2012

Community-Level Consequences of Plant-Herbivore Interactions

Tania N. Kim
COMMUNITY-LEVEL CONSEQUENCES OF PLANT-HERBIVORE INTERACTIONS

By

TANIA N. KIM

A dissertation submitted to the Department of Biological Science in partial fulfillment of the requirements for the degree of Doctor of Philosophy

Degree Awarded: Fall Semester, 2012
Tania Kim defended this dissertation on October 17, 2012.
The members of the supervisory committee were:

Nora Underwood
Professor Directing Dissertation

Frederick R. Davis
University Representative

Brian D. Inouye
Committee Member

Thomas E. Miller
Committee Member

Alice A. Winn
Committee Member

The Graduate School has verified and approved the above-named committee members, and certifies that the dissertation has been approved in accordance with university requirements.
I dedicate this dissertation to BJS, RPD, and Nugget.
ACKNOWLEDGEMENTS

I would like to thank my advisor, Nora Underwood, who has been a wonderful role model, mentor, and friend. This dissertation would not have been possible without her tireless support, enthusiasm, and encouragement over the past six years. Next, I thank my committee members, Drs. Brian Inouye, Tom Miller, Alice Winn and Fritz Davis, for reading my dissertation and challenging me to think hard about difficult questions. I also thank current and past members of the Underwood-Inouye labs for their encouragement and feedback. In addition, I thank the staff at the Mission Road Research Facilities (Karen Graffius, C.D. Smith, and Theresa Jepsen), Virginia Hellman, and Judy Bowers for logistical support.

This project was funded by various sources, including the Robert K. Godfrey award in Botany, the Dissertation Research Grant from the FSU Graduate School, and the National Science Foundation.

Finally, I thank my family and friends for their love and support. In particular, I thank Brian J. Spiesman and Reginald P. Doggie for their unconditional love, patience, and humor.
# TABLE OF CONTENTS

List of Tables ........................................................................................................................................ viii
List of Figures ........................................................................................................................................ ix
Abstract ................................................................................................................................................ x

1. INTRODUCTION .......................................................................................................................... 1
   1.1 Study system .......................................................................................................................... 3
   1.2 Plant preparation protocol ..................................................................................................... 4

2. INSECT HERBIVORES CHANGE THE OUTCOME OF PLANT COMPETITION THROUGH EFFECTS ON DEMOGRAPHIC PROCESSES ............................................... 6
   2.1 Methods .................................................................................................................................. 8
      2.1.1 Experimental design and data collection ....................................................................... 8
      2.1.2 Data analysis and fitting competition models to data .................................................... 9
      2.1.3 Simulating herbivores effects on the outcome of competition .................................... 11
   2.2 Results ...................................................................................................................................... 11
      2.2.1 Fitting competition models to *Solanum* data ............................................................ 12
      2.2.2 Fitting competition models to *Solidago* data ............................................................ 12
      2.2.3 Variation in model parameters ....................................................................................... 13
      2.2.4 Simulation of herbivore effects on longer-term community dynamics ..................... 13
   2.3 Discussion ............................................................................................................................... 14
      2.3.1 Herbivore effects on intrinsic rates of population growth ........................................... 14
      2.3.2 Herbivore effects on per capita competitive ability ....................................................... 15
      2.3.3 Temporal variation in the importance and magnitude of parameters ....................... 16
      2.3.4 Long term effects of herbivores ..................................................................................... 16
      2.3.5 Conclusions ..................................................................................................................... 17

3. NON-LINEAR EFFECTS OF PLANT NEIGHBORHOOD COMPOSITION ON INSECT HERBIVORE DAMAGE ......................................................................................................................... 24
   3.1 Methods .................................................................................................................................... 26
      3.1.1 Experimental design ......................................................................................................... 26
   3.2 Results ....................................................................................................................................... 26
   3.3 Discussion ............................................................................................................................... 27

4. THE EFFECTS OF NEIGHBORHOOD COMPOSITION ON MECHANISMS OF ASSOCIATIONAL RESISTANCE AND SUSCEPTIBILITY ................................................................. 32
   4.1 Methods .................................................................................................................................... 34
      4.1.1 Basic experimental design ............................................................................................... 34
      4.1.2 Leaf damage and numerical responses of herbivores and predators ......................... 35
      4.1.3 Microclimate effects ........................................................................................................ 35
      4.1.4 Constitutive and induced plant resistance ..................................................................... 36
      4.1.5 Herbivore foraging strategies ......................................................................................... 37
4.2 Results ........................................................................................................................................39
  4.2.1 Associational effects ........................................................................................................39
  4.2.2 Predator community .........................................................................................................39
  4.2.3 Microclimate ....................................................................................................................40
  4.2.4 Plant resistance ..............................................................................................................40
  4.2.5 Herbivore foraging behavior ..........................................................................................40
4.3 Discussion ..................................................................................................................................41
  4.3.1 Frequency-dependent mechanisms in damage ..............................................................41
  4.3.2 Density-dependent mechanisms of damage ..................................................................43
  4.3.3 Long-term consequences of context-dependent herbivory ....................................44

5. LATITUDINAL VARIATION IN PLANT DAMAGE AND PALATABILITY OF TWO
   OLD-FIELD PLANT SPECIES ......................................................................................52
  5.1 Methods ...................................................................................................................................54
    5.1.1 Field survey .................................................................................................................54
    5.1.2 Plant quality .................................................................................................................55
    5.1.3 Statistics .......................................................................................................................56
  5.2 Results ......................................................................................................................................57
    5.2.1 Damage ........................................................................................................................57
    5.2.2 Insect herbivore communities ......................................................................................58
    5.2.3 Nutrient content ............................................................................................................58
    5.2.4 Bioassays ......................................................................................................................58
  5.3 Discussion ..................................................................................................................................59
    5.3.1 Herbivore responses are complex ...............................................................................60
    5.3.2 Incorporating plant and herbivore phenology .............................................................61
    5.3.3 Previous studies .............................................................................................................61
    5.3.4 Conclusions ....................................................................................................................62

6. CONCLUSIONS ............................................................................................................................68

APPENDICES ...............................................................................................................................70
  A. CHAPTER 2: Response surface design ..................................................................................70
  B. CHAPTER 2: Detailed description of statistical methods and ANOVA tables ...................71
  C. CHAPTER 2: AIC weights (w) for five standard competition models .................................74
  D. CHAPTER 2: Recruitment data ............................................................................................75
  E. CHAPTER 2: Importance weights .........................................................................................76
  F. CHAPTER 3: Response surface design ...............................................................................77
  G. CHAPTER 4: Neighborhoods in pair-wise preference experiments ..................................78
LIST OF TABLES

2.1. ΔAICc and AICc weights (in parentheses) for the 16 candidate Law and Watkinson (LW) models. .........................................................................................................................19

2.2. Point estimates and 95% confidence intervals (in parentheses) for parameters of best fit models in Table 2.1...............................................................................................................20

3.1. Effects of Solanum density and frequency of Solidago on mean leaf tissue damage........31

4.1. Summary of neighborhood effects on mechanisms suspected to generate associational effects........................................................................................................................................51
LIST OF FIGURES

2.1. Spray treatment effects on leaf tissue damage (A), biomass (B), and stem densities of *Solanum* (C) and *Solidago* (D) ..................................................................................................................................................21

2.2. Relationship between the proportion of heterospecific competitors and density responses of *Solanum* (A) and *Solidago* (B) ..................................................................................................................................................22

2.3. Frequency distribution of *Solanum* and *Solidago* final densities (see text for details) from replicate simulations (n=100) of best fit competition models (Table 2.1)..........................................................................................23

3.1 Leaf tissue damage on *Solanum carolinense* and *Solidago altissima* .................................................................29

3.2. Effect of *Solidago* frequency on *Solanum* leaf tissue loss (mean percent leaf area removed per plant) at four different total plant densities per 1m$^2$ quadrat ........................................................................................................30

4.1. Response surface designs for three experiments ........................................................................................................46

4.2. Percent leaf damage of *Solanum* and *Solidago* ........................................................................................................47

4.3. The effect of *Solidago* frequency on *Solanum* leaf damage. ..................................................................................48

