidae), two leaf miners: the polyphagous serpentine miner *Liriomyza trifolii* Burgess (Diptera: Agromyzidae) and the oligogophagous blotch miner *Amauromyza maculosa* Malloch (Diptera: Agromyzidae); the monophagous stem boring plume moth *Oidaematophorus balanotes* Meyrick (Lepidoptera: Pterophoridae); and the myrmecophilous *Aphis coreopsidis* (Hemiptera: Aphidinae). The aphids are preyed upon by a suite of coccinellids, both larvae and adults, and syrphid larvae. The ant attendants on the host plant were either the native *Camponotus floridanus* or the exotic *Linepithema humile*.

Ant attendance on hemipterans well documented. The degree of association between hemipterans and ants can vary from untended hemipterans, which may be preyed upon by ants, to facultative species that may be tended by multiple species of ants, to obligate myrmecophiles that are mutualists with particular species of ants (Buckley 1987). Myrmecophilous hemipterans provide the ant foragers with honeydew in exchange for protection from predators and parasites (Buckley 1987). Of the myrmecophilous aphids, the subfamily Aphidinae contains the largest proportion of myrmecophiles and these are mostly facultative in nature with a few species that exhibit an obligate mutualism with ants (Stadler et al. 2003). Some or all of the following are considered to be important benefits to ant-tended hemipterans: (1) protection against parasites and predators; (2) reduction of fungal infections that can result from an

accumulation of honeydew; (3) increases in feeding rates and fecundity (Addicott 1979, Buckley 1987); and (4) reduction of potential competition from other non-myrmecophilous herbivores on the host plant (Messina 1981). Potential costs of attracting ant attendant are (1) the potential for predation by ants, (2) restriction to habitats where ant attendants are present (Stadler 2004), and (3) production of competitively superior honeydew (Addicott 1979, Sakata and Hashimoto 2000, Engel et al. 2001, Woodring et al. 2004). Ant-aphid mutualisms are conditional (Cushman and Whitham 1989) and may vary in time and space and by species of host plant, aphid and ant (Messina 1981, Fritz 1983, Mooney and Tillberg 2005). Ant-tended aphids may be less sensitive, in terms of altering their growth rates, to changes in host plant quality relative to untended species, a consequence which may work as both a cost and benefit (Stadler et al. 2002). Further, ant attendants can be both a limited and limiting resource for myrmecophilous aphids (Cushman and Addicott 1989).

CHAPTER 2

MYRMECOPHILY ON *BACCHARIS HALIMIFOLIA*

Synopsis

The main objective of this experiment was to evaluate the effects of aphid-tending ant density myrmecophilous and non-myrmecophilous herbivores of *Baccharis halimifolia,* via field manipulations of ant attendance levels. High and low levels of ant attendance were established for a five month evaluation of the effects of ant densities on *Aphis coreopsidis*, aphidophages, and the two leaf miners, *Amauromyza maculosa* and *Liriomyza trifolii*. High levels of ant attendance resulted in significantly higher densities of both aphids and their predators over the course of the five month experiment. The densities of the two leaf miners were reduced on high attendance host plants although this trend was not significant despite a consequent significant increase in ant-damaged mines. In a complementary short-term (20-day) experiment, aphid populations in ant-attended colonies increased in size and persisted longer than those in non-ant attended colonies; and aphid predators remained more abundant on non-ant attended aphid colonies until the colonies went locally extinct. The results of this experiment suggest that ant tending by *L. humile* on *B. halimifolia* more strongly affects insects normally involved in the ant-aphid mutualism.

Introduction

Often in ant-hemipteran mutualisms there is a direct relationship between aphid colony size and number of ants tending the colony with the strength of the relationship varying according to the species of ant and/or aphid involved in the mutualism (Cushman and Addicott 1989, Engel et al. 2001, Fischer et al. 2001). Generally, ants increase their level of attendance on larger aphid colonies; colonies that receive attendance by a greater number of ants, i.e. a greater ant-aphid ratio, receive greater fitness benefits such that the tending level of ants is an important determinant of aphid fitness and colony persistence (Cushman and Addicott 1989, Breton and Addicott 1992). Previous studies have primarily relied on ant exclusion methods to elucidate patterns and mechanisms in ant-hemipteran mutualisms. This experiment manipulated ant densities in the field by both increasing and decreasing tending ant densities on open honeydew-producing hemipteran populations in order to evaluate the responses of hemipterans, their predators and non-myrmecophilous herbivores of a host plant. The design of this experiment is unique and provides several benefits. Manipulating ant densities on host plants in the field allows for a more biologically relevant interpretation of the dynamics of ant-hemipteran-natural enemy interactions as compared with greenhouse studies in which environmental heterogeneity is not incorporated. The duration of this study also encompassed the time period during which hemipterans at this site are most abundant, namely spring and summer, and the effects of level of ant tending are evaluated across time in search of generalizations about the broad consequences of ant tending for a community of insects on a host plant.

Specifically, this experiment was designed to address the following questions: (1) what are the consequences to aphids of variable levels of ant attendance on a host plant; (2) how do differences in aphid abundances affect the distribution of aphid predators among host plants; and (3) what is the effect of variable degrees of myrmecophily on other non-myrmecophilous herbivores of the host plant?

Methods

Two experiments were conducted in fulfillment of the objectives just listed. The first of these, hereby referred to as Experiment 1, was initiated in April 2003 at which time 24 *B. halimifolia* trees were selected The trees ranged in height from 1-2 m and trees were a minimum of 1 m apart. Each tree was randomly assigned to one of three treatments. The three treatment levels consisted of the following: (1) ant reduction via the application of Tanglefoot® adhesive at the base of experimental trees; (2) ant enhancement via the use 4, 0.76 m long (2.5 cm diameter) PVC pipes half-buried vertically in the ground around the base of experimental trees; and (3) control, or ambient ant densities.

Tanglefoot® is a sticky non-toxic substance that immediately traps insects and is often used in ant exclusion experiments because it effectively restricts foraging ants. Tanglefoot® was applied to experimental ant removal trees by applying the substance to the base of the trees and removing foraging ants on the foliage with a large soft-bristle brush. Surrounding vegetation, such as grass blades and branches from neighboring trees, were clipped to prevent ants from circumventing the Tanglefoot® and foraging on treatment trees. Ant enhancement was carried out by inserting 4, 0.76 m long PVC pipes

half-buried vertically around the base of experimental trees in a front-back-side-side arrangement. The use of PVC pipes, typically for plot demarcation, in other salt marshes around Tampa Bay has been found to increase local ant densities because the pipes become colonized by ants (Altfeld, personal observation). At the end of the experiment all PVC pipes were inspected for ant colonization.

Post-treatment sampling was carried out monthly from May- September 2003. On each sampling date, 25 randomly selected branches per tree were visually inspected for numbers of ants, *A. coreopsidis*, coccinellid adults and larvae, and syrphid larvae. Due to difficulty in counting individuals in the field, aphid abundances were estimated using the following categories: 0, 1-10, 11-100, and 101-1000 individuals per branch.

Leaf mine densities were estimated each month by counting the number of leaf mines on 200 randomly selected leaves per tree. Leaf miners were identified to species based on the morphology of the leaf mine; *A. maculosa* creates blotch mines and *L. trifolii* creates serpentine mines. Ant-damaged mines encountered in the 200-leaf sub-sample were also included in the data to represent the proportion of total mines ripped/destroyed by foraging ants.

In July 30th, 2004, Experiment 2 was initiated. This experiment represented an evaluation of the short-term dynamics of ant exclusion on aphid and predator abundance. For this experiment, 5 pairs of branches from four *B. halimifolia* trees that supported ant-tended aphid colonies were selected. Each branch consisted of several separate stems all with their own growing tips. One branch from each of the 5 pairs received a band of Tanglefoot® at the base of the branch where it met with the first division of the tree trunk and all ants on the branch were removed using a soft bristle brush. The second branch of

the pair was left un-manipulated. As such, each pair of branches represented an un-tended aphid colony and a tended aphid colony on a single host plant. The number of ants, aphids, syrphid larvae, coccinellid larvae and coccinellid adults were recorded once a day on days 1 - 4 and 20, post-treatment. Aphid abundance was recorded using abundance categories similar to the method used in Experiment 1 but with a finer scale of estimation that would enable smaller changes in aphid population size to be detected. The abundance categories were as follows: 0, 1-25, 26-50, 51-100, 100-200, +200. As in Experiment 1, the midpoint of each abundance category was used in the analysis of aphid data.

Statistical analysis was carried out using SPSS® version 12 for MS Windows®. All variables were subject to Kolmogorov-Smirnov normality testing and Levene's homogeneity of variance test. Transformations were used when variables did not readily meet assumptions of normality and homoscedasticity for ANOVA testing. The relevant comparisons in Experiment 1 were between high and low levels of ant attendance. Prior to analysis, the categorical data on aphid abundance was transformed for use as continuous data by taking the median of each category and transforming it using a fourth root transformation ($(a + 0.5)^{1/4}$) (for similar method see Sloggett and Majerus 2000). Aphid predator densities, however, were unable to be transformed to meet assumptions of homoscedasticity and normality and were analyzed using the non –parametric Mann-Whitney U. In Experiment 2, time was an important factor in the analysis of response by aphids and their predators to ant removal. As such, aphid and predator abundances in the second experiment were analyzed using repeated-measures ANOVA. For both experiments, $\alpha = 0.05$ was designated as an appropriate level of statistical significance.

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Results

Experiment 1

The experiment was initially designed to provide eight replicate host plant trees within each ant attendance level. However, owing to heterogeneity in the distribution and behavior of ants across the field site, not all trees with PVC pipes were colonized and one control tree failed to maintain foraging ants. The following numbers of replicates were used in the analysis of the data: high n = 6, control n = 9, and low n = 9.

Ant abundances were effectively altered on experimental trees via field manipulations. During the experimental season, mean ant density in the high attendance level treatment was 3x greater than in the control (natural) attendance treatment (Table 2.1), 2.5x fewer in the low attendance level treatment and the difference between the high and low treatments was significant ($F_{1,13} = 27.726$, $P < 0.001$).

Ant attendance level significantly affected the seasonal abundance of *A. coreopsidis* and their predators (Figure 2.1). Aphids were more abundant in the high attendance level treatment compared to the low attendance level treatment (Table 2.1, $F_{1,13} = 7.781$, $P = 0.015$). Aphid predators consisted of 3.6% larval coccinellids, 44.4% adult coccinellids and 52% larval syrphids (Table 2.1). Predator densities were greater on trees with higher densities of their prey, namely trees in the high ant density treatment ($U = 48.5$, $P = 0.010$).

The densities of the two species of leaf miners were not significantly affected by level of ant attendance (Table 2.1, *A. maculosa* $F_{1,13} = 2.418$; $P = 0.144$; *L. trifolii* $F_{1,13} = 0.04$; $P = 0.845$), despite a significantly greater number of ant-damaged mines on trees in the high ant density treatment ($F_{1,13} = 13.787$; $P = 0.003$).

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Table 2.1. Mean ± SE abundances of myrmecophilous and non-myrmecophilous insects on the host plant in each ant attendance level treatment.

	High	*Control*	*Low*
Ants	770.0 ± 150.4	249.7 ± 71.8	100.9 ± 32.8
A. coreopsidis	2986.7 ± 1278.8	1161.7 ± 502.4	194.4 ± 89.4
Predators	14.7 ± 6.2	10.0 ± 2.0	4.4 ± 0.5
Coccinellids	6.3 ± 2.3	7.0 ± 0.78	3.4 ± 0.69
Syrphids	14.8 ± 7.3	5.0 ± 2.7	1.0 ± 0.29
Other Herbivores			
Intact Mines	103.2 ± 19.4	84.2 ± 7.8	74.9 ± 4.7
A. maculosa	81.0 ± 17.8	65.2 ± 6.2	51.8 ± 3.4
L. trifolii	22.2 ± 3.4	19.0 ± 3.9	23.1 ± 3.1
Ant Damaged Mines	65.0 ± 11.3	48.6 ± 9.4	24.8 ± 4.8
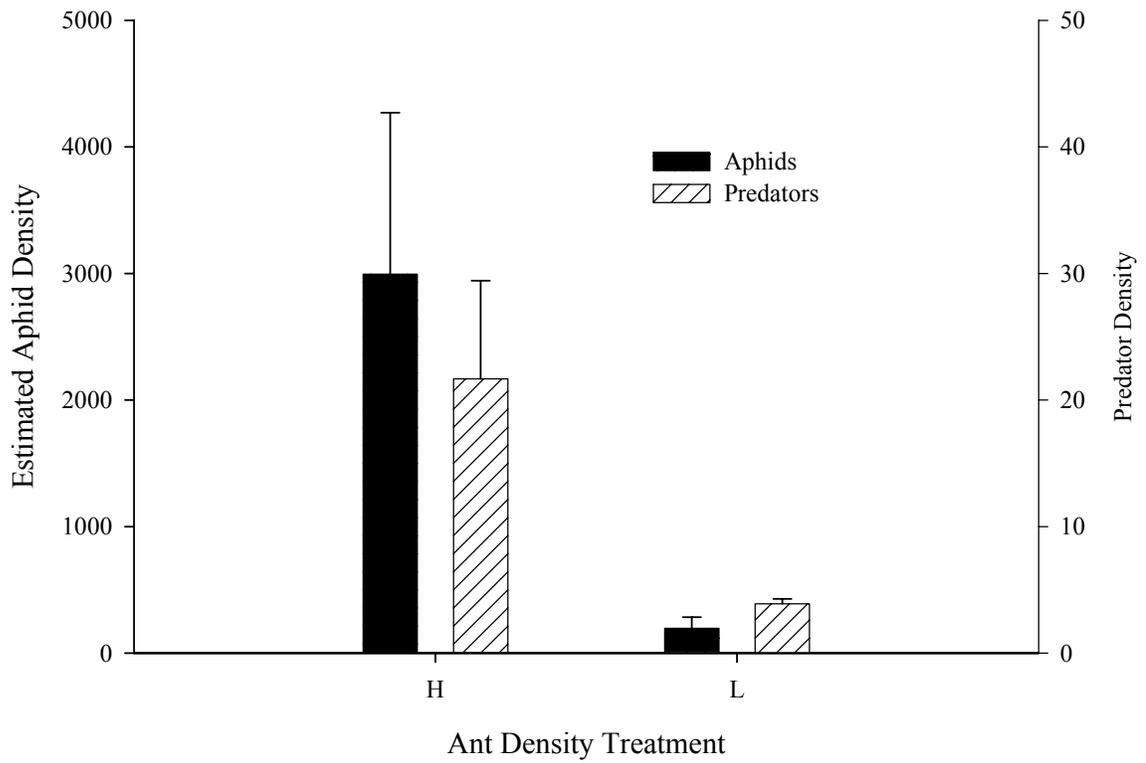
Figure 2.1. Seasonal mean density of aphids and aphid predators ± 1 standard error on 25

B. halimifolia branches per tree from May through September 2003 in the high (H; n = 6)

versus low (L; n = 9) ant density treatments.