4.4. Effects of neighborhood composition on induced resistance measured using the relative growth rates of *Leptinotarsa juncta* beetle larvae........................................................................................................49

4.5. Preference of adult *Leptinotarsa juncta* beetles for different neighborhood types ..................................................50

5.1. Locations of latitudinal surveys ......................................................................................................................................63

5.2. Latitudinal gradients in herbivory (% leaf damage) for *Solanum* (grey) and *Solidago* (black) .................................................................................................................................................................64

5.3. Relationships between latitude and percent nutrient (cumulative and standardized, A, B respectively) and carbon to nitrogen ratios (cumulative and standardized, C, D, respectively) for *Solanum* (grey) and *Solidago* (black). ........................................................................................................................................................................65

5.4. Relationships between latitude and the relative growth rates of *Solanum* specialists (*Manduca sexta*, *Leptinotarsa juncta*) and generalists (*Spodoptera exigua* and *Schistocerca americana*) feeding on *Solanum* diet. ..........................................................................................................................................................66

5.5. Relationships between latitude and (A) the number of eggs per clutch for a *Solidago* specialist (*Trirhabda virgata*) (B) the relative growth rates of generalists *Spodoptera exigua* and (C) *Schistocerca americana* feeding on *Solidago* diet..................................................................................................................67
ABSTRACT

Ecological systems are dynamic, yet many experimental studies examine plant-herbivore interactions as from a simple, static, or single perspective. Reciprocal interactions can have profound effects on communities, and ignoring such feedbacks can result in mismatches between theoretical predictions and experimental results. In this dissertation, I examined reciprocal interactions between two plant species, *Solanum carolinense* and *Solidago altissima* and their insect herbivores.

In chapter 2, I examined how insect herbivores influenced plant competition and coexistence. Theory suggests that herbivores influence plant communities by altering competitive interactions. Because the outcome of competition is influenced by both the per capita competitive ability of plants and demographic processes including density dependence and intrinsic population growth rates, measuring herbivore effects on all these processes is necessary to understand the mechanisms by which herbivores influence plant communities. I fit alternative competition models to data from a response surface experiment conducted over four years to examine how herbivores affected the outcome of competition between two perennial plants, *Solidago altissima* and *Solanum carolinense*. Within a growing season, herbivores reduced *Solanum* plant size, but did not affect *Solidago*, which exhibited compensatory growth. Across seasons, herbivores did not affect the density of *Solanum* but reduced both the density and population growth of *Solidago*. The best fit models indicated that the effects of herbivores varied with year. In some years, herbivores increased the per capita competitive effects of *Solidago* on *Solanum*; in other years herbivores influenced the intrinsic population growth rates of *Solidago*. I examined herbivore effects on the longer-term outcome of competition (over the time-scale of a typical old-field habitat) using simulations based on the best fit models. In the absence of herbivores, plant coexistence was observed. In the presence of herbivores, *Solanum* was excluded by *Solidago* in 60% of the simulations. I demonstrated that herbivores can influence the outcome of competition through both changes in per capita competitive effects and changes in demographic processes. I discuss the implications of these results for ecological succession and biocontrol.

In chapter 3, I examined how plant community composition influenced damage patterns on plants. Neighboring plants can increase (associational susceptibility) or decrease
(associational resistance) the likelihood of damage to a focal plant but their long-term consequences for plant competition and coexistence are unclear. Neighbor effects on damage can occur through changes in the relative density of the focal plant (i.e., frequency of the focal plant), the absolute density of the focal plant, or through the total density of plants, because the different mechanisms known to influence damage patterns (e.g., pest suppression by predators, herbivore foraging behavior, plant quality) respond to different features of the neighborhood. To examine the long-term consequences of neighbor effects for plant communities, an understanding of how density and frequency of plants influence damage is needed. Using a response surface experimental design, I examined the effects of plant density and frequency on damage to *Solanum carolinense*. I found non-linear effects of the frequency of heterospecific neighbors (*Solidago altissima*) on *Solanum* damage, and a positive effect of *Solanum* density on damage. The non-linear pattern suggests that multiple mechanisms may be operating to influence damage. Non-linear patterns may be common in other habitats but might be overlooked because traditional neighborhood studies use a very narrow range of densities in their experiments. I encourage future neighborhood studies to use response surface designs to determine the prevalence of non-linear relationships in nature.

In chapter 4, I examined how neighborhood composition (i.e. plant density and frequency) influenced four mechanisms known to influence damage to plants (predator suppression, foraging behavior of herbivores, plant quality, and microclimate) using a response surface experimental design. An associational effect was observed between *Solanum* damage and the frequency of a heterospecific neighbor (*Solidago altissima*). Predator abundance and richness, soil moisture, and herbivore foraging strategies were all influenced by the frequency of *Solidago*, suggesting that these mechanisms may contribute to associational susceptibility in this interaction. Other mechanisms (microclimate and plant quality) were influenced by *Solidago* and total plant densities, respectively. This study showed that different mechanisms can be influenced by different components of the neighborhood and most likely interacts to influence damage to plants. I discuss the implications of these finding for agriculture and for understanding the long-term consequences of damage for plant communities.

In chapter 5, I examined how herbivory, herbivore community composition, plant nutrient content, and herbivore performance varied with latitude. A longstanding theory in biogeography is that species interactions, including herbivory, are stronger in southern latitudes
compared to those in the north. Because of this, the latitudinal gradients (LG) hypothesis in damage and plant defenses predicts that plants should be better defended in the tropics because selection for plant defenses is greater. Recent empirical studies suggest that the predictions from this hypothesis may be limited to a narrow range of systems (e.g. salt marshes). In efforts to understand why LG in herbivory and plant defenses are not prevalent as once thought, I examined relationships between herbivore abundance and richness, plant nutrient content, and latitude in old-field systems. I also examined latitudinal gradients in herbivore performance using generalist and specialist herbivores. Some relationships with latitude matched predictions from the LG hypothesis (e.g. plant nutrient content, damage to *Solidago altissima*), while others had opposite relationships (e.g. herbivore abundance and richness, damage to *Solanum carolinense*), and some relationships varied with leaf longevity. Herbivore responses varied with diet specialization and the exact relationship with latitude (linear, non-linear, positive, negative, or no relationship) varied with herbivore species. These results suggest that the predictions from the LG hypothesis are too simple; a more thorough investigation of relationships between herbivore abundance, damage, and plant resistance in other wide-ranging systems is needed.
CHAPTER ONE
INTRODUCTION

Ecological systems are dynamic, yet many ecological studies treat species interactions as simple, static, or examine them from one perspective. Interactions between consumers and resources have long been recognized as important forces shaping communities (e.g. predator mediated coexistence (Caswell 1978), apparent competition (Holt 1977), trophic cascades (Paine 1980)), however experimental studies typically ignore feedbacks or reciprocal interactions that frequently occur, which can result in mismatches between theoretical predictions and experimental results (Doak et al. 2008). Plant-herbivore interactions are examples of dynamic consumer-resource interactions that have often been examined simplistically or from one direction. In a review by Hambäck and Beckerman (2003), the authors classified plant-herbivore studies into two groups: plant-based or herbivore-based studies. Plant-based studies are experimental or observational studies that examine herbivore effects on plant traits, such as growth, reproduction and survival. Herbivore-based studies, which are less frequent, examine how plants influence herbivore growth, reproduction or survival. Rarely do studies integrate both perspectives to examine reciprocal interactions between plants and herbivores (particularly at the community-level) even though reciprocal interactions or feedbacks are inherent features of these dynamic systems (e.g. coevolution (Ehrlich and Raven 1964), induced defenses (Karban and Carey 1984)).