Experiment 2

The results from the short-term ant-exclusion experiment showed that the application of Tanglefoot® on ant-exclusion branches was fully effective. Ants were completely excluded on branches where the sticky substance was applied. The abundance of aphids on branches that excluded ants showed steady decline (Figure 2.2) and by day 20 the estimated number of aphids in the ant-exclusion treatment was significantly lower than in corresponding tended colonies. A repeated measures ANOVA provided significant time and time-treatment effects ($P=0.003$ and $P=0.028$ respectively). The treatment effect alone, however, was not significant ($P=0.095$) because it wasn't until day 20 of ant exclusion that untended aphid colonies were sufficiently reduced to show a significant difference from the tended colonies. The abundance of aphidophages, namely coccinellid adults, larvae and syrphid larvae, also responded to ant exclusion (Figure 2.3). Repeated measures ANOVA for predators produced significant time ($P=0.035$), time-treatment ($P=0.028$), and treatment effects ($P=0.001$). Predator abundance responded to ant exclusion by day 2 of the experiment with predators remaining more abundant in untended aphid colonies until the aphids disappeared.
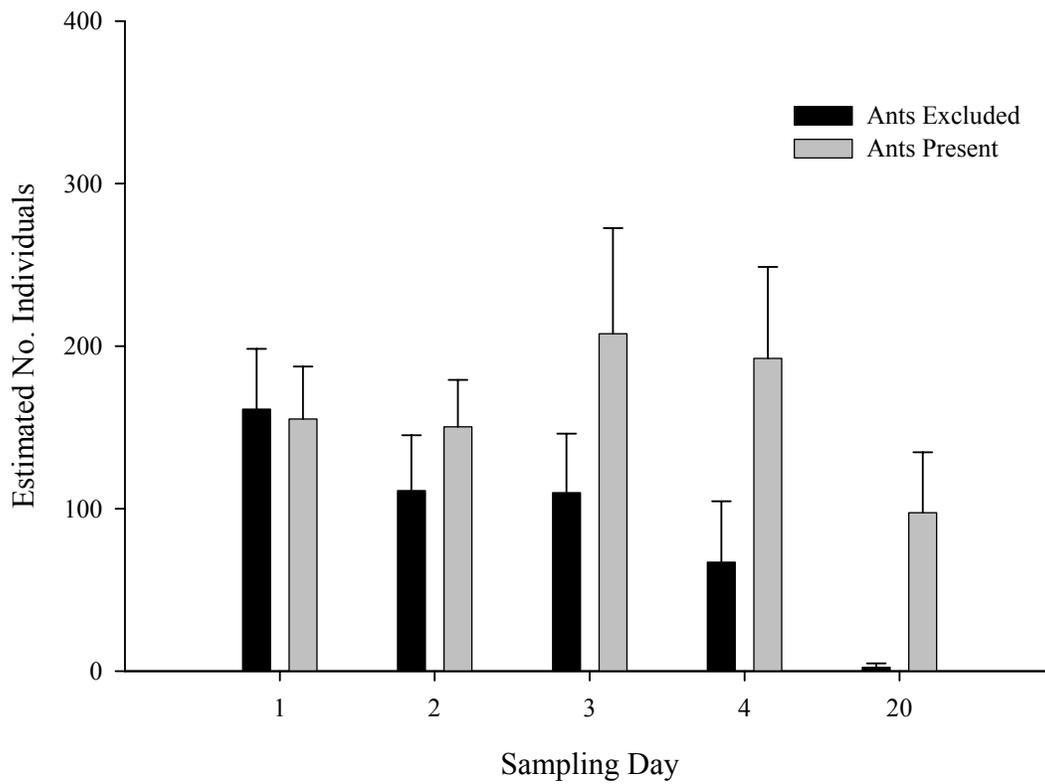
Figure 2.2. Mean ± 1 standard error estimated number of aphids in paired ant-tended/untended populations.
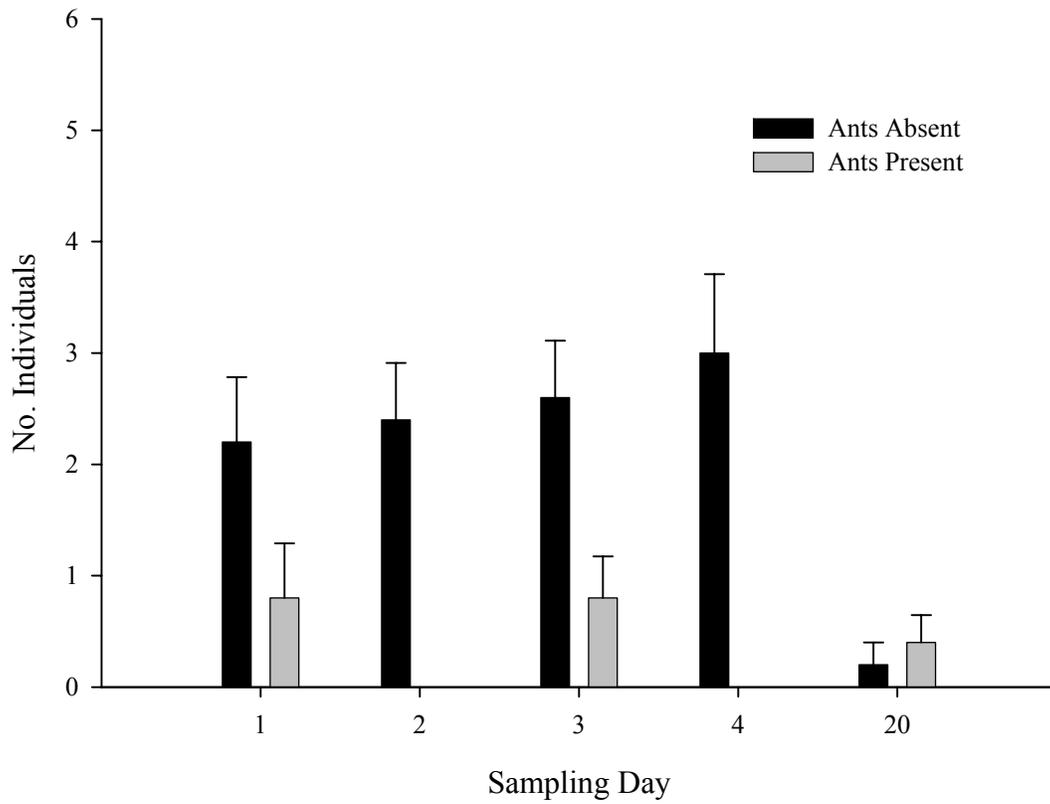
Figure 2.3. Comparison of the mean ± 1 standard error number of aphid predators in ant-tended versus untended aphid populations.

Discussion

Using Tanglefoot® to exclude ants in the field was challenging because of the physical disturbances caused by weather and tides that were frequent at the field site and because the ants were persistent in their determination to forage in the canopy of host trees. However, I was able to create a treatment which resulted in 59.6% fewer foraging ants as compared to control trees over the course of the experiment. The reduction in ant abundance was biologically relevant to aphids and aphidophages, which had statistically lower abundances in this treatment. Restricting ant foragers from reaching the aphids they tended prevented aphid persistence on the host plant over the course of the season, i.e. late spring and summer. When aphid populations were left untended they were more efficiently preyed upon by coccinellids and syrphid larvae as was shown in the rapid demise of untended aphid populations concurrent with the increase in predator abundance in Experiment 2. In tended aphid populations, however, the efficiency of predators was either inhibited by ant attendants, or mortality by predators was compensated for by population growth enhancement due to ant tending, or both.

Examples of both negative and positive density dependence have been shown to exist in ant-hemipteran mutualisms. Addicott (1979) suggests that ants seem to have the greatest positive effect on relatively small aphid populations via predator exclusion and increases to aphid feeding rates while the positive effects of ants on relatively large aphid populations diminish due to low ant-aphid ratios. Breton and Addicott (1992) showed that small aphid populations (<30 individuals) of *Aphis varians* on fireweed benefited more from ant attendance than did large aphid populations (>30 individuals) in terms of increased growth of local populations that was attributed to the per capita increase of ant

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attendants in small aphid colonies. However, large colonies of the ant tended membracid, *Publilia modesta,* received increased benefits of 36 - 46% relative to small colonies (Cushman and Addicott 1991). On *B. halimifolia*, *A. coreopsidis* populations persist on host plants longer when tended by *L. humile* than when left untended, even when aphid populations are large (> 30 individuals).

When evaluating the accumulated effects of ant exclusion on the abundances of aphids and their predators, an understanding of the relevant time frame of the system is important. Aphid predators in this system do seem to prefer foraging on untended aphid colonies. However, results from the short term experiment suggest that colonies of aphids are quickly consumed to extinction. These results concur with other studies that show the rapid extinction of aphid colonies by coccinellid and syrphid predators in the absence of ant attendants (Addicott 1979, Flatt and Weisser 2000, Shingleton and Foster 2000, Yao et al. 2000). However, results from Experiment 1 also showed that in the relative absence of untended aphid colonies the predators are more abundant on trees where their prey more consistently persists – in ant-tended colonies. The results of this study are similar to those of Sloggett and Majerus (2000) in which a greater proportion of predators were found on aphid colonies tended by *Formica rufa* during times of untended aphid scarcity and the persistence of tended aphid colonies provided an alternative source of food, a situation which they called aphid-mediated coexistence of ladybird beetles and ants.

An additional aim of the current study was to look at potential predation on leaf miners by aphid-tending ants. The two common leaf miners, *A. maculosa* and *L. trifolii,* were unaffected by increased density of *L. humile* on the host plant despite increases in

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the number of ant-damaged mines. This suggests that either ant predation is not critical

or that compensatory mortality is occurring at some later stage in the life cycle.

Clearly, the presence of ant attendants can have dramatic effects on those

organisms which are involved in the mutualism. But in terms of effects of the mutualism

on other herbivores the patterns are less clear. Studies of ant guards on ant plants have

produced equivocal results. Herbivory on plants with extra-floral nectaries has been

shown to be reduced (Dyer and Letourneau 1999) or unaffected (Mody and Linsenmair

2004) in the presence of ant guards. On plants that host ant-hemipteran mutualisms, the

evidence supports a reduction in herbivory in the presence of the mutualism, particularly

when the herbivores are foliage feeding beetles and their larvae (Dansa and Rocha 1992,

Floate and Whitham 1994). This effect of reduced herbivory, however, depends in part

on whether or not the tending ants are aggressive (Messina 1981).

CHAPTER 3

NITROGEN LIMITATION, COMPETITION AND MYRMECOPHILY

Synopsis

Here I test the effects of (1) nitrogen enrichment, (2) competition by *Trirhabda*

bacharidis (Coleoptera: Chrysomelidae) and (3) aphid-tending by *Linepithema humile*

(Hymenoptera: Dolichoderinae) on insects of *B. halimifolia* using a fully factorial design.

The presence of ants had a greater effect on herbivore densities than either *T. bacharidis*

larvae presence or nitrogen enrichment: aphids were more abundant but leaf miners and

stemborers were less abundant. Ant presence increased tree survival because stemborers

frequently killed host plants. Competition by *T. bacharidis* affected aphids and their

predators which were more abundant on trees with reduced herbivory. Nitrogen

fertilization had no effect on most herbivores although *T. bacharidis* larvae achieved

higher densities and earlier pupation on fertilized trees. These results indicate that aphid

tending by *L. humile* affects other insects on *B. halimifolia* more so than herbivory by an

exploitative competitor such as *T. bacharidis* or nitrogen limitation.