Part of the challenge in examining plant-herbivore population or community dynamics is that most studies are conducted over very short periods. Very few long-term plant-herbivore studies exist (mean duration = 15.23 months calculated from studies used in Hambäck and Beckerman 2003 review), however there are some notable exceptions (e.g., Brown and Heske 1990, Carson and Root 2000). This lack of long-term data prevents examining the importance of reciprocal effects in structuring communities. Instead, models can be fit to short-term experimental data to examine reciprocal interactions between plants and herbivores and make predictions for how their effects will play out with time. Models have been successful in following dynamics between mammalian herbivores and plants (e.g., Coughenour 1991), however the use of models for understanding insect herbivore and plant population or
community dynamics is rare (but see Underwood and Rausher 2002, Stephens and Myers 2012), with the exception studies managing pest outbreak and spread (Wallin and Raffa 2004). Of course, connecting models with experimental data requires appropriate experimental designs that allow parameters to be estimated across a broad range of conditions to account for any variation that may occur in space and in time. Many plant-herbivore studies use experimental designs that are too narrow in scope to adequately parameterize models. In this dissertation, I used a combination of field observations, experiments (field, behavior, and greenhouse), and modeling approaches to describe community-level consequences of feedbacks between plants and insect herbivores and how those interactions vary with space and time (Fig. 1.1).

In chapter 2, I examined how insect herbivores influenced competition and coexistence between two perennial plants, *Solanum carolinense* and *Solidago altissima*. Theory suggests that herbivores influence plant communities not through direct mortality of plants but rather through competitive interactions (Louda et al. 1990, Pacala and Crawley 1992). However the effects of competition can transpire through changes in the per-capita competitive ability of plants (e.g. changes in sizes, resource extraction rates), or through numerical changes in abundance (which are influenced by demographic processes). Previous experimental studies have focused on how herbivores affect the per-capita competitive ability of plants but ignore herbivore effects on demographic parameters including growth rates and density dependence. By fitting competition models to data from a four year response surface experiment, I examined how herbivores influenced both per-capita competition and demographic parameters. Using model simulations and estimated parameters, I was able to determine how herbivore effects on parameters would play out over a time-scale longer than the course of this experiment (50 years).

In chapter 3 and 4, I examined how differences in plant communities, in turn, influenced herbivore abundance and damage. Plant neighborhood studies have often considered features of the neighborhood such as size, density, and nearest neighbor distance, to be important for plant growth (Silander and Pacala 1985). However, few studies have examined how these neighborhood features can influence herbivore communities and damage patterns on host plants. It is known that neighborhoods can influence damage patterns on plants beyond the inherent properties of the host plant (Tahvanainen and Root 1972), and neighborhood effects can be associational (dependent on the density of the host plant relative to other plants) or through changes in the absolute density alone. In chapter 3, I examined how neighborhood composition
(density and frequency of host plants) influenced damage to a focal plant (*Solanum*). In chapter 4, I examined how neighborhood composition influenced four mechanisms known to generate neighbor effects in damage (e.g. predator abundances, plant quality, microclimate, and foraging behavior). Because the composition of communities change as succession or competition proceeds, examining the relationship between damage and neighborhood composition will help to understand dynamic feedbacks occurring between plants and herbivores.

Reciprocal interactions between plants and herbivores can vary in strength across space and time. One of the largest and well known spatial gradients of species interactions are latitudinal gradients in plant-herbivore interactions (Schemske et al. 2009). Theory suggests that because the abundance of herbivores is typically higher in the tropics than temperate areas, selection should favor the production of plant defenses (latitudinal gradients (LG) hypothesis). Although earlier works on latitudinal gradients in herbivory and plant defenses support the LG hypothesis (Coley and Aide 1991, Coley and Barone 1996), recent reviews have suggested that systems conforming to the LG hypothesis may not be as wide-spread and common as once thought (Moles et al. 2011a, Moles et al. 2011b). In Chapter 5, I explored the LG hypothesis in plant damage and defenses in old-field habitat. I explored how *Solanum* and *Solidago* damage, herbivore abundance and richness, plant quality varied across a latitudinal gradient from Florida to New York (>10 degrees). I also examined LG in herbivore responses to damage since most traits measured in previous studies may not actually confer resistance. Examining herbivore responses might help us understand why LG patterns in damage and defenses exist in some habitats (e.g. salt marshes) while in others they do not.

In short, the goals of this dissertation were to: (1) examine herbivore effects plant competition and coexistence between two perennial plants, *Solanum carolinense* and *Solidago altissima*; (2 & 3) examine how neighborhoods of varying in composition influence damage and mechanisms known to generate damage, and (4) examine latitudinal gradients in damage, herbivore load, plant quality, and herbivore responses.

### 1.1 STUDY SYSTEM

The two plant species at the center of my research are *Solanum carolinense* (Carolina horsenettle) and *Solidago altissima* (Tall goldenrod). *Solanum* (Solanaceae) and *Solidago*
(Asteraceae) are perennial herbaceous plants native to the eastern United States but considered invasive in other parts of the US, Europe, and Asia (Werner et al. 1980, Wise et al. 2008). Both species reproduce vegetatively and by seed, and co-occur in disturbed areas and early successional agricultural fields. The phenologies of *Solanum* and *Solidago* vary. In Florida, *Solanum* sprouts early in the spring (April-May) and flowers shortly thereafter and throughout the growing season. The primary pollinators are bumblebees and digger bees. *Solanum* berries typically become mature in the late summer and fall (August-September), and are dispersed by rodents and birds. *Solidago* on the other hand, sprouts in June, and flowers in the fall (September). *Solidago* is pollinated by an assortment of wasps, bees, and beetles. The light-weight seeds are wind dispersed.

*Solanum* and *Solidago* support a diversity of generalist and specialist insect herbivores, including leaf chewers, phloem feeders, gall makers, and leaf miners. For *Solanum*, the primary herbivores are specialist leaf chewing insects including the false potato beetle, *Leptinotarsa juncta*, tobacco hornworm *Manduca sexta* and eggplant flea beetle *Epitrix fuscula*. For *Solidago*, some of the common herbivores include sap suckers (e.g. red goldenrod aphids *Uroleucon* sp, spittle bugs *Clastoptera* sp) and internal feeders (e.g., gall making midges *Eurosta solidaginis* and *Rhopalomyia solidaginis*). In northern latitudes, two leaf chewing chrysomelid beetles (*Trirhabda virgata* and *Microrhopala vittata*) are commonly found on *Solidago* and at times in outbreak numbers, but their southern limit is northern Georgia. In addition to specialist herbivores, both *Solanum* and *Solidago* are fed upon by generalist insects including beet army worm (*Spodoptera exigua*) and cabbage looper (*Trichoplusia ni*), and grasshoppers (*Melanoplus* and *Aptenopedes* sp). Both plant species have chemical and physical traits suspected to deter herbivores (Bosio et al. 1990, Cipollini and Bergelson 2002), and herbivores are known to affect plant performance (Root 1996, Wise and Sacchi 1996), population growth (Carson and Root 1999, Underwood and Halpern 2012), and natural selection (Meyer 1993, Wise and Cummins 2006) of both plant species.

### 1.2 PLANT PREPARATION PROTOCOL

The following protocol was used to prepare plants for experiments. *Solanum* and *Solidago* root cuttings were planted at the Mission Road Research Facility greenhouse at Florida State
University (Tallahassee, FL; 30.52°N, 84.4°W). Cuttings (1.5 ± 0.2 g) were taken from field and greenhouse-grown plants collected from natural populations in north Florida and south Georgia between 2001 and 2011. Each cutting was placed in a 530 mL nursery pot with a 3:1 mixture of Fafard 3 soil (Conrad Fafard Inc, Agawan, MA) to coarse sand, and kept in a greenhouse for approximately five to six weeks (plant heights approximately 12-17 cm).
Numerous studies have documented herbivore effects on plant abundance and community composition (Brown and Heske 1990, Carson and Root 2000). Because herbivory rarely results in plant mortality, theory suggests that herbivores influence plant community structure by altering the competitive ability (i.e. ability to acquire resources) of one species with another (e.g. Crawley 1983, Louda et al. 1990). For example, herbivores could mediate coexistence by feeding on dominant plant species, weakening their competitive effects on others and leading to higher diversity. Alternatively, if herbivores selectively feed on inferior competitors, this could exacerbate the negative effects of competition, accelerating rates of competitive exclusion and reducing plant diversity. While in theory selective feeding can change plant community structure by influencing interspecific competition, empirical support for this particular mechanism is weak. Because herbivores also influence other processes important for determining the outcome of competition such as intrinsic growth rates (Maron and Crone 2006) and density dependence (Underwood and Halpern 2012), herbivore effects on demographic processes must be considered as well.

Herbivores could affect the outcome of interspecific competition in at least two ways: through changes in the per-capita competitive ability of plants, and changes in their total population size. This can be illustrated with a simple equation describing the outcome of competition between two species, X and Y.

\[ X_{t+1} = f(X_t) - \beta Y_t. \]  

The dynamics of species X are a function of intraspecific interactions, \( f(X_t) \), and interspecific competition, \( \beta Y \), (for simplicity, the analogous equation for species Y is not shown). The net competitive effect of species Y on X is the product of two components: the per capita competitive ability of species Y on X (\( \beta \)) and the total population size of Y, both of which can be influenced by herbivores (Louda et al. 1990, Chase et al. 2002). Many studies have examined the
effect of herbivores on the per capita competitive ability of plants (reviewed by Hambäck and Beckerman 2003). Per capita effects are typically measured in terms of traits associated with resource intake, such as individual plant size, growth rates, or fitness, across one or two growing seasons (reviewed by Goldberg and Barton 1992). It is generally thought that herbivores decrease the competitive ability of plants by consuming plant tissue (thus reducing resource intake), making resources more available to undamaged plants (Crawley 1983, Louda et al. 1990). However, resource intake can sometimes increase following damage through compensatory growth or increased photosynthesis (i.e. tolerance to herbivory; Whitham et al. 1991, Strauss and Agrawal 1999), leaving fewer resources for undamaged plants.

While several studies examine herbivore effects on the per capita competitive ability of plants, it is unclear how changes in per capita competitive ability alone relate to changes the outcome of competition and thus plant community structure. To my knowledge no empirical studies have examined how herbivory might affect the outcome of competition through changes in demographic processes (i.e., intrinsic rates of growth and density dependence), yet many studies do suggest that herbivory can affect plant demography (Maron and Crone 2006). Changes in intrinsic growth rates have been documented in plant populations following release from herbivory (Fagan and Bishop 2000) and may explain how non-native plants spread in novel environments (enemy-release hypothesis, Keane and Crawley 2002). Recent work suggests that herbivores can also change density dependence in plant populations, and that the strength and form of herbivore effects on plants may vary with plant size (Underwood and Halpern 2012). Because the outcome of competition is determined by both the per-capita competitive ability of plants and their population sizes, measuring herbivore effects at both of these levels is necessary to separate their contributions.

To measure per capita competitive ability, intrinsic rate of population growth, and density dependence simultaneously, competition models must be fit to data so that parameters for each of these processes can be estimated. A comparison of model parameters estimated in the presence and absence of herbivores would then disentangle the mechanisms by which herbivores influence plant communities. These models would also allow results from experiments conducted over a few seasons to be extrapolated across many seasons, the timescale necessary to observe community dynamics. Measuring density dependence, intrinsic rates of growth, and per capita competition requires experimental designs that simultaneously manipulate both plant
densities and frequencies. Previous experimental studies have examined herbivore effects across a limited range of plant densities (examples in Hambäck and Beckerman 2003) so that density dependence and intrinsic growth rates cannot be estimated for both plant species. These experiments have also confounded inter and intraspecific density effects on plant growth. The necessary data for dissecting different mechanisms for herbivore effects on plant communities can be gathered using response surface experimental designs that simultaneously vary the densities and frequencies of both plant species over a wide range of values (Law and Watkinson 1987, Inouye 2001).

The goal of my study was to examine how insect herbivores affect a simple two species plant community. I asked whether herbivore effects on the relative abundance of these two plants are mediated through changes in their per capita competitive ability and/or through other demographic processes. I carried out a response surface field experiment over four years, allowing us to include the effects of herbivores on processes that occur only across years and to estimate across-year variance due to ontogeny or environmental variation. I measured plant densities across years in the presence and absence of insect herbivores and fit competition models to my experimental data, to (1) identify which processes (model parameters) were most influenced by herbivores and how herbivore effects varied with time, and (2) examine whether the magnitude of parameters varied with time. Using model simulations I (3) examine how herbivore-mediated changes to these processes might play out over timescales longer than the length of the experiment.

2.1 METHODS

2.1.1 Experimental design and data collection
In May 2007, *Solanum* and *Solidago* plants were prepared following the plant preparation protocol in the Introduction. In June 2007, *Solanum* and *Solidago* were transplanted into 1m$^2$ field quadrats, each with a particular combination of plant densities. A response surface experiment with 17 density combinations of *Solanum* and *Solidago* was planted (densities were 1, 6, 12, and 18 individuals per 1m$^2$ quadrat in various combinations Appendix A). I crossed each density treatment with the presence/absence of insect herbivores. Densities were chosen to span the range of natural densities (T Kim, unpublished data). The 17 treatments within the response
surface design (hereafter referred to as a set) were clustered together spatially (quadrats were separated by 1.5 m of weed mat). There were six replicate sets arranged as three pairs (paired sets were separated by 5-7 m of weed mat, and each pair was separated by 12-30m). Thus the experiment encompassed a total of 102-1 m² quadrats (1092 planted individuals), arranged in three spatial blocks, each block consisting of a pair of sets, each set comprising 17 density treatments.

To manipulate the presence of herbivores, one of the sets in each block was sprayed bi-weekly with a non-systemic insecticide, N-methyl carbamate (Sevin, GardenTech, Lexington, KY) to greatly reduce insect damage (20 ml of Sevin per 3.14 l of water); control sets were sprayed with equal amounts of water throughout the growing season (May-October). Sevin has been shown to have little or no effects on plant growth or reproduction in other systems (Lau and Strauss 2005), and does not reduce pollinator visits or pollen germination of Solanum in the field in N. Florida (A. Winn and K. Kilcourse, unpublished data). To ensure that competition occurred only between Solanum and Solidago, other plant species were gently removed by hand. For grass culms not easily removed by hand, the broad-spectrum herbicide Glyphosate (Roundup, The Scotts Company LLC, Marysville, OH) was applied using a sponge or paint brush. To confine roots, I trenched the perimeter of each 1 m² quadrat once per month using a shovel. I measured the number of stems of each species and plant damage (percent leaf area removed) in each 1 m² quadrat from 2007-2010 in June when most stems had emerged from the soil. As a proxy for plant biomass, I measured the total stem length for each plant. Total length of stems was correlated with the total above- and below-ground biomass of each plant species ($r^2 = 0.80$ for Solanum, $r^2 = 0.66$ for Solidago, T. Kim unpublished data). A non-destructive measure of plant biomass was necessary to allow continued plant growth.

2.1.2 Data analysis and fitting competition models to data

ANOVA was used to test for the effects of spraying and initial planting density on plant damage, plant biomass, and the final densities of Solanum and Solidago (PROC GLM and PROC MIXED, SAS Institute 2010; see Appendix B for further details). Although ANOVA results provide an overview of the significance of herbivory and/or competition, they tell us little about the mechanism by which herbivores influence the outcome of competition, and do not allow us to make long-term predictions. To achieve these ends, I fit competition models to the data.
Model fitting was a two-step process: finding the most appropriate competition model and then incorporating herbivore effects. First, from a set of five standard competition models, I selected one model that best described interactions between *Solanum* and *Solidago*. These models have all been commonly applied in ecology and include both linear (Ricker 1954, May 1974) and non-linear (Leslie 1958, Hassell and Comins 1976, Law and Watkinson 1987) density effects (Appendix C). Analyses were based on the total number of stems of each plant species in each quadrat (hereafter, stem density) and were performed in R 2.12 using the bbmle package (Bolker 2010, R Development Core Team 2010). The model parameters were estimated using maximum likelihood and assuming a normal error distribution. For each transition period (change in density from one year to the next), I fit the models assuming no effect of herbivores (i.e., stem densities from sprayed and unsprayed treatments were pooled). I determined the second order Akaike Information Criterion (AICc) for each model and used ΔAICc to select the best fit models. AICc weights (w), which sum to 1, were used to indicate the relative support for each model (Burnham and Anderson 2002). The model that received the highest average support across the three transition periods was the Law and Watkinson competition model (\( \bar{w} = 0.25 \) for *Solanum* and \( \bar{w} = 0.29 \) for *Solidago*, Appendix C) and was therefore used in the following analyses.