Introduction

Fertilizing host plants with nitrogen often results in increased herbivore densities

because of the frequency of nitrogen limitation for insect herbivores (Mattson 1980,

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Waring and Cobb 1989, Awmack and Leather 2002). However, the absence of increased herbivore densities on fertilized host plants can indicate that other factors, such as competition or predation, may be preventing the expression of positive effects from nitrogen fertilization (Kytö et al 1996, Strengbom et al. 2005, Moe et al. 2005). Predator manipulations, unlike manipulations of host plant quality, often result in either species-specific effects on herbivore densities because of the unique interactions between herbivores and their natural enemies or unpredicted responses in herbivore densities caused by environmental heterogeneity (Moon and Stiling 2002). In addition, the outcomes of interspecific interactions among co-occurring herbivores can be affected by both host plant quality and predators (Strauss 1987, Inbar et al. 1995, Denno et al. 2000, Vestergård et al. 2004). No one theory of community dynamics predicts the outcomes of species interactions among multiple species of herbivores, mutualists and predators that share a host plant nor how host plant quality can affect those species interactions.

Here I evaluated how host plant quality affects competition among herbivores, the intensity of a mutualism between aphids and ants, and predation by ants. The community of common insects on the groundsel tree, *Baccharis halimifolia* Linnaeus (Asteraceae) provides a model for evaluation of the relative effects of nitrogen limitation, competition between herbivores, and predation by ants because each of these factors have previously been found to be important. Common insects of the host plant were nitrogen limited (Moon and Stiling 2004), the presence of aphid-tending ants led to predation on leaf miners (Altfeld and Stiling 2006), and the presence of an early-season herbivore, *Trirhabda bacharidis* (Coleoptera: Chrysomelidae), negatively affected late-season herbivores (Hudson and Stiling 1997).

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Specifically I tested whether nitrogen fertilization alleviated or enhanced (1) competition between *T. bacharidis* and other herbivores and (2) predation on other herbivores by aphid-tending ants. My hypotheses were that, (1) if fertilized trees maintained higher densities of *T. bacharidis* larvae, then the densities of at least some of the other herbivores would be lower on those trees because of greater exploitative use of the host plant; and (2) ant presence would have positive effects on aphids and their predators but negative effects on leaf miners because of mine predation by the ants. Thus, nitrogen fertilization might not elicit increases in the densities of all insects utilizing the host plant because of interactive effects of predation and competition.

Methods

All experimental trees were between 1-2 m in height and were located within a 3.2 km long stretch of coastline shoreward of a mangrove fringe along the east coast of Mullet Key.

In December 2003, a total of 40 *B. halimifolia trees*, 20 trees with primarily smooth bark and 20 trees with primarily grooved bark, were selected, based on size and the presence of aphids, for random assignment to experimental treatments in a 2 x 2 x 2 factorial design with five replicates. The three factors were nitrogen fertilization (added versus control), *T. bacharidis* larvae abundance (grooved versus smooth bark), and ant attendants (present versus absent). The experiment was conducted for 9 months from January through August and October 2004. The passage of several tropical storms in September precluded data collection.

Nitrogen fertilization was accomplished via monthly applications of 40g granular nitrogen fertilizer (46-0-0 urea fertilizer, PCS Sales Skokie, IL) around the base of experimental trees. The density of *T. bacharidis* larvae was manipulated by arbitrarily selecting host trees with either primarily smooth or grooved tree bark. The selection of one of two bark phonologies provided a natural treatment for *T. bacharidis* larvae presence / absence because female beetles tend to deposit eggs in the grooves of host tree bark (Boldt 1989, Hudson and Stiling 1997) such that host trees with primarily smooth bark have few to no larvae. Ant attendance was manipulated by excluding ant foragers on experimental trees using a band of Tanglefoot® (The Tanglefoot Company, Grand Rapids, MI) around the trunk of experimental trees and surrounding vegetation was clipped to prevent ants from bypassing the Tanglefoot® and foraging in the trees.

Insect abundances were estimated at the beginning of each month from January through October using three census methods. First, 25 branches, each a minimum of 10 cm in length, were arbitrarily chosen and the numbers of individual *T. bacharidis* larvae and adults, ants, aphids, coccinellids and syrphid larvae were determined by visual inspection. Aphid abundance on each branch was assigned to the following categories: 0, 1-25, 26-50, 51-100, 101-200, 201+ individuals. Second, 200 leaves were inspected for leaf mines and were categorized by leaf miner species and as intact or ant-damaged. Third, 200 different branches, also 10 cm minimum length, were examined for the number of galls. Finally, a single count of recent stemborer emergence holes on host plant branches was made by visually inspecting all branches on each host tree in August during the peak in stemborer activity. Recent emergence holes were identified by the presence of frass around the holes.

In order to quantify differences in foliar nitrogen between fertilized and unfertilized trees, foliar nitrogen was analyzed monthly for 10 randomly collected leaves per tree. Leaves were oven dried at 50° C for 3 days, ground in a Wiley mill, and analyzed for total nitrogen as percent dry mass (CN 2100 Soil Analyze, CE Elantech, Inc. Lakewood, NJ).

Treatment effects were tested on monthly abundances of insects using fully factorial, repeated measures ANOVA. Prior to analysis, the categorical data on aphid abundance were transformed for use as continuous data by taking the median of each category to the fourth root $((a + 0.5)^{1/4}$, for similar method see Sloggett and Majerus 2000). The abundance of stemborer holes was tested using a univariate ANOVA. Main factors for ANOVA tests were nitrogen fertilization (+/-), *T. bacharidis* larvae (+/-) and ants (+/-). The effect of the presence of ants on stemborer-induced mortality among host trees was tested by chi-square with the Yates correction for continuity (Zar 1999). Prior to analysis all variables were subjected to Kolmogorov-Smirnov normality testing and Levene's homogeneity of variance test. All statistical tests were carried out using SPSS Version 13 for Windows (SPSS, Inc. 2004).

Results

The addition of nitrogen fertilizer significantly increased foliar nitrogen in *B. halimifolia* from 1.67% ± 0.05 (standard error) to 1.84% ± 0.05 ($F_{1,32}=6.364, P=0.017$). Abundance of *T. bacharidis* larvae on host trees with smooth bark was significantly lower, 33 ± 7 SE ($F_{1,32}=4.211, P=0.048,$) than on host trees with grooved bark, 55 ± 14 SE. Tanglefoot® effectively reduced the number of foraging ants, 16 ± 5 SE, on

exclusion trees ($F_{1,32}=39.323$, $P<0.001$) compared to 108 ± 21 ants on control trees. In addition, Tanglefoot® also captured some *T. bacharidis* larvae such that there was a significant Tanglefoot® by tree type interaction with the lowest densities of larvae on smooth trees banded with Tanglefoot®.

The presence of *L. humile* attendants influenced abundances of aphids, both species of leaf miners, ant-damaged mines, and stemborers. Aphids were present in significantly higher densities on trees with ant attendants ($F_{1,32}=9.557$, $P=0.004$). The presence of ants significantly reduced the abundances of both species of leaf miners, *A. maculosa* ($F_{1,32}=4.996$, $P=0.033$) and *L. trifolii* ($F_{1,32}=4.885$, $P=0.034$) (Fig. 3.1), and the stemborer, *O. balanotes* ($F_{1,32}=25.835$, $P<.001$). The reduction in the abundances of intact leaf mines coincided with significantly higher numbers of ant-damaged mines on trees with ant foragers ($F_{1,32}=20.308$, $P<0.001$) (Fig. 3.1). The abundance of *N. lathami* galls was unaffected by the presence of ant attendants.

The abundance of *T. bacharidis* larvae on *B. halimifolia* had no effects on any of the insects in this study, apart from *T. bacharidis adults,* where adults were more abundant on grooved trees. However, the abundances of ants, aphids and coccinellids were highest on trees with reduced numbers of *T. bacharidis* larvae when the tree had ant attendants (ants: $F_{1,32}=4.497$, $P=0.042$; aphids: $F_{1,32}=4.648$, $P=0.03$; coccinellids: $F_{1,32}=4.477$, $P=0.042$) (Fig. 3.2). In addition, *Trirhabda bacharidis* larvae were more abundant and left their hosts earlier on fertilized trees (Fig. 3.3; significant time x nitrogen interaction: $F_{2, 64} = 3.093$, $P = 0.052$).

Finally, there was 47.5% mortality of experimental trees during September and October of 2004 from stemborers. Of the trees that died from stemborer damage, significantly more (15 out of 19) were ant-exclusion trees ($\chi^2 = 5.2632, P<0.025$).
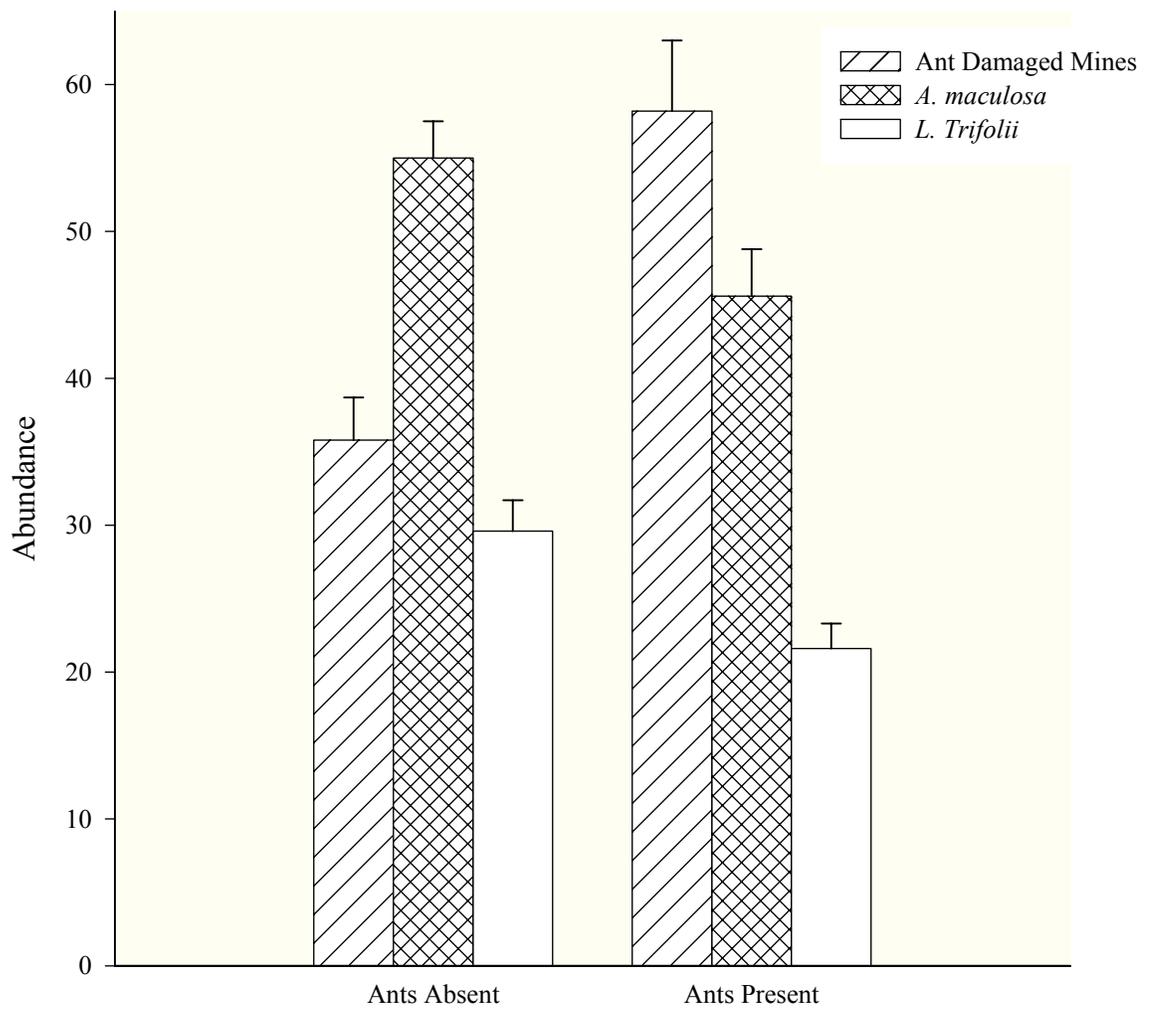
Figure 3.1. Mean seasonal abundances of ant-damaged mines, *A maculosa* and *L. trifolii* in the presence and absence of ant attendants. Bars represent 1 standard error.
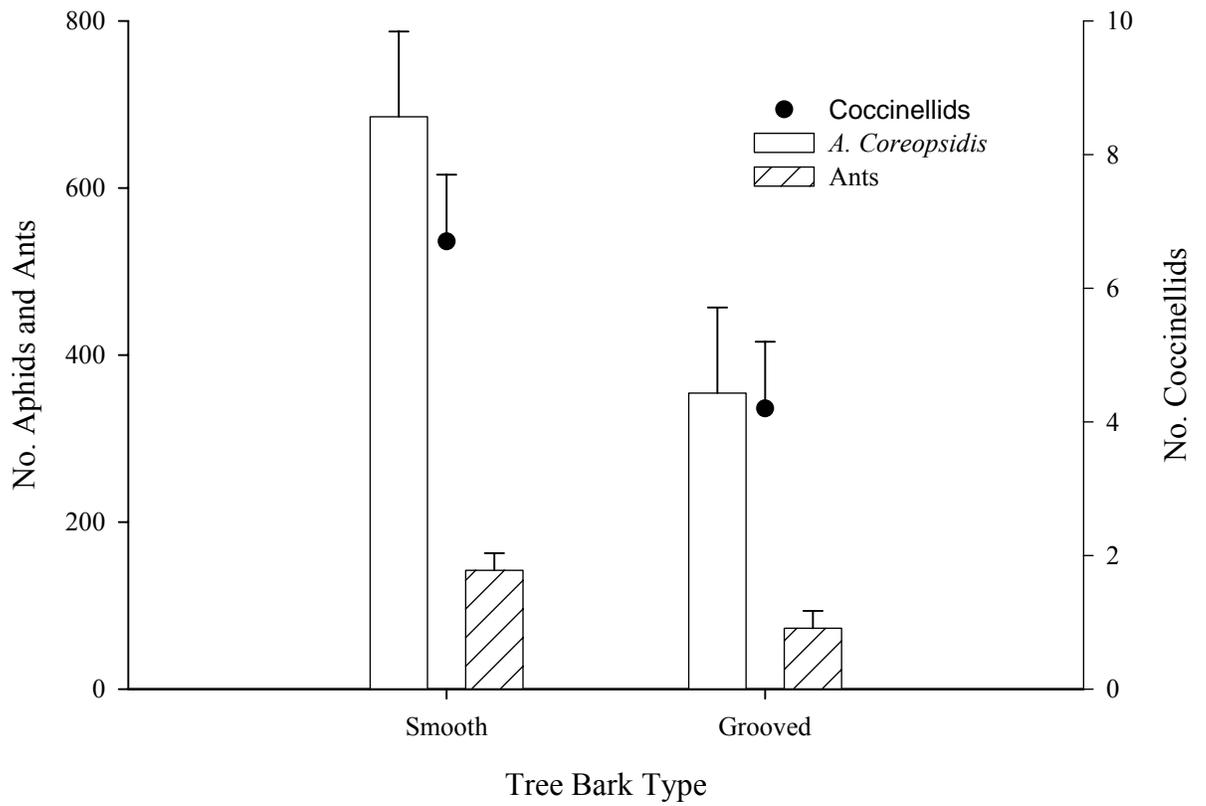
Figure 3.2. Mean seasonal abundances of aphids, ants and coccinellids on smooth and