The second step involved incorporating herbivore effects into the Law and Watkinson competition model (1987) to determine which, and to what extent, model parameters were affected by herbivores. The parameters in this model are \( \lambda \) (per capita growth rate at low densities), \( \beta_{ij} \) (competition coefficient, per capita effect of species j on species i), and c (a constant that describes the total density response). I assumed a normal error distribution. I introduced herbivory terms (\( \gamma \)) into the model, adding a unique \( \gamma \) to each of the model parameters either alone or in all possible combinations with others, creating a series of 16 alternative models embodying different ways in which herbivores might affect plant populations (Table 1). Models were fit to stem density data for each transition period separately. I used ΔAICc and AICc weights (w) to select the best fit model. In cases where multiple models had similar fits (ΔAICc < 2), I selected the most parsimonious model (Burnham and Anderson 2002). To determine the relative importance of each herbivory term (\( \gamma \)) across all models, importance weights (w+) of each \( \gamma \) parameter were calculated by summing AICc weights across all models in which each \( \gamma \) parameter occurred (Burnham and Anderson 2002). Unlike AICc weights, these importance weights (w+) sum to >1 because some models contained multiple \( \gamma \) parameters, thus
the AICc weights of these models were counted multiple times.

2.1.3 Simulating herbivores effects on the outcome of competition
To examine how herbivore effects might play out over periods longer than the length of this experiment, I ran stochastic simulations using the best fit competition models with herbivore effects, chosen in step two. Simulations ran for 50 time steps, an appropriate time-scale for examining *Solanum* and *Solidago* persistence in old-fields (Hartnett and Bazzaz 1985). I calculated 95% confidence intervals (CI) for each parameter using *profile* and *confint* functions in R (Table 2). For the first time step, all parameter values were drawn from a uniform distribution covering the 95% CIs of parameters estimated in transition 1, since processes associated with initial establishment in the field occurred during this transition period. In subsequent time steps, parameter values were randomly drawn from uniform distributions covering the 95% CIs of parameters estimated in either transition 2 or 3, with equal probability, reflecting environmental and ontogenetic variability. I recorded the mean densities of *Solanum* and *Solidago* in the last 25 times steps of each simulation, a period in which densities appeared to stabilize (hereafter referred to as final densities). Separate simulations were run using parameter estimates from the best fit models in the presence and absence of herbivores, each replicated 100 times.

2.2 RESULTS

The spray treatment was effective in reducing insect damage on both plant species ($F_{1,148} = 107.02$, $P < 0.0001$; Fig. 1A). Herbivore damage differed between plant species ($F_{1,148} = 252.40$, $P < 0.0001$). In control plots, leaf damage was generally higher on *Solanum* than *Solidago* (Fig. 1A). *Solanum* was frequently attacked by leaf chewing insects such as *Manduca sexta*, *Leptinotarsa juncta*, and *Spodoptera exigua* throughout the growing season with a mean of 37% leaf tissue loss. In contrast, leaf damage on *Solidago* was minimal (10% mean leaf tissue loss), but attacks by aphids (*Uroleucon* sp) and gall-forming flies (*Eurosta solidaginis, Rhopalomyia solidaginis*) were observed (20% mean gall occurrence in *Solidago*). Herbivores affected within- and across-season growth. In 2007, sprayed *Solanum* plants were larger than control plants ($P = 0.05$) but minimal differences were observed for *Solidago* ($P = 0.25$; Fig. 1B). Across seasons,
herbivores reduced the mean density of Solidago ($F_{1, 70} = 5.29, P = 0.025$; Fig. 1D) but had little
effect on Solanum density ($F_{1, 71} = 1.14, P = 0.28$; Fig. 1C), despite high leaf damage and within-
season reductions in biomass. Competition between Solanum and Solidago was asymmetric (Fig. 2).
Solidago had strong effects on Solanum ($F_{1, 44} = 77.80, P < 0.0001$) but Solanum had weaker
effects on Solidago ($F_{1, 44} = 12.79, P = 0.0009$). Specifically, as the proportion of Solidago
planted within each treatment increased, the density of Solanum in following years decreased.
The effect of Solidago on Solanum was strongest in high density treatments ($F_{1, 44} = 21.86, P = 
<0.0001$). Solanum had similar effects on Solidago in high or low density treatments (see
Appendix B for further details).

2.2.1 Fitting competition models to Solanum data
The best fit model varied among the transition periods (Table 1). In transition 1 (2007 - 2008),
three models were similar in fit ($\Delta$AICc < 2, in boldface in Table 1); I selected the most
parsimonious of these as the best fit model (Burnham and Anderson 2002). For transition 1, the
presence of herbivores increased the variance in stem densities ($w = 0.22$, Model 9). For
transition 2 (2008 - 2009), herbivores increased the per capita competitive effect of Solidago on
Solanum, and the variance in Solanum stem densities ($w = 0.62$, Model 16). For transition 3
(2009 - 2010), three models were similar in fit ($\Delta$AICc < 2, Table 1). I therefore considered the
most parsimonious model as the best fit model. For this model, herbivores had no effects on
model parameters ($w = 0.21$, Model 1). The best fit models captured 76% to 90% of the variation
in the observed data (Appendix D). To ensure that the models selected above best described
herbivore effects on plant growth, I compared the importance of each herbivory parameter ($\gamma$
) across all models using importance weights ($w^{+}$). The $\gamma$ parameter that collectively received the
highest support across all models for each transition period match those found in the best fit
models above (Appendix E).

2.2.2. Fitting competition models to Solidago data
For Solidago, the best fit models varied with transition period (Table 1). In transition 1 (2007 -
2008), the selection process indicated that herbivores increased the variance in Solidago density
but reduced Solidago growth rate ($w = 0.45$, Model 9). In transition 2 (2008 - 2009), two models
were of similar fit and I selected the most parsimonious model as the best fit model ($w = 0.26,$
Model 1). In transition 2, herbivores had no effects on model parameters. Finally, in transition 3, herbivores reduced the growth rate of *Solidago* (*w* = 0.33, Model 4). The best fit models captured 66% to 87% of the variation in the observed data (Appendix D). The γ parameters that collectively received the highest support across all models for each transition period match those found in the best fit models above (Appendix E).

### 2.2.3 Variation in model parameters

I compared the magnitude of parameters from the best fit models among years and between plant species (Table 2). The magnitude of intrinsic growth rates (λ) and density responses (c) decreased over time for both plant species. The magnitude of competition (β) also varied through time but only for the effect of *Solidago* on *Solanum* (β_{SG}). When model parameters are averaged across transition periods, there were species-level differences. For *Solidago*, the mean intrinsic rate of growth in the absence of herbivores was greater than for *Solanum* (\( \lambda_G = 5.09 \) versus \( \lambda_S = 1.74 \)). The competitive effect of *Solidago* on *Solanum* was more than twice (\( \beta_{SG} = 1.66 \)) the effect of *Solanum* on *Solidago* (\( \beta_{GS} = 0.6 \)) indicating asymmetric competition. The density responses of *Solidago* was twice as large as *Solanum* (\( c_S = 0.01 \), \( c_G = 0.02 \)) indicating that total density dependence was stronger in *Solidago* than *Solanum*.

### 2.2.4 Simulation of herbivore effects on longer-term community dynamics

To examine how the effects of herbivory and competition would play out beyond the four years of my experiment, I performed simulations using the best fit models. By incorporating variation around parameter estimates and performing replicate simulations, I generated a range of competitive outcomes and the estimated probability of competitive exclusion over 50 years in the presence and absence of insect herbivores (Fig. 3). Simulations showed that herbivores reduced the mean final densities of *Solanum* (32.6 stems per m\(^2\) without herbivores, 2.4 stems per m\(^2\) with herbivores), but had little effect on mean final *Solidago* densities (~103 stems per m\(^2\)). Simulation results differ from the mean densities observed during the last year of the experiment, particularly in the presence of herbivores (Fig. 3), suggesting that a longer experiment is needed to observe the ultimate outcome of competition. Simulations also showed that herbivores influenced the probability of competitive exclusion. In the absence of herbivores, competitive exclusion was never observed. In the presence of herbivores, competitive exclusion (stem
densities < 1) of *Solanum* by *Solidago* was observed in 60% of the simulations and 96% of the mean final densities of *Solanum* were less than 10 stems.