grooved trees in the presence of ant attendants. Bars represent 1 standard error.
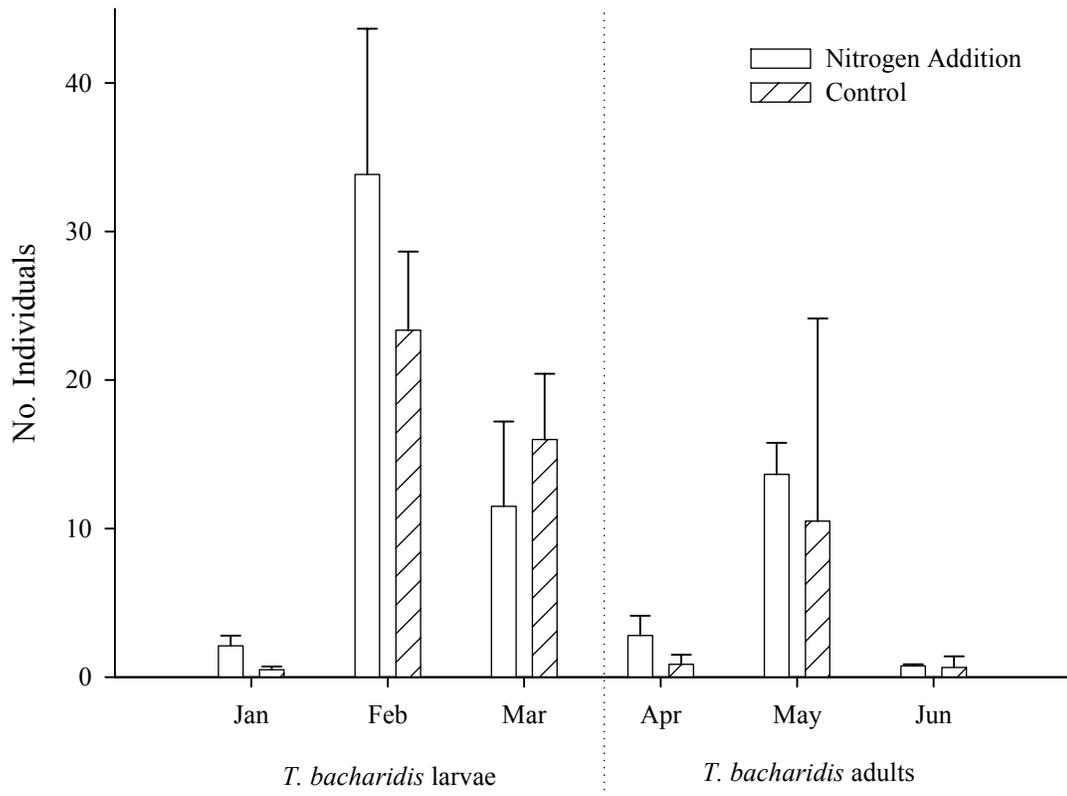
Figure 3.3. Mean monthly abundance of larval and adult *T. bacharidis*, on control and fertilized trees. Bars represent 1 standard error.

Discussion

The ant attendants, *L. humile*, on myrmecophilous aphids of *B. halimifolia,* had significant positive effects on aphids and coccinellids but negative effects on leaf miners and stemborers. Nitrogen did not affect the densities of ant attendants nor affect the outcome of competition from *T. bacharidis* larvae. In fact, only *Trirhabda* larvae responded to nitrogen addition inferring that *T. bacharidis* larvae may be nitrogen limited and experience decreased development time and/or increased survivorship on fertilized trees.

Invasion of non-native habitats by *L. humile* often causes significant decreases in native arthropod diversity (Holway et al. 2002, Sanders et al. 2003). However, for honeydew producing myrmecophiles, *L. humile* can have positive effects. *Linepithema humile* makes an exceptional partner because they recruit to honeydew sources quickly, tend 24 hours a day and have a modified proventriculus that increases honeydew uptake rates and carrying capacity, and assists in food sharing among nestmates (Holway et al. 2002, Davidson et al. 2004, Ness and Bronstein 2004).

Aphid-tending ants, whether native or non-native, have significant effects on aphid colony size via predator exclusion in a variety of systems (Addicott 1979, Flatt and Weisser 2000, Shingleton and Foster 2000, Yao et al. 2000). On *B. halimifolia*, *L. humile* has a positive effect on aphid density but differentially affects coccinellids depending on the spatial scale used for observation. On individual host trees, the presence of *L. humile* reduces coccinellid densities; among a stand of host trees, coccinellid densities are positively affected by the presence of *L. humile* by providing alternative resources when untended aphid populations are rare (Altfeld and Stiling 2006). The positive effects of

ant attendants on coccinellids is facilitated by the relatively higher densities of aphids on trees with ant attendants (Sloggett and Majerus 2000) and a positive relationship between aphid density and oviposition preference by female coccinellids (Evans and Dixon 1986).

The mechanism by which ants benefit plants by removing herbivores is complex and often strongly related to the species of ant and the presence of myrmecophilous aphids (Skinner and Whittaker 1981, Del-Claro and Oliveira 2000, Suzuki et al. 2004). Two other *Trirhabda* spp. on *Solidago* were differentially affected by the presence of ant attendants, depending on the size and aggressiveness of the species of ant present. The larger and more aggressive *Formica* sp. had significant negative effects on beetles but the smaller ant species, *Myrmica* sp.and *Prenolopis* sp., had no effects (Messina 1981). Even herbivores that feed within protective structures such as mines are not necessarily protected from predation by ants (Faeth 1980, Fowler and MacGarvin 1985, Pezzolesi and Hager 1994, Fagundes et al. 2005). *Camponotus* sp. and *Crematogaster* sp. of ant attendants have significant negative effects on a psyllid gall fly of *Baccharis dracunculifolia* (Fagundes et al. 2005). *Linepithema humile*, in particular, can have strong negative effects on herbivory levels experienced by a host plant via herbivore exclusion or predation (Way 1963, Way et al. 1992, Way et al. 1999) especially because they can reach high densities where they tend honeydew-producing insects (Holway et al. 2002). On *B. halimifolia*, the presence of *L. humile* was responsible for a trophic cascade because the presence of ants significantly reduced stemborer-induced tree death.

CHAPTER 4

PHOSPHORUS LIMITATION

Synopsis

This experiment was designed to evaluate the limiting value of phosphorus for

insect herbivores on *B. halimifolia*. Experimental trees were fertilized with phosphorus

and nitrogen + phosphorus and insect densities compared on experimental trees relative

to untreated control plants. As predicted, *T. bacharidis* larvae responded positively to

phosphorus fertilization. However, adult beetles showed no effects of fertilization.

Aphids and the two species of leaf miners responded negatively to phosphorus

fertilization although this result is considered to be an artifact of host trees not re-flushing

with leaves after *T. bacharidis* larval herbivory. Results suggest that *T. bacharidis* is

phosphorus limited, likely due to the rapid development of this univoltine insect, but the

limiting value of phosphorus of the other insect herbivores, especially *A. coreopsidis*,

bears further investigation.

Introduction

Phosphorus is an important limiting nutrient for herbivores. Phosphorus

represents only about 0.1 to 0.8% of plant tissue by mass but is an essential element in

the construction of nucleic acids, amino acids and energy transferring molecules such as

ATP and NADP (Sterner and Elser 1998). While the positive effects of nitrogen

fertilization have frequently been reported for insect herbivores, the effects of phosphorus

fertilization on insect herbivores are much less well documented. However, due to the

evidence of phosphorus limitation of organisms such as *Daphnia* and the theory that

rapidly growing organisms are more likely to be phosphorus limited due to the high

phosphorus demand of RNA production during growth, more studies that evaluate the

role of phosphorus as a limiting nutrient are being conducted. The insects on *B.*

halimifolia that may be most sensitive to phosphorus limitation due to characteristic rapid

growth are the specialist beetle *T. bacharidis*, which completes its entire life cycle within

6 months, and aphids. Phloem feeders in particular have been suggested to experience

extreme stoichiometric imbalances, a condition which may be exaggerated in aphids.

The objectives of this experiment were to evaluate (1) whether herbivores on *B.*

halimifolia exhibit phosphorus limitation and (2) if nitrogen and phosphorus fertilization

would have additive effects on herbivore densities.

Methods

In February, 2004 12 *B. halimifolia* host trees, ranging in height from $1 - 2$ m and

separated by a minimum distance of 2 m, were assigned to one of two fertilization

treatments (n = 6). The treatments were (1) phosphorus fertilization or (2) nitrogen +

phosphorus fertilization. All trees were fertilized with a one-time application of 74 g of

dry calcium phosphate fertilizer (total phosphoric acid 16%, Loncola Inc., High Springs,

FL). Trees in the nitrogen + phosphorus treatment were also fertilized with an additional 50 g of nitrogen fertilizer (46-0-0 urea fertilizer, PCS Sales Skokie, IL).

The densities of *T. bacharidis* larvae and adults, *A. coreopsidis*, ants, aphid predators, *A. maculosa*, *L. trifolii* and *N. lathami* were estimated monthly from March through October. Insect densities were measured using 3 census methods. First, 25 branches, each a minimum of 10 cm in length, were arbitrarily chosen and the numbers of individual *T. bacharidis* larvae and adults, ants, aphids, coccinellids and syrphid larvae were determined by visual inspection. Aphid abundance on each branch was assigned to the following categories: 0, 1-25, 26-50, 51-100, 101-200, 201+ individuals. Second, 200 leaves were inspected for leaf mines and were categorized by leaf miner species. Third, 200 different branches, also 10 cm minimum length, were examined for the number of galls.

Foliar nitrogen and phosphorus content were not measured for host trees in this experiment because most trees did not re-flush with leaves after larval herbivory by *T. bacharidis*.

The densities of insects on the host plant were compared among the following treatments: control, phosphorus fertilization and nitrogen + phosphorus fertilization. Data for insect abundances on control, unfertilized, host plants came from 6 randomly selected host trees that were also being used in a concurrent experiment (see Chapter 3). Treatment differences were evaluated with ANOVA. The densities of *A. coreopsidis* were fourth root (x + 0.5) transformed and *L. humile* square root (x + 0.5) transformed to meet assumptions of normality and homoscedasticity.

Results

The densities of *T. bacharidis* larvae were higher on host plants fertilized with phosphorus and nitrogen + phosphorus relative to control ($F_{2,15}$ = 4.745, P = 0.025). There were no additive effects for the combination of nitrogen and phosphorus fertilization (Figure 4.1). *Trirhabda bacharidis* adults exhibited no significant effects of fertilization by either phosphorus or nitrogen + phosphorus (Figure 4.1). The densities of *A. coreopsidis* and *L. humile* were negatively affected by phosphorus and nitrogen + phosphorus fertilization relative to control host trees ($F_{2,15}$ = 4.044; P = 0.055 and $F_{2,15}$ = 4.437; P = 0.031, respectively) but aphid predators were unaffected (Figure 4.2). Leaf miners were also negatively affected by phosphorus and nitrogen + phosphorus fertilization treatments (Figure 4.3. *A. maculosa*: $F_{2,15}$ = 7.249; P = 0.006 and *L. trifolii*: $F_{2,15}$ = 4.046; P = 0.039). The gall fly, *N. lathami*, was unaffected by phosphorus and nitrogen + phosphorus fertilization treatments.
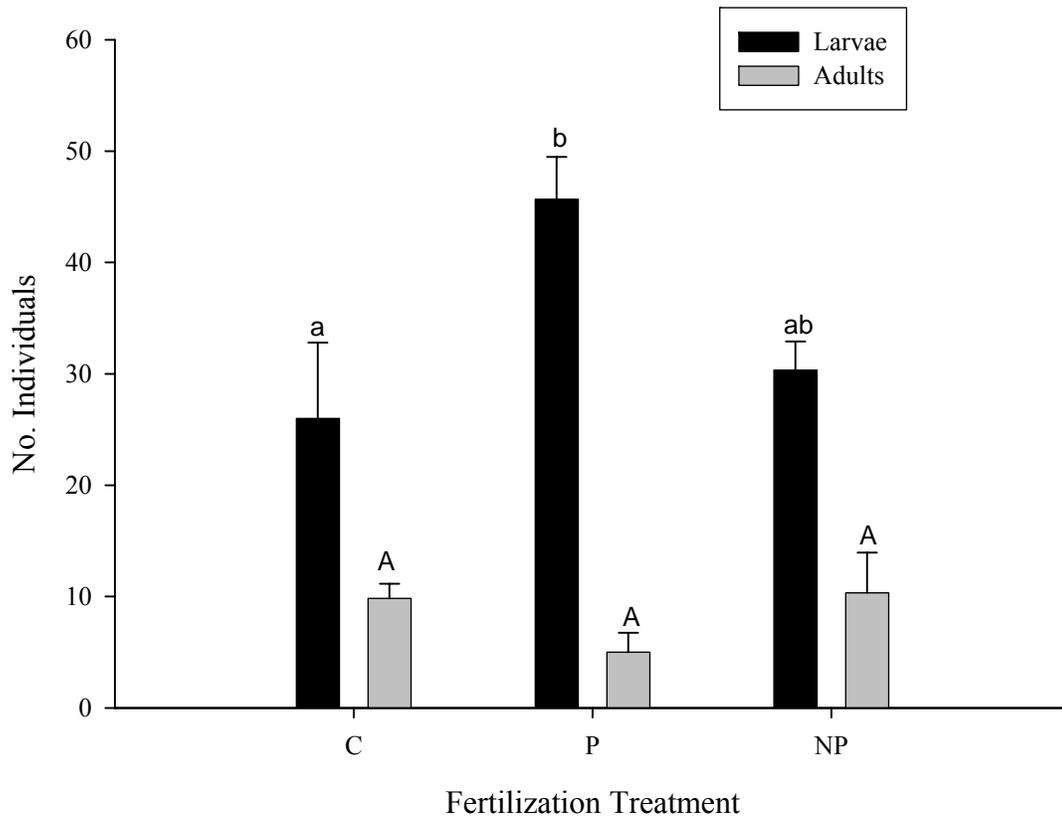
Figure 4.1. Mean ± 1 SE abundances of *T. bacharidis* on host plants under different

fertilization treatments.
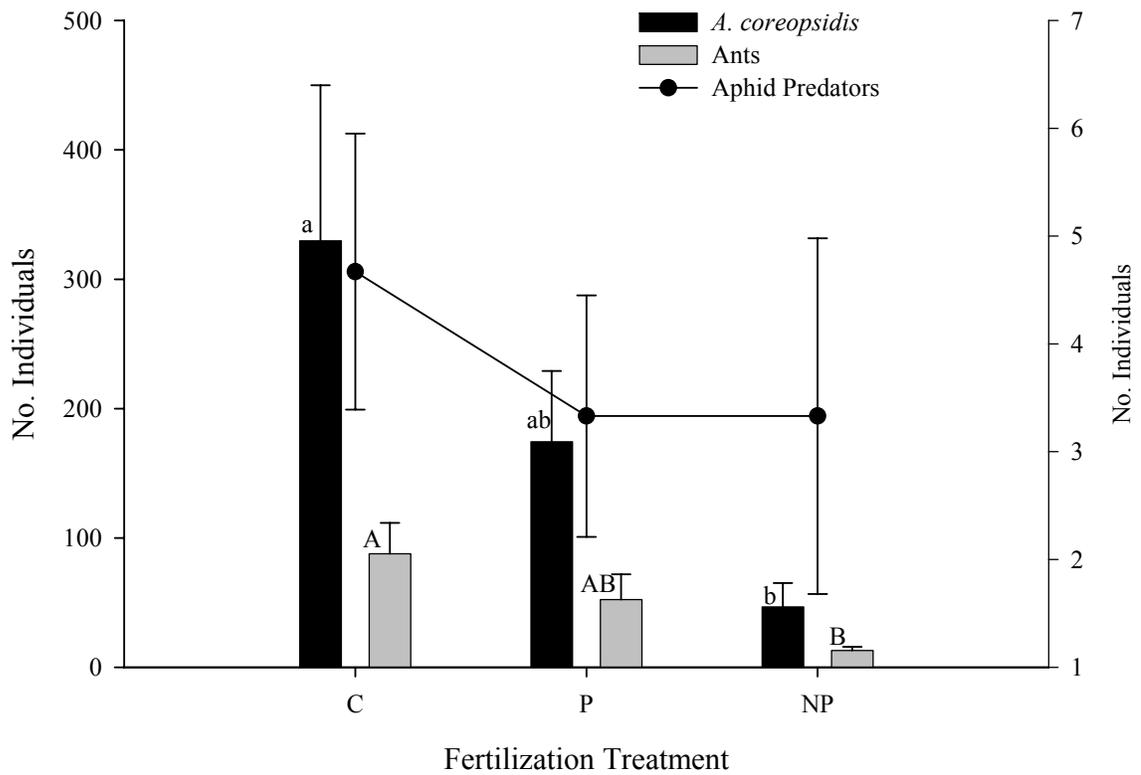
Figure 4.2. Mean ± 1 SE abundances of *L. humile*, *A. coreopsidis* and aphid predators on host plants under different fertilization treatments.
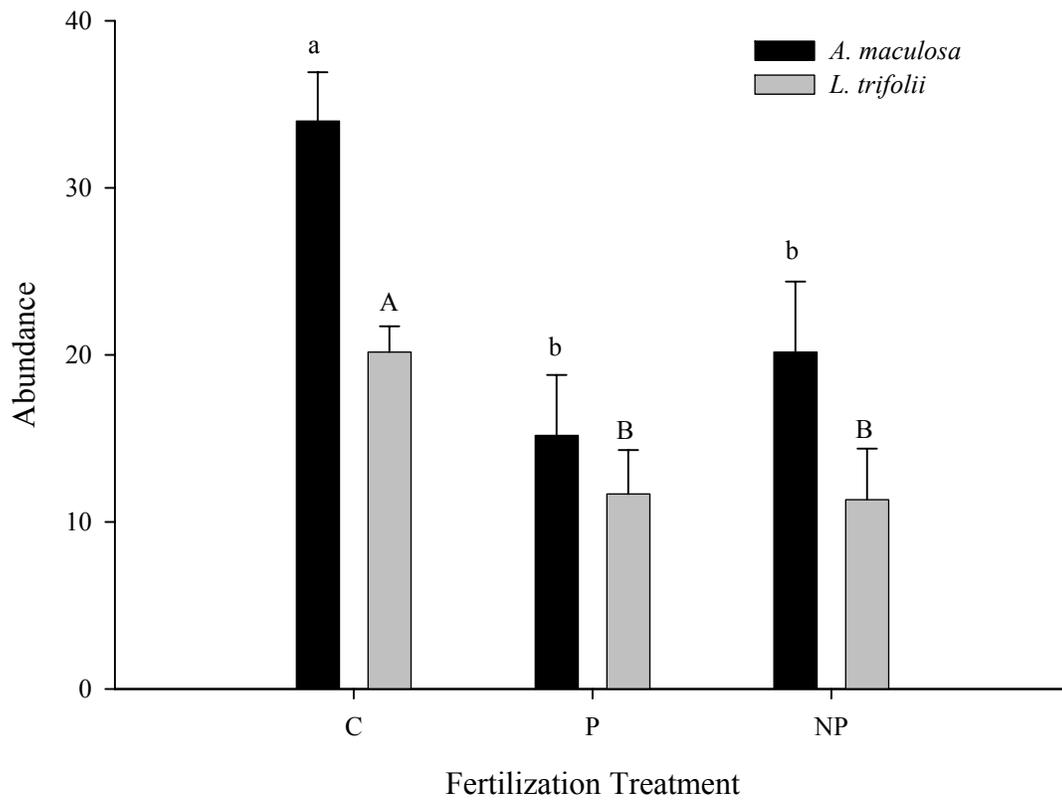
Figure 4.3. Mean ± 1 SE abundances of *A. maculosa* and *L. trifolii* on host plants under different fertilization treatments.

Discussion

Trirhabda bacharidis was the only herbivore positively affected by phosphorus fertilization and only during the larval stage. This insect was predicted to respond positively to phosphorus enrichment of the host plant because this beetle is univoltine and has rapid growth during its larval stage. Adult beetles, however, showed no preference for fertilized trees. The majority of host plants in this experiment did not recover from *T. bacharidis* larval herbivory by re-flushing with new leaves. This lack of recovery from larval herbivory is more likely to have caused the observed negative effects of phosphorus fertilization in *A. coreopsidis*, ants, *A. maculosa* and *L. trifolii* than changes in host plant quality.

CHAPTER 5

EXOTIC VERSUS NATIVE ANTS

Synopsis

I compared the effects of native ants, *Camponotus floridanus*, and exotic ants,

Linepithema humile, on plant-insect interactions on *B. halimifolia*. I used a nested design

to determine whether (1) the identity of aphid-tending ant matters to co-occurring insects

on the host plant, (2) the species of ant changes the effects of early-season herbivory on

herbivores that occur on the host plant later in the year, and (3) if the strength of bottom-

up and top-down factors changes in the presence of an exotic species of ant, compared to

the presence of a native ant.

Densities of all insects except the stem-galling fly *Neolasioptera lathami* were

increased on host plants with exotic ants. The negative effects of early-season herbivory

on later feeding leaf miners and a gall fly were more pronounced on host plants with

native ants than on host plants with exotic ants. On plants with exotic ants, only the gall

fly was significantly reduced by early-season herbivory. In addition, bottom-up effects of

foliar nitrogen increases were more likely to be translated into increased densities of leaf

miners on host plants with native ants. Top-down effects of ant predation were only

important for herbivores when exotic ants were present on the host plant. These results

suggest that community-level processes can be significantly affected by identity of ants and early-season herbivory on a host plant.

Introduction

Ants are among the most common omnivores in terrestrial systems (Holldobler and Wilson 1990). Ant species vary in their abilities to act as attendants to myrmecophilous insects or as predators on other insects (Messina 1981, Buckley 1987, Freitas and Oliveira 1996, Mody and Linsenmair 2004). In its native range, the Argentine ant, *Linepithema humil*e (Hymenoptera: Dolichoderinae), establishes mutualisms with honeydew producing hemipterans in their native areas (Holway et al. 2002) and makes an excellent mutualist because it recruits to honeydew sources quickly, tends 24 hours a day and has a modified proventriculus that increases honeydew uptake rates and carrying capacity (Holway et al. 2002, Davidson et al. 2004, Ness and Bronstein 2004). Outside its native range, however, this ant reduces native ant and arthropod diversity and has been associated with outbreaks of honeydew-secreting hemipterans (Way 1963, Ness and Bronstein 2004). In the U.S., *L. humile* has spread widely and has the potential to impact many native insect communities.

The direct and indirect effects of ants on insects that co-occur on a host plant differ depending on the feeding guild of the insect and its association with ants (Mahdi and Whittaker 1993). Myrmecophilous insects benefit from the presence of ants because ants provide protection from natural enemies, reduce incidences of fungal infections, increase feeding rates and fecundity (Addicott 1979, Buckley 1987); and reduce competition from other non-myrmecophilous herbivores on the host plant (Messina

1981). In Florida, the presence of *L. humile* on the host plant, *Baccharis halimifolia*

(Asteraceae), strongly affects the myrmecophilous aphid *Aphis coreopsidis* and its

predators and, potentially, other members of the insect community (Altfeld and Stiling

2006). There are, however, many other selective pressures which may generate in this

system. To begin with, not all host plants are patrolled by exotic Argentine ants. Many

support only patrols of the native *Camponotus floridanus*, a much larger species. Host

plants tend to have only one species of ant, not both. In addition, the community can also

be negatively affected by early-season herbivory from larvae of the specialist beetle,

Trirhabda bacharidis which defoliates plants and reduces subsequent densities of

herbivores which appear after the leaves re-flush (Hudson and Stiling 1997). Most

herbivores are also affected by increases in foliar nitrogen (Moon and Stiling 2004).

Here I evaluated the extent to which the responses of the insect community on *B.*

halimifolia to both host plant quality and predators are changed in the presence of native

or exotic ants. Specifically I examined how the species of ant on a host plant affects

interspecific interactions among herbivores under differing conditions of early-season

herbivory (present / absent), host plant quality (increased / control) and predation by ants

(present / absent).

I manipulated ant species, early-season herbivory, foliar nitrogen and ant

predation using a nested design and made the following predictions. (1) The presence of

an exotic ant on the host plant will affect the densities of all insects utilizing the host

plant. The direction of the effects of the exotic ant will differ depending on whether the

insects are or are not involved in the ant-aphid mutualism. (2) Early-season herbivory

will negatively affect all herbivores of the host plant, regardless of the species of ant on

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the host plant. (3) Bottom-up factors will be important for all insects of the host plant but will increase in importance in the absence of early-season herbivory and for non-myrmecophilous herbivores. (4) Top-down effects of ants will be species-specific, affecting only those insects either closely associated with ants or more vulnerable to predation.