2.3 DISCUSSION

Herbivores influence plant community structure (reviewed by Huntly 1991) and these effects are thought to arise through changes to interspecific competition (Louda et al. 1990). Because herbivores can influence both the per capita competitive ability of plants and demographic processes important for determining population sizes, we need to consider how herbivores influence all these processes to understand and predict the long-term consequences of herbivory for plant communities. I found that herbivores reduced individual *Solanum* growth within a growing season but had minimal effects on individual growth of *Solidago*. Across seasons, the pattern was reversed; herbivores reduced population growth of *Solidago* but had little effects on the population growth of *Solanum*. Models fit to these experimental data showed that herbivores increased the per capita competitive ability of *Solidago* in some years, and reduced the intrinsic population growth rates of *Solidago* in other years. My simulations predicted that the presence of insect herbivores increases the probability of competitive exclusion of *Solanum* by *Solidago*, and decreases the final population sizes of both plant species. I demonstrated that herbivores can affect the outcome of interspecific competition, and that this can occur both through per capita competitive ability and through other demographic processes.

2.3.1 Herbivore effects on intrinsic rates of population growth

In this study, herbivores lowered population growth at low densities (\(\lambda\)) for *Solidago* but not for *Solanum*. The disparity in intrinsic population growth responses between *Solanum* and *Solidago* could be due to different tolerance mechanisms, arising from a different suite of herbivores feeding on each plant species. The apical meristem of *Solidago* was frequently attacked by gall-makers at the start of the growing season. In this study and others (Wise and Abrahamson 2008, T. Kim personal observation), the production of lateral stems following apical gall damage was observed in *Solidago*. The cost of compensatory growth could reduce stem numbers in following years, resulting in a reduction in \(\lambda\) when herbivores are present. In contrast, *Solanum* was damaged by foliar-feeding insects throughout the growing season. I did not observe herbivore
effects on $\lambda$ for *Solanum*, even though damaged plants were smaller in size than undamaged plants. The lack of change in $\lambda$ was surprising because another study in this system (Underwood and Halpern 2012) demonstrated a positive relationship between plant size and asexual reproduction in *Solanum* from one year to the next, so I expected damaged (i.e., smaller) plants to produce fewer stems in later years than undamaged (i.e., larger) plants. Damaged plants may have been able to produce as many stems as undamaged plants over the four-year span of my experiment by increasing photosynthetic rates in remaining leaves (Trumble et al. 1993) or by re-alloca- ting resources from above- to belowground growth following herbivory (McNutt et al. *In press*). The ability to increase when rare despite the presence of herbivores may serve not only as a mechanism to cope with herbivory but may also have allowed *Solanum* to persist and remain competitive throughout the course of my experiment. Tolerance of this kind may explain why biocontrol is not effective in reducing stem densities in other systems.

### 2.3.2 Herbivore effects on per capita competitive ability

I found that herbivores exacerbated the negative effects of *Solidago* on *Solanum* (Table 2). These negative effects could have come from herbivores either increasing the per capita competitive effect of *Solidago* on *Solanum*, or weakening competitive effects of *Solanum* on *Solidago*. Herbivores increased the per capita effect of *Solidago* on *Solanum* (Table 2), which may have occurred because *Solidago* increased the production of lateral stems following damage, reducing the amount of light reaching *Solanum* in the understory. Alternatively, *Solidago* may have increased nutrient and water uptake from the soil following herbivory and compensatory growth to meet aboveground demand for resources (Ritchie et al. 1998). Both these responses of *Solidago* to herbivory could result in an increased per capita competitive effect of *Solidago* on *Solanum*, leaving *Solanum* with fewer resources for growth (Strauss and Agrawal 1999). I found that herbivores did not reduce the per capita competitive ability of *Solanum*, despite causing high tissue damage and reduced plant biomass (Fig. 1). This may have occurred because competition was strongly asymmetric, so further reduction in plant size, individual growth rates, or overall performance of *Solanum* by herbivores could have had little impact on *Solidago*. Alternatively, overcompensation in stem production following damage may have allowed *Solanum* to remain competitive in the presence of herbivores.
2.3.3 Temporal variation in the importance and magnitude of parameters

Over the four-years of my experiment, I found differences in the magnitude of parameter estimates and the effects of herbivores on those parameters. In the presence of insect herbivores, I initially observed a reduced population growth rate of *Solidago* (transition 1, 2007-2008), followed by an increase in the competitive effect *Solidago* on *Solanum* (transition 2, 2008-2009), ending with a reduced population growth rate of *Solidago* in transition 3 (Table 2). These differences could reflect plasticity in tolerance mechanisms to herbivore damage that vary across among years and/or with plant age over the course of succession (Whitham et al. 1991). Because both *Solanum* and *Solidago* are perennial and long-lived, tolerance mechanisms may change with time, as plant responses to damage in previous years could influence plant responses in later years (Whitham et al. 1991, Boege and Marquis 2005). Therefore, following plant responses through time may be required to characterize the dynamic interactions occurring between these plants and their insect herbivores, and to examine the ecological and evolutionary consequences of those interactions for plant populations.

2.3.4 Long term effects of herbivores

In the presence of herbivores, competitive exclusion of *Solanum* by *Solidago* was frequently predicted to occur over 50 years whereas in the absence of herbivores, coexistence was predicted (Fig. 3). In my experimental system, *Solanum* and *Solidago* were the only two species present; non-target species were manually removed. In nature, however, old fields are successional habitats where *Solanum* and *Solidago* are eventually outcompeted by woody plants unless recurring disturbance allows them to persist. Although results from my simulations may seem artificial, they indicate where this system may be heading and offer insight into how herbivores might influence rates of succession. *Solidago* is a dominant plant in old-fields and can form dense monospecific stands with thick litter layers (Hartnett and Bazzaz 1985). *Solidago* stands may inhibit colonization of woody species, slowing rates of succession (Carson and Root 1999). Reduction of *Solidago* population growth by herbivores could lengthen the time required for *Solidago* to become dominant (typically 5-20 years after establishment), potentially facilitating colonization of woody species and increasing the rate of succession. In old-fields in NY, insect herbivores are thought to increase plant diversity by feeding on *Solidago* leaves and allowing light to reach inferior competitors in the understory (Carson and Root 2000). The release from
competition in the NY system may have allowed persistence of early successional plant species that would have otherwise been outcompeted by Solidago and could increase rates of succession by facilitating colonization of woody plant species. Although herbivore-mediated changes in competitive effects could have lead to changes in diversity patterns and succession in NY, it is unclear how changes in the competitive effect of Solidago on other plant species relate to changes in their population sizes. In contrast, my study in FL showed that phloem-feeding and gall-forming insects triggered compensatory growth that decreased the population growth rates of Solidago in some years but increased its competitive ability against Solanum in other years. Together these processes could accelerate rates of competitive exclusion of Solanum by Solidago, facilitate the formation of dense Solidago stands, and potentially slow rates of succession.

Herbivore effects on demographic processes and competition have implications for biocontrol. Both Solidago and Solanum are considered invasive in parts of the US, Asia and Europe, and biocontrol might be considered as a tool for decreasing their population sizes or reducing their spread (Weber and Schmid 1998, Follak and Strauss 2010). In my study, Solidago intrinsic growth rates (\(\lambda\)) decreased following damage in the first year of my study, which would support the use of biocontrol to reduce Solidago population sizes. However, in the second year of the study, I observed an increase in the per capita competitive effect of Solidago (\(\beta\)) following damage, which would offset any negative effects of biocontrol on Solidago, and suggest that biocontrol for Solidago after the first year of establishment would be ineffective. Furthermore, the increased competitive effect of Solidago on competitively inferior plants could result in unintended negative consequences for neighboring plants. Because the goal of reducing invasive plant populations is often coupled with increasing neighboring native plant populations (Mack et al. 2000), it may be necessary to follow the effects of herbivory on the invasive species and changes in their competitive interactions with native or non-target species for multiple seasons to determine the full effects of biocontrol measures.