Methods

All experimental trees were located within Fort De Soto Park on Mullet Key, St. Petersburg, Florida, USA. Host plants selected for inclusion in this experiment were between 1 – 2 m in height, a minimum of 2 m apart and had either native *C. floridanus* or exotic *L. humile* ants tending *A. coreopsidis*. In January 2005, 80 *B. halimifolia* trees were assigned to experimental groups based on a 3-tier hierarchical design. The main factor (1st tier) was aphid-tending ant species, *C. floridanus* or *L. humile*. Nested within ant species was the presence of absence of early-season herbivory by *T. bacharidis* larvae (2nd tier). Nested within ant species and early-season herbivory were foliar nitrogen (control and enriched) and ant foragers (absent and present) applied in a 2 x 2 design. Data was collected for 4 months from April to July 2005, when insect densities were highest on the host plant.

Ant attendance and early-season herbivory by *T. bacharidis* larvae were manipulated by applying either a temporary or permanent band of Tanglefoot® (The Tanglefoot Company, Grand Rapids, MI) around the base of experimental trees. To prevent early-season herbivory and exclude ants, a permanent band of Tanglefoot® was placed around the base of the trunks of experimental trees, but above where the *T.*

bacharidis eggs were laid. To prevent early-season herbivory but allow ants, a temporary band of Tanglefoot® was placed on trees only for the three months, January through March, when *T. bacharidis* larvae were actively hatching and feeding on host trees. After the larvae left host trees at the end of March, the temporary Tanglefoot® was removed from trees to allow the ants access to foliage. To allow early-season herbivory and exclude ants, a band of Tanglefoot® was placed on trees after the larvae left host trees in late March. Host trees with early-season herbivory and ants present were free of Tanglefoot® manipulations.

The temporary bands of Tanglefoot® consisted of a band of tape wrapped around the trunk with Tanglefoot® placed over the tape. The tape was easily cut and peeled off host trees for removal when necessary. Bands were made permanent by applying the Tanglefoot® directly to host trees and reapplying when necessary. In addition, vegetation surrounding ant-exclusion trees was clipped to prevent ants from bypassing the Tanglefoot®.

Foliar nitrogen enrichment was achieved via monthly applications of 60g granular nitrogen-based fertilizer (46-0-0 urea fertilizer, PCS Sales Skokie, IL) around the base of experimental trees. In order to quantify differences in foliar nitrogen between fertilized and unfertilized trees, foliar nitrogen was analyzed monthly for 10 randomly collected leaves from all trees at both sites. Leaves were oven dried at 50° C for 3 days, ground in a Wiley mill, and analyzed for total nitrogen as percent dry mass (CN 2100 Soil Analyzer, CE Elantech, Inc. Lakewood, NJ).

Beginning in April, insect abundances at each site were estimated monthly using three census methods. First, 25 branches, each a minimum of 10 cm in length, were

arbitrarily selected and the numbers of individual *T. bacharidis* adults, ants, aphids, coccinellids and syrphid larvae were recorded. Aphid abundance on each branch was assigned to the following categories: 0, 1-25, 26-50, 51-100, 101-200, 201+ individuals. Second, 200 leaves were inspected for leaf mines, which were categorized by species and presence or absence of ant damage. Third, 200 different stems, each a minimum of 10 cm in length, were examined for galls. In addition, a single count of recent stemborer emergence holes on host plant branches was made by visually inspecting all branches on each host tree in August during peak stemborer activity. Recent emergence holes were identified by the presence of frass around the holes. In September, host tree mortality due to stemborer damage was evaluated.

Data were analyzed using a nested ANOVA design with ant species as the main factor, early-season herbivory by *T. bacharidis* larvae nested within ant species, and foliar nitrogen (control / enriched) and ant foragers (present / absent) fully crossed and nested within larval herbivory. The abundances of aphids and aphid predators were square root (x + 0.5) transformed to meet the assumptions of normality and homogeneity of variance. Prior to analysis all variables were subjected to Kolmogorov-Smirnov normality testing and Levene's homogeneity of variance test. All statistical tests were carried out in SPSS Version 13 for Windows (SPSS, Inc. 2004).

<div align="center">Results</div>

The densities of all insects, except the specialist gall fly, *N. lathami*, were significantly affected by the species of ants foraging on the host plant (Table 5.1). The densities of ants, *A. coreopsidis* and aphid predators were higher on host plants with the

exotic *L. humile* as compared to insect densities on host plants with the native ant *C. floridanus* (Figure 5.1a). The densities of herbivores not involved in the ant-aphid mutualism, namely the leaf miners, gall fly, and stem borer, were also higher on host plants with *L. humile* as compared to host plants with *C. floridanus* (Figure 5.1b.).

Table 5.1. Ant species effects on insects of *B. halimifolia*. Results from Nested ANOVA with ant species as the main factor.

Insect	$F_{1,64}$	P
Ants	46.908	**< 0.001**
A. coreopsidis	60.118	**< 0.001**
Aphid Predators	30.822	**< 0.001**
T. bacharidis Adults	52.519	**< 0.001**
A. maculosa	123.737	**< 0.001**
L. trifolii	357.328	**< 0.001**
N. lathami	0.197	0.659
O. balanotes	43.888	**< 0.001**
Ant-Damaged Mines	8.897	**< 0.001**

Early-season feeding by *T. bacharidis* larvae affected the densities of *A. coreopsidis*, *A. maculosa*, *L. trifolii*, and *N. lathami* (Table 5.2). On host plants with native *C. floridanus*, the densities of *A. maculosa*, *L. trifolii* and *N. lathami* were increased and the density of *A. coreopsidis* decreased when early-season herbivory by *T. bacharidis* larvae was prevented (Figure 5.2). When exotic *L. humile* was present on host plants, however, only the specialist gall fly, *N. lathami*, was negatively affected by early-season herbivory (Figure 5.2).

Table 5.2. Effects of early-season feeding by *T. bacharidis* larvae on herbivores of *B. halimifolia*. Results from Nested ANOVA with Larval Herbivory as nested factor within Ant Species.

Insect	$F_{2,64}$	P
Ants	1.442	0.244
A. coreopsidis	3.248	**0.045**
Aphid Predators	2.746	0.072
T. bacharidis Adults	0.245	0.784
A. maculosa	7.441	**0.001**
L. trifolii	4.338	**0.017**
N. lathami	17.588	**0.001**
O. balanotes	0.431	0.652

Foliar nitrogen increased on fertilized trees by an average of 17.25%. This increase in foliar nitrogen affected the densities of *A. maculosa*, *L. trifolii*, *N. lathami* and aphid predators (Table 5.3). However, species of ant and the presence or absence of early-season herbivory by *T. bacharidis* larvae influenced the extent to which herbivore densities were affected by increased foliar nitrogen (Figure 5.3). Aphid predators increased in response to nitrogen fertilization only on host plants with native *C. floridanus*. However, on host plants with exotic *L. humile*, aphid predator densities were unaffected by fertilization while *A. coreopsidis* densities decreased. *Amauromyza maculosa*, *L. trifolii*, and *N. lathami* increased in response to nitrogen fertilization only in the absence of early-season herbivory by *T. bacharidis* larvae.

Table 5.3. Bottom-up effects from nitrogen fertilization on insects of *B. halimifolia*.
Results from Nested ANOVA with Fertilization nested within Larval Herbivory (nested within Ant Species).

Insect	$F_{4,64}$	P
Ants	0.216	0.929
A. coreopsidis	1.789	0.142
Aphid Predators	2.714	**0.037**
T. bacharidis Adults	0.731	0.574
A. maculosa	5.504	**0.001**
L. trifolii	7.035	**< 0.001**
N. lathami	16.151	**< 0.001**
O. balanotes	1.393	0.246

The presence of ants affected *A. coreopsidis*, aphid predators, *L. trifolii* and ant-damaged mines (Table 5.4). The effects, however, were species-specific. Aphid predators were less abundant in the presence of *C. floridanus* but more abundant in the presence of *L. humile* (Figure 5.4). Herbivores not involved in the ant-aphid mutualism were unaffected by the presence of ants when the ant was the native *C. floridanus* but *L. trifolii* was less abundant in the presence of ants on host plants with exotic *L. humile* because the ants preyed on leaf mines (Figure 5.5). There were no significant interactions observed between bottom-up and top-down manipulations for any insects except *L. trifolii*, which showed the higher densities on nitrogen enriched, ant-exclusion host plants compared to host plants that were either nitrogen enriched or ant-exclusion.

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Table 5.4. Top-down effects of ants on insects of *B. halimifolia*. Results from Nested

ANOVA with Ant Foragers nested within Larval Herbivory (nested within Ant Species).