2.3.5 Conclusions

In the 1960-70s, herbivores were thought to be unimportant for structuring plant communities (Hairston et al. 1960). Since then, studies have documented herbivore effects across a wide range of systems and with different herbivore taxa (reviewed by Huntly 1991), and focus has now
shifted to understanding the mechanisms by which herbivores influence plant community structure. Because herbivory rarely results in plant mortality, the prevailing theory is that herbivores influence plant communities by affecting interspecific plant competition (Crawley 1983). Yet, surprisingly, few empirical studies have thoroughly examined the mechanisms leading to changes in plant communities (final conclusions in Louda et al. 1990, Hulme 1996). To my knowledge, this is the first experimental study to tease apart these mechanisms by simultaneously measuring herbivore effects on per-capita competitive effect and demographic processes. In my two species plant community, the presence of herbivores affected the abundance of both plant species through changes in per capita plant competition, and intrinsic rates of population growth. The effects of herbivores on demographic processes have been largely ignored when examining herbivore effects on plant communities (Louda et al. 1990, Hulme 1996); studies have focused instead on how herbivores change the per capita competitive ability of plants. Because per capita competition is not the only factor important for affecting the outcome of competition and thus plant communities, it is also necessary to examine herbivore effects on demographic factors to determine the generality of this well-accepted mechanism.
Table 2.1: ΔAICc and AICc weights (in parentheses) for the 16 candidate Law and Watkinson (LW) models. Models were fit to Solanum or Solidago stem density recruitment data and arranged by transition periods. Herbivore effects (γ) were incorporated into the LW models by modifying one or more model parameters. Parameters include: X (focal plant densities); Y (competitor plant densities); competition coefficient β_{XY} (effect of species Y on species X); λ_X (population growth rate of species X at low densities); and c_X describes the total density response. K is the number of parameters in a model. Parameters were estimated using maximum likelihood and assuming a normal error distribution, where the standard deviation (σ) was also an estimated parameter that could be influenced by herbivores (models 9-16). Best fit models and models of similar fit (ΔAICc < 2) are in bold. Models with asterisks were used in simulations.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameters affected by herbivores, γ</th>
<th>K</th>
<th>Model equation</th>
<th>Solanum</th>
<th>Solidago</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>none</td>
<td>4</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>3.2 (0.06)</td>
<td>15.4 (&lt;0.01)</td>
</tr>
<tr>
<td>2</td>
<td>( \beta )</td>
<td>5</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + (\beta_{XY} + \gamma_{XY}) Y_i)} )</td>
<td>2.4 (0.10)</td>
<td>2.3 (0.19)</td>
</tr>
<tr>
<td>3</td>
<td>( \lambda, \beta )</td>
<td>6</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + (\beta_{XY} + \gamma_{XY}) Y_i)} )</td>
<td>18.0 (0.01)</td>
<td>4.1 (0.08)</td>
</tr>
<tr>
<td>4</td>
<td>( \lambda )</td>
<td>5</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>5.2 (0.02)</td>
<td>13.1 (&lt;0.01)</td>
</tr>
<tr>
<td>5</td>
<td>( c )</td>
<td>5</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>3.8 (0.05)</td>
<td>13.4 (&lt;0.01)</td>
</tr>
<tr>
<td>6</td>
<td>( \lambda, c )</td>
<td>6</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>18.5 (&lt;0.01)</td>
<td>13.9 (&lt;0.01)</td>
</tr>
<tr>
<td>7</td>
<td>( c, \beta )</td>
<td>6</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>18.5 (&lt;0.01)</td>
<td>3.9 (0.09)</td>
</tr>
<tr>
<td>8</td>
<td>( \lambda, c, \beta )</td>
<td>7</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>18.5 (&lt;0.01)</td>
<td>8.6 (0.01)</td>
</tr>
<tr>
<td>9</td>
<td>( \sigma )</td>
<td>5</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td><strong>0.8 (0.22)</strong></td>
<td>11.8 (&lt;0.01)</td>
</tr>
<tr>
<td>10</td>
<td>( \beta, \sigma )</td>
<td>6</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td><strong>0.0 (0.32)</strong></td>
<td><strong>0.0 (0.62)</strong></td>
</tr>
<tr>
<td>11</td>
<td>( \lambda, \beta, \sigma )</td>
<td>7</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>18.5 (&lt;0.01)</td>
<td>33.3 (&lt;0.01)</td>
</tr>
<tr>
<td>12</td>
<td>( \lambda, \sigma )</td>
<td>6</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>18.5 (&lt;0.01)</td>
<td>10.3 (&lt;0.01)</td>
</tr>
<tr>
<td>13</td>
<td>( c, \sigma )</td>
<td>6</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>1.6 (0.14)</td>
<td>11.1 (&lt;0.01)</td>
</tr>
<tr>
<td>14</td>
<td>( \lambda, c, \sigma )</td>
<td>7</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>18.5 (&lt;0.01)</td>
<td>10.4 (&lt;0.01)</td>
</tr>
<tr>
<td>15</td>
<td>( c, \beta, \sigma )</td>
<td>7</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>18.5 (&lt;0.01)</td>
<td>12.0 (&lt;0.01)</td>
</tr>
<tr>
<td>16</td>
<td>( \lambda, c, \beta, \sigma )</td>
<td>8</td>
<td>( X_{i+1} ) = ( \frac{X_{i-1}}{1 + c_i(X_i + \beta_{XY} Y_i)} )</td>
<td>18.5 (&lt;0.01)</td>
<td>18.2 (&lt;0.01)</td>
</tr>
</tbody>
</table>
Table 2.2: Point estimates and 95% confidence intervals (in parentheses) for parameters of best fit models in Table 2.1. Parameters were estimated using stem density recruitment data for (A) *Solanum*, *S* and (B) *Solidago*, *G* and arranged by transition periods.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_S$</td>
<td>1.99 (1.42, 2.73)</td>
<td>2.1 (1.75, 2.51)</td>
<td>1.14 (1.08, 1.21)</td>
<td>1.74</td>
</tr>
<tr>
<td>$c_S$</td>
<td>0.01 (0.003, 0.03)</td>
<td>0.015 (0.01, 0.02)</td>
<td>0.00064 (0.0003, 0.006)</td>
<td>0.01</td>
</tr>
<tr>
<td>$\beta_S$</td>
<td>3.75 (0.65, 5.15)</td>
<td>0.006 (-0.22, 0.22)</td>
<td>1.22 (0.72, 2.94)</td>
<td>1.66</td>
</tr>
<tr>
<td>$\sigma_S$</td>
<td>6.04 (5.02, 7.46)</td>
<td>6.64 (5.36, 7.47)</td>
<td>8.20 (7.19, 9.47)</td>
<td>6.96</td>
</tr>
<tr>
<td>$\gamma_{\lambda S}$</td>
<td>-</td>
<td>0.59 (0.30, 1.03)</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_G$</td>
<td>11.07 (8.73, 14.39)</td>
<td>2.53 (2.11, 3.09)</td>
<td>1.67 (1.30, 2.23)</td>
<td>5.09</td>
</tr>
<tr>
<td>$c_G$</td>
<td>0.03 (0.01, 0.06)</td>
<td>0.007 (0.004, 0.01)</td>
<td>0.008 (0.004, 0.01)</td>
<td>0.02</td>
</tr>
<tr>
<td>$\beta_G$</td>
<td>0.88 (0.32, 2.21)</td>
<td>0.66 (0.48, 2.07)</td>
<td>0.26 (0.13, 1.42)</td>
<td>0.60</td>
</tr>
<tr>
<td>$\sigma_G$</td>
<td>12.94 (10.78, 15.94)</td>
<td>20.99 (18.41, 24.24)</td>
<td>17.05 (14.96, 19.70)</td>
<td>16.99</td>
</tr>
<tr>
<td>$\gamma_{\lambda G}$</td>
<td>-1.5 (-2.77, -0.39)</td>
<td>-</td>
<td>-0.36 (-0.57, -0.20)</td>
<td>-</td>
</tr>
</tbody>
</table>