Insect	$F_{4,64}$	P
A. coreopsidis	39.299	**< 0.001**
Aphid Predators	6.546	**< 0.001**
T. bacharidis Adults	2.629	**0.042**
A. maculosa	2.083	0.093
L. trifolii	28.987	**< 0.001**
N. lathami	1.681	0.165
O. balanotes	1.859	0.129
Ant-Damaged Mines	8.897	**< 0.001**
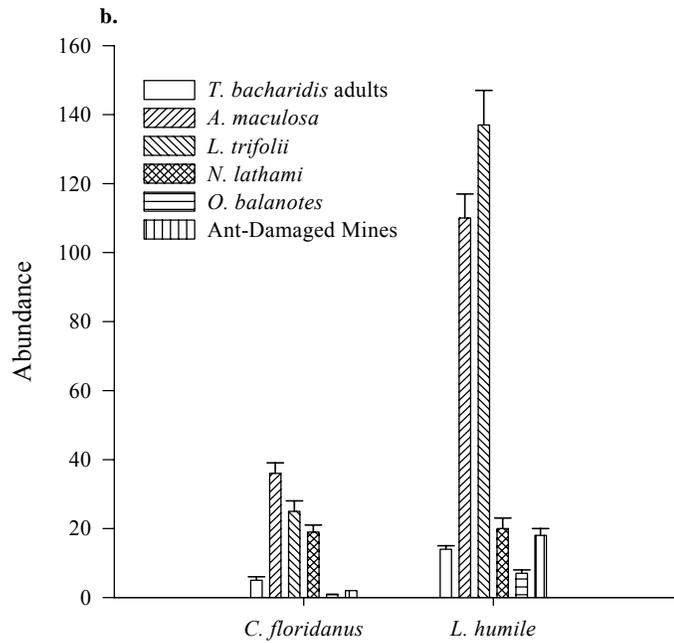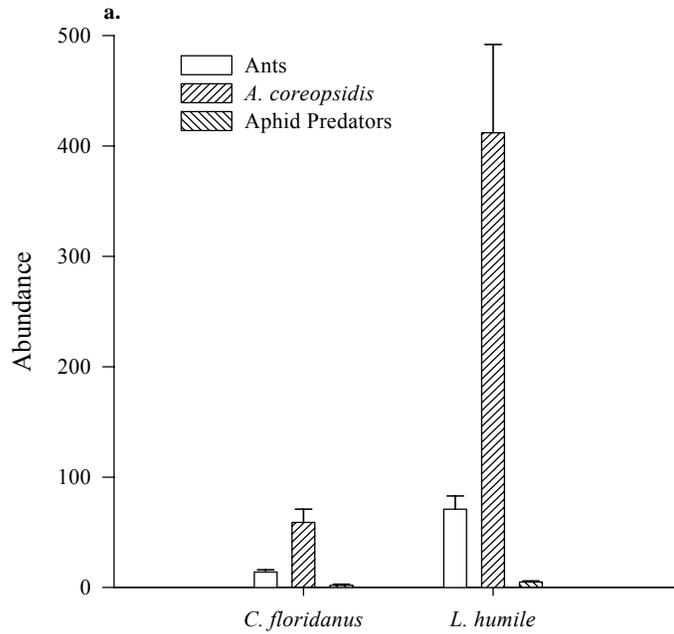
Figure 5.1. Comparison of mean ± 1 SE abundances of (a.) insects involved in the ant-aphid mutualism and (b.) other herbivores not involved in the ant-aphid mutualism, when the ant foragers were either the native *C. floridanus* or the exotic *L. humile*.
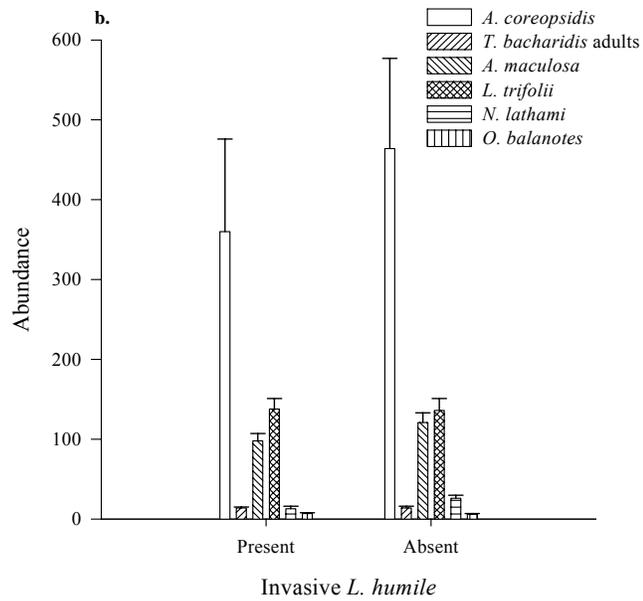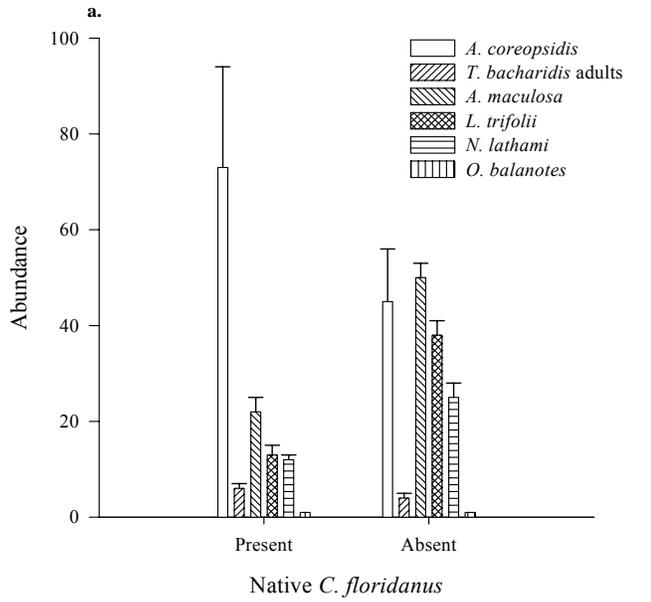
Figure 5.2. Comparison of mean ± 1 SE abundances of herbivores on host plants with the presence and absence of early-season herbivory by *T. bacharidis* larvae. Results are presented for host trees with **(a.)** native *C. floridanus* and **(b)** exotic *L. humile* ants.
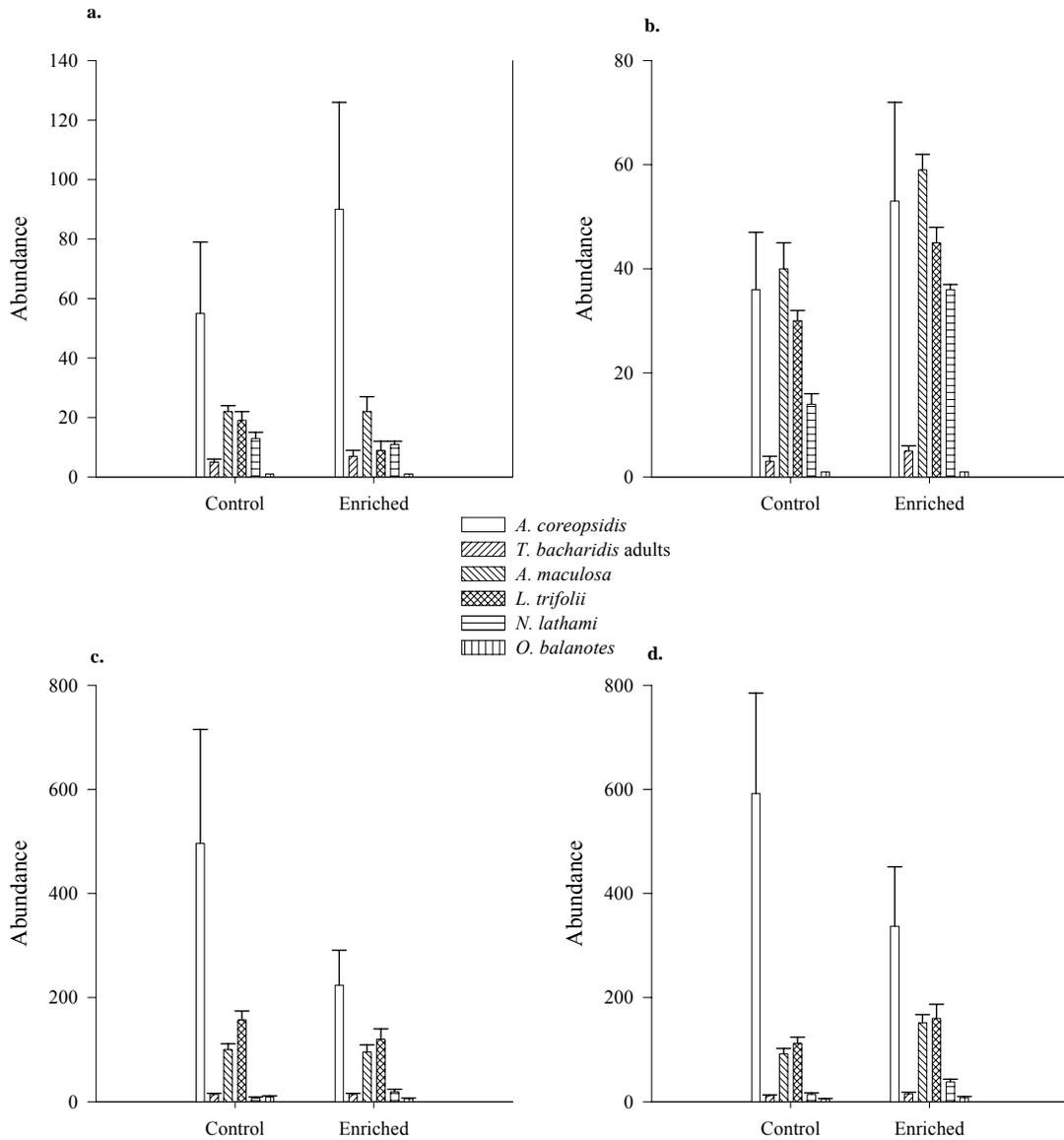
Figure 5.3. Comparison of mean ± 1 SE abundances of herbivores on control and nitrogen enriched host plants with **(a.)** native *C. floridanus* and early-season herbivory, **(b.)** native *C. floridanus* but no early-season herbivory, **(c.)** exotic *L. humile* and early-season herbivory, and **(d.)** exotic *L. humile* but no early-season herbivory.
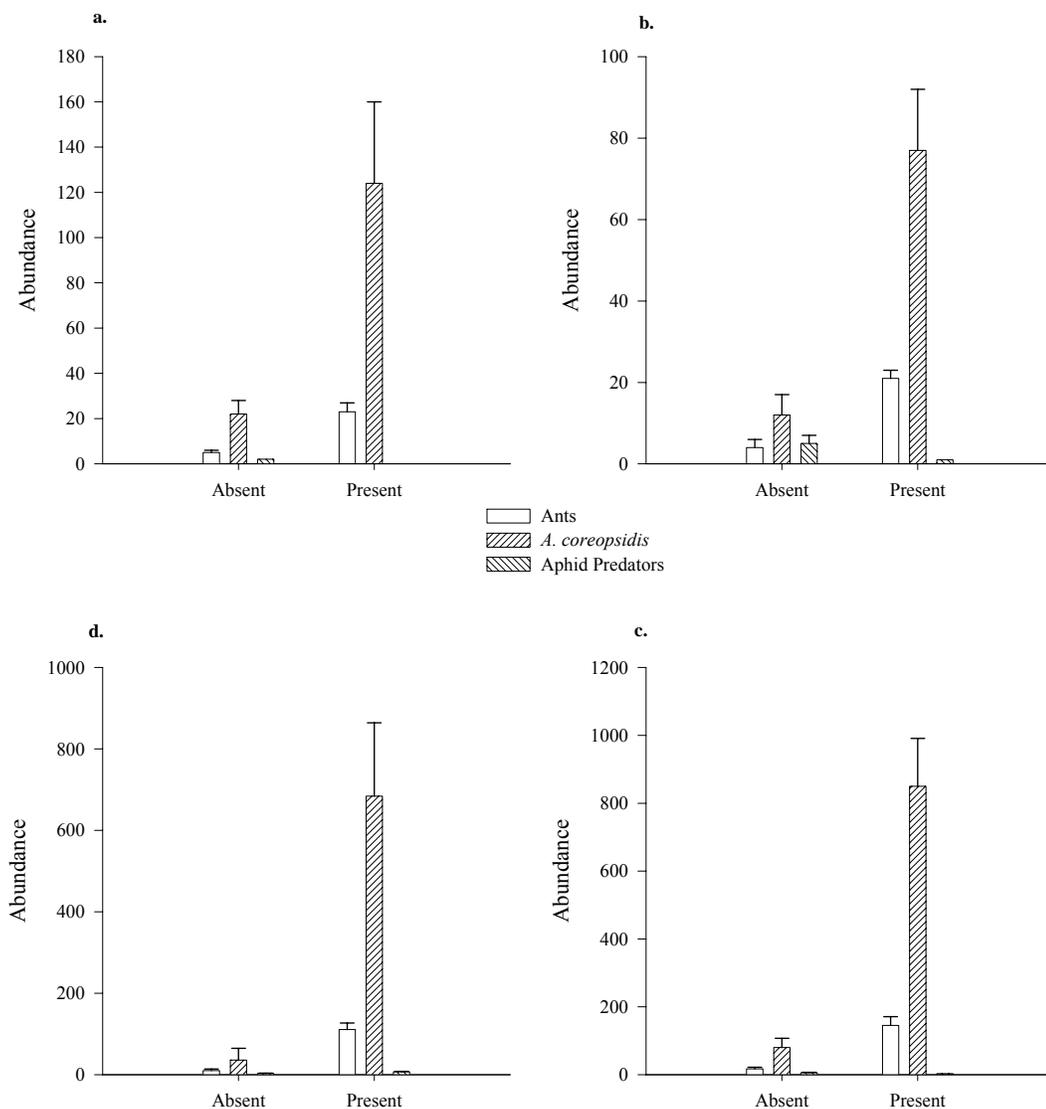
Figure 5.4. Comparison of mean ± 1 SE abundances of insects involved in the ant-aphid mutualism when ants were present or absent on host plants with **(a.)** native *C. floridanus* and early-season herbivory, **(b.)** native *C. floridanus* but no early-season herbivory, **(c.)** exotic *L. humile* and early-season herbivory, and **(d.)** exotic *L. humile* but no early-season herbivory.
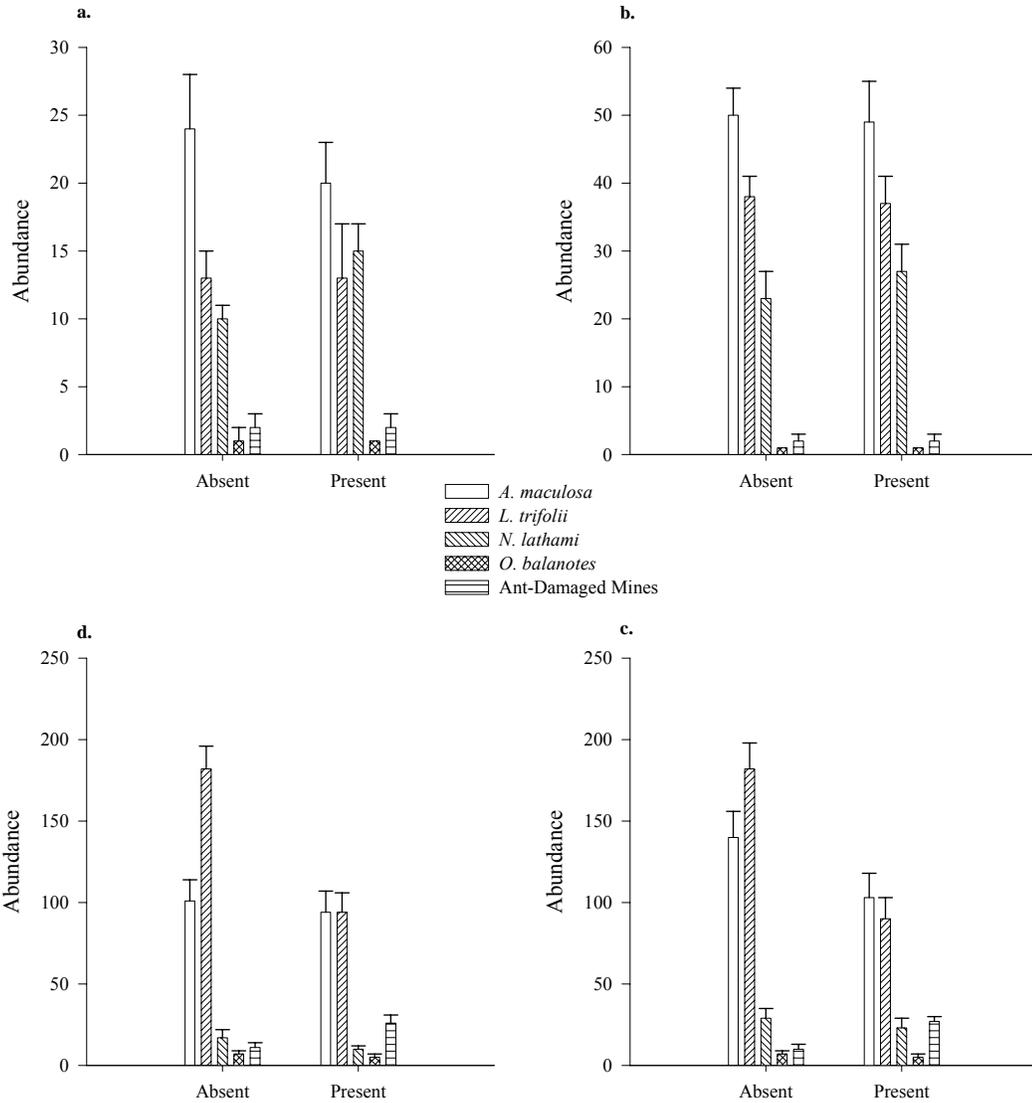
Figure 5.5. Comparison of mean ± 1 SE abundances of herbivores not involved in the ant-aphid mutualism when ants were present or absent on host plants with **(a.)** native *C. floridanus* and early-season herbivory, **(b.)** native *C. floridanus* but no early-season herbivory, **(c.)** exotic *L. humile* and early-season herbivory, and **(d.)** exotic *L. humile* but no early-season herbivory.

Discussion

The presence of the exotic *L. humile* on *B. halimifolia* affected all of the insects, except the specialist gall fly *N. lathami*, on the host plant. By comparison with trees patrolled by the native ant *C. floridanus*, trees containing the exotic *L. humile* maintained greater densities of all observed insects. Aphids were 7 times more abundant in the presence of *L. humile*. The exotic *L. humile* makes an exceptional partner for honeydew-producing hemipterans, enabling them to have very high densities in the ants' presence (Altfeld and Stiling 2006, Davidson et al. 2004, Ness and Bronstein 2004, Murdoch et al. 1995). The higher relative densities of aphid predators, especially coccinellids, were likely due to female ladybird beetles using honeydew and aphid presence as cues for oviposition to increase larval densities where aphids are abundant (Evans and Dixon 1986). Coccinellids feeding on aphids tended by *Formica rufa* also showed higher densities in the presence of ant attendants when untended aphid populations were rare (Sloggett and Majerus 2000). Higher relative densities of leaf miners, despite leaf mine predation, suggest compensatory mortality when *L. humile* is on the host plant, as may be produced if parasitism is reduced by this exotic ant (Inouye and Agrawal 2004).

Negative indirect effects of early-season herbivory by *T. bacharidis* larvae were observed for the leaf miners and gall fly on host trees with the native ant, *C. floridanus*, but, when *L. humile* was on the host plant, were observed only for the gall fly. The mechanism by which *T. bacharidis* early-season herbivory affects later occurring insects on *B. halimifolia* is indirect and thought to be chemical in nature because host trees fully re-flush with leaves after the larvae feed on the plants (Hudson and Stiling 1997).

Bottom-up effects of host plant quality were more important to herbivores in the absence of early-season herbivory. However, for aphids the results were variable depending on whether they were tended by native or exotic ants. In addition, increases in foliar nitrogen trickled up to the third trophic level in the native insect community. Regardless of the species of ant on the host plant, the specialist gall fly, *N. lathami*, was positively affected by increases in foliar nitrogen and unaffected by the removal of ants, suggesting that this herbivore's success on its host is tightly linked to host plant quality and the fly larvae are susceptible only to specialized parasitoids not generalist predators such as ants.

Top-down effects of ant predation were unaltered by early-season herbivory but were strongly affected by the species of ant on the host plant. Native ants had negative effects on aphid predator abundance and no effects on other herbivores of the host plant. *L. humile*, however, dramatically increased aphid densities, aphid predator densities and preyed on leaf mines, reducing the densities of the leaf miner *L. trifolii*.

Leaf mine predation by ants is not uncommon. *Liriomyza commelinae*, a congener of *L. trifolii*, is preyed upon by *Crematogaster* ants with mortality rates of 21.2% (Freeman and Smith 1990). The delicate mines of *Eriocraniella* sp., which mine young oak leaves, suffer significant mortality by arboreal ants; however, *Cameraria* sp., which mine mature oak leaves, are better protected within thicker mines and do not suffer mortality by ants (Faeth 1980). Leaf mining beetles on bamboo suffer predation by *Pseudomyrmex gracilis* in Costa Rica (Memmott et al. 1993), but leaf miners on bracken fern, a plant with extra-floral nectaries, suffer no attacks by ants (Heads and Lawton 1985, Rashbrook et al. 1992). *Coleophora serratella* miners on birch are also unaffected

by ants(Fowler and MacGarvin 1985). Furthermore, larvae of the leaf mining beetle *Odontota* have higher survivorship in the presence of membracid-tending ants because the ants deter an important predator of the beetle larvae (Fritz 1983).

Community-level processes can be strongly influenced by the presence of an exotic species, such as *L. humile* (Way and Khoo 1992). On *B. halimifolia*, nutrient limitation, predation and competition were all changed by the presence of this ant. *Linepithema humile* had direct and indirect effects on most herbivores. Predicted negative effects of early-season herbivory were less pronounced on host trees with exotic ants because the generalist herbivores were more abundant on those host trees and bottom-up factors were more important in the absence of early-season herbivory. Only the specialist *N. lathami* responded as predicted to early-season herbivory regardless of the identity of ant on *B. halimifolia*. Top-down effects of ant predation were only important for leaf miners in the presence of exotic ants. Clearly, the effects of this exotic ant are persistent, significant, direct and indirect, and permeate all levels of the community. The long-term consequences of *L. humile* presence on *B. halimifolia* are unknown but may be to alter adaptive behaviors of herbivores that co-occur on this host plant.

CHAPTER 6

CLOSING REMARKS

The presence of invasive species in communities can have profound consequences for native organisms in the communities where the exotic species invade. Otherwise adaptive strategies of native organisms can become disadvantageous when invasive species enter communities because the invasive species alter community dynamics producing what Schlaepfer et al. (2002) called an evolutionary trap. The reverse may also be true whereby the outcomes of interactions between native and invasive species benefit either or both organisms, a result which is known as evolutionary release (Schlaepfer et al. 2005). Interactions among native species and *Linepithema humile* have been both positive and negative. Whereas native arthropod diversity is typically reduced, especially ant diversity, other insects, such as scale insects on citrus benefit from reduced parasitism in the presence of *L. humile* (Holway et al. 2002, Sanders et al. 2003). On *B. halimifolia*, *L. humile* presence dramatically increases the mean annual abundance of *A. coreopsidis*, a facultative myrmecophile, and subsequently alters aphid predator foraging by providing large populations of prey. The invasive ant also preys on leaf miners, sometimes reducing their densities and sometimes not, and is capable of a trophic cascade enabling *B. halimifolia* to survive periods of intense damage by the specialist stem borer

O. balanotes. Temporally variable effects of ant predation are, however, common in many systems (Del-Claro and Oliviera 2000, Mooney and Tillberg 2005).

Despite the abovementioned effects, the specialist herbivores, *T. bacharidis* and *N. lathami*, are unaffected by the presence of this exotic ant. Larvae of *N. lathami* are well protected within its galls and adults are, evidently, undeterred from ovipositing on host trees with ants. Larvae of *T. bacharidis* are likely unpalatable, secreting haemolymph when disturbed and adult beetles are able to fly off host plants when disturbed by ants (Altfeld personal observation). Host use by herbivores of *B. halimifolia*, then, may only change in response to *L. humile* presence when the herbivores are myrmecophilous or are vulnerable to predation. The evolutionary consequences of *L. humile – A. coreopsidis* mutualism on *B. halimifolia* may be facilitation of each species by the other. *Linepithema humile* is widespread on Mullet Key and its spread may have been facilitated by honeydew collection from myrmecophiles such as *A. coreopsidis*. In other areas, such as Australia, where both *B. halimifolia* and *L. humile* are invasive, the ant may interfere with biological control of the plant because *O. balanotes* is used as a biological control agent. Both scenarios represent examples of evolutionary release. However, for generalist leaf miners, such as *L. trifolii*, *B. halimifolia* host use can be reduced because of predation by *L. humile*, an example of an evolutionary trap.

The temporal variability in leaf mine predation observed for *L. humile* on *A. maculosa* and *L. trifolii* may have been, at least in part, a result of density dependence because the densities of leaf miners were higher on host plants with *L. humile* than on host plants with *C. floridanus*. In order to evaluate the density dependent nature of leaf mine predation by ants as a function of overall leaf mine abundance, I used the densities

of intact and damaged leaf mines from control trees in all experiments from 2003 – 2005

at the field site that contained *L. humile.* I plotted that data and then tested the functional

relationship against the following models: linear, S, quadratic and exponential. The

quadratic model best fit the data (Figure 6.1). The nature of the quadratic relationship

may help explain the temporal variation in leaf mine predation on leaf miner abundance.

Leaf mine predation was greatest when miners were at a density between 50 – 100 mines

per 200 leaves. Below and above this range leaf mine predation was decreased either

because leaf mines were rarely encountered or overly abundant on host plants.
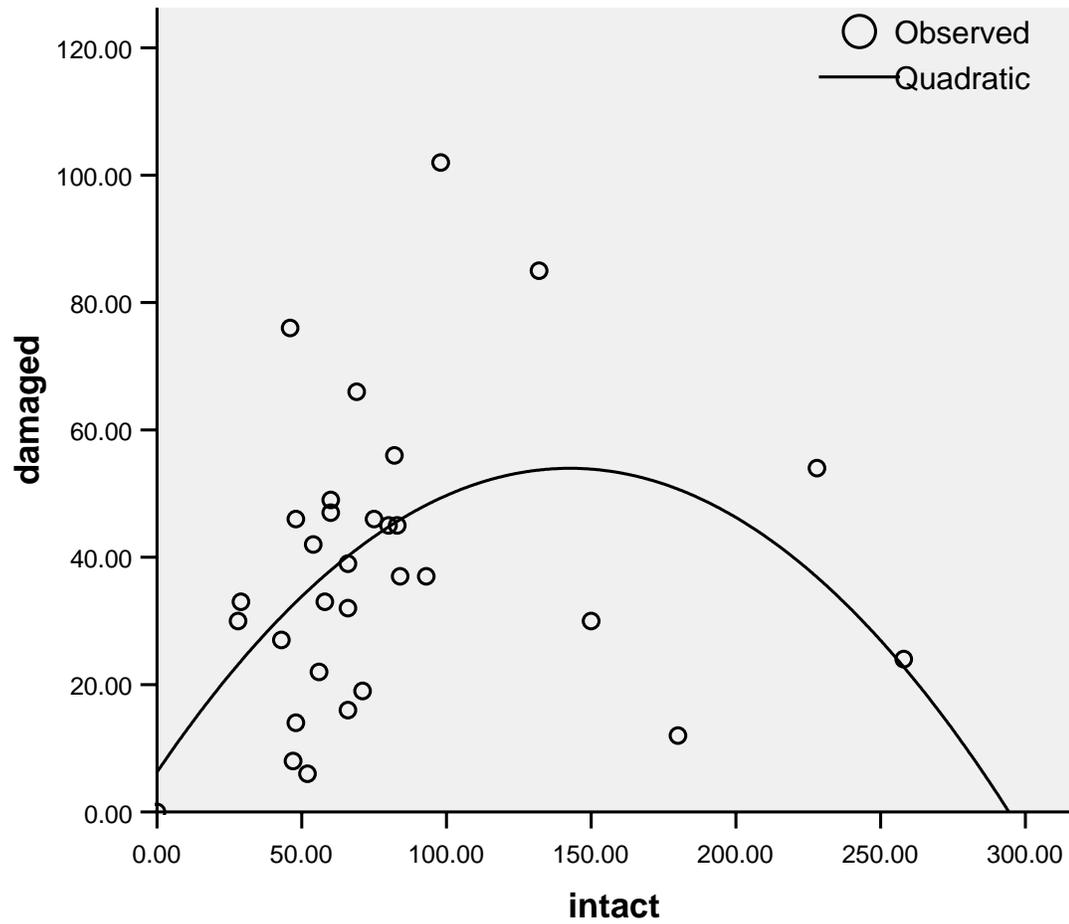
Figure 6.1. Abundance of ant-damaged leaf mines as a quadratic function of the abundance of intact leaf mines on the host plant, *B. halimifolia*.

Interspecific interactions among insects on *B. halimifolia* varied only for some insects, usually polyphagous, and depended on whether or not *L. humile* was present. Early-season herbivory by *T. bacharidis* was clearly an important factor for herbivores on the host plant. This side-to-side interaction affected the relative importance of host plant quality but host plant quality did not affect the relative importance of competition for later feeding herbivores. The effects of early-season herbivory were most pronounced when native *C. floridanus* were present but, even when *L. humile* was present, *N. lathami* predictably decreased in density due to *T. bacharidis* larval herbivory. Top-down effects of ant predation were unaffected by host plant quality but host plant quality was affected by the presence of predation by exotic ants. The leaf miner, *L. trifolii*, was particularly vulnerable to decreases in density when *L. humile* was present. The previous series of experiments involving *B. halimifolia* have shown that the presence of an ant-aphid mutualism has significant effects on community-level dynamics. However, the effects that the mutualism has depend on what species of ant is tending the aphids.

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ABOUT THE AUTHOR

Laura Francine Altfeld, née Hensey, was born to Rose Marie and Daniel Hensey, April 20th, 1970. Raised in Florida, Laura attended Eckerd College, where she completed a senior thesis on ichthyofauna in created versus natural wetlands and earned a Bachelor's of Science degree in Marine Science. In keeping with her interests in wetlands, Laura pursued a Master's of Science degree in Biology with Peter Stiling, PhD, at the University of South Florida, where she began studying insect herbivory on salt marsh plants. In 2003, Laura began work on her PhD, also under the supervision of Peter Stiling. While at USF, Laura was a graduate and teaching assistant for the Biology and Biology Honors Labs. Laura is expected to complete her doctorate in 2006 and continue to pursue research in the area of plant-animal interactions.