20
Figure 2.1: Spray treatment effects on leaf tissue damage (A), biomass (B), and stem densities of *Solanum* (C) and *Solidago* (D). White boxes = herbivores present, Grey boxes = herbivores reduced. Thick horizontal lines indicate medians and whiskers encompass 1.5 times the interquartile range from the boxes. Leaf damage was averaged for plants in each 1m$^2$ quadrat. Biomass was the sum of all stem lengths in each 1m$^2$ quadrat. Stem densities for all 17 density treatments are included in the box plots. Asterisks indicate significant differences interactions (P < 0.05) between spray treatments (see Appendix B for details).
Figure 2.2: Relationship between the proportion of heterospecific competitors and density responses of *Solanum* (A) and *Solidago* (B). The proportion of heterospecific competitors is the number of heterospecific competitors planted per quadrat in 2007 divided by the total number of individuals planted per quadrat in 2007. Density responses of *Solanum* and *Solidago* in high initial density treatments (filled symbols and solid lines, 18 individuals / m²), and low initial density treatments (open symbols and dashed lines, 6 individuals / m²). Each point represents density responses of *Solanum* and *Solidago* in 2008, 2009, and 2010. Asterisks indicate significant interactions (P < 0.05) between initial density x proportion of heterospecific competitors (see Appendix B for details).
Figure 2.3: Frequency distribution of *Solanum* and *Solidago* final densities (see text for details) from replicate simulations (n=100) of best fit competition models (Table 2.1). Models parameters were drawn randomly from a uniform distribution encompassing the 95% CIs of parameter estimates (Table 2). Distribution in the absence (A) or presence (B) of herbivores. Numbers in parentheses represent final densities averaged across all 100 simulations. Hatchings indicate locations of the mean densities of *Solanum* and *Solidago* at the end of the four-year study.
CHAPTER THREE

NON-LINEAR EFFECTS OF PLANT NEIGHBORHOOD COMPOSITION ON INSECT HERBIVORE DAMAGE

Simple and still commonly used models of plant population dynamics assume all individuals experience the same conditions (Harper 1977, Mack and Harper 1977). In nature, of course, we know that plants are heterogeneously distributed and the conditions in local neighborhoods can affect individual growth, reproduction, and survival. One way by which local neighborhoods influence plant performance is through changes in herbivore abundance and plant damage. For example, neighboring plants can reduce the likelihood of damage (associational resistance, AR), or increase the likelihood of damage to plants (associational susceptibility, AS) (Tahvanainen and Root 1972). Although a large literature tests for the existence of neighbor effects, examines potential mechanisms (e.g. predator attraction, host-plant apparency), and discusses the application of neighbor effects to agroecosystems (e.g. diversified planting, trap-cropping), the long-term consequences of neighbor effects for plant competition and coexistence are poorly understood (reviewed by Barbosa et al. 2009).

To examine the long-term consequences of neighbor effects for plant communities, an understanding of how components of the neighborhood influence damage is required. Neighborhood modeling studies have spent considerable efforts trying to determine which aspects of the neighborhood including the spatial extent, neighbor arrangement, and the absolute and relative densities of plants, influence plant performance (Silander and Pacala 1985, Pacala 1986, Molofsky et al. 2002). A similar approach should be used to examine how these factors influence damage. Neighbor effects on damage can transpire through changes in the relative density of the focal plant (i.e., frequency of the focal plant), the absolute density of the focal plant, or through the total density of plants, because the different mechanisms generating damage patterns are responding to different features of the neighborhood. For example, effective pest suppression by predators may rely on the frequency of focal plants, whereas foraging behavior of the herbivores may depend more on the density of the host plant. Similarly, plant quality may depend on neither the frequency nor density of the host plants but rather the total density of plants in the neighborhood. Previous studies examining associational resistance and
susceptibility have not made those neighborhood distinctions, considering all neighbor effects (regardless of neighbor identity) as associational. Because frequency- and density dependent mechanisms can lead to different long-term outcomes for plant communities, making those distinctions is important. Therefore, I refer to associational effects (AE) as damage generated by frequency-dependent processes only, and distinguish AE from damage due to density-dependent processes including resource concentration (Root 1973) and dilution effects (Otway et al. 2005).

To determine whether neighbor effects on damage are associational or through density-dependent processes, experimental studies need to manipulate both the density and frequency of the focal plant. While previous neighborhood studies can tell us that neighborhood composition matters, in most cases they do not pinpoint which aspects of the neighborhood (i.e., the total, focal, or neighbor plant densities) are responsible for damage pattern because they confound plant density and frequency (e.g. substitutive designs (Letourneau 1995, Orians and Bjorkman 2009); additive designs (Rand 1999, Hambäck et al. 2000)). This problem is not limited to manipulative experiments but also applies to observational studies that measure neighbor densities and correlate those densities with damage patterns (Sholes 2008). To determine whether damage in different neighborhoods is indeed associational (frequency-dependent), or occurs through changes in focal plant density (density-dependent), we need to tease apart these two components of the neighborhood (hereafter referred to as neighborhood composition). These confounding issues can be overcome by adopting a response surface experimental design (Inouye 2001) which simultaneously varies the density and frequency of plants across a broad range.

Although the importance of neighbor density and identity for plant competition has been studied since the 1960s (Yoda et al. 1963, Harper 1977, Tilman 1982), how these effects might be mediated through herbivores is less well understood. To my knowledge, no study has effectively addressed how damage changes with the density and frequency of neighbors. Using a response surface experimental design, I will examine how plant density and frequency of neighbors affects damage to a focal plant Solanum carolinense. As the relative and absolute densities of the plants change in response to competition, the strength and direction of damage effects may shift with time. Therefore understanding how damage changes with the density and frequency of plants in the neighborhood is critical for evaluating dynamic feedbacks between herbivory and plant competition.
3.1 METHODS

3.1.1 Experimental design
In 2007, I examined how neighborhood composition (i.e. plant density and frequency) influenced leaf damage on *Solanum* using a response surface experimental design. Four total densities of plants (1, 6, 12, 18 individuals per 1m$^2$ quadrat) at varying densities of *Solanum* and *Solidago* were established in the field (13 density combinations in total, Appendix F). Densities of *Solanum* and *Solidago* spanned the range of naturally occurring densities in surrounding areas, and each density combination was replicated three times (39-1m$^2$ quadrats in total). Plants were clonally propagated from root cuttings following the protocol in the Introduction. Plants were then transplanted into 1m$^2$ field quadrats. Quadrats were separated by 1.5 m of weed mat and arranged into three spatial blocks separated by 12-30 m.

At the end of the growing season in September, percent damage was assessed on all leaves of all plants. The type of damage (mining, chewing, galls, skeletonized) found on all plants was recorded as well. The effects of total plant density, density of *Solanum*, and relative density (frequency) of *Solidago* on damage to *Solanum* (including all two-way interactions) were analyzed using a generalized linear model in R 2.12 (R Development Core Team 2010). I suspected a non-linear relationship between *Solanum* damage and the frequency of *Solidago* so both linear and quadratic terms were used as predictor variables. An AIC-based step-wise elimination process was used to select the best fit model.

3.2 RESULTS

As expected, damage varied with plant species (t = -11.67, d.f. = 104, P < 0.001, Fig.3.1). Leaf damage to *Solanum* was extensive (3.3% to 62.2%, mean = 27%). *Solidago* damage was low (0.15 to 23.4%, mean = 6.15%). *Solanum* damage was largely due to leaf feeding insects with minimal damage by aphids and leaf miners (< 1% of all *Solanum* plants). Several aspects of neighborhood composition appeared to influence *Solanum* damage. First, a positive relationship was observed between the density of *Solanum* and damage (F$_{1,35}$ = 6.64, P = 0.014, Table 3.1). Second, a unimodal relationship was observed between the frequency of *Solidago* and *Solanum* damage (significant quadratic effect of *Solidago* frequency, F$_{2,35}$ = 5.49, P = 0.008). As the
frequency of *Solidago* increased, *Solanum* damage increased reaching peak damage levels when neighborhoods were 30-50% occupied by *Solidago* (Fig. 3.2), and then declining with further increases in *Solidago* frequency. *Solanum* growing in the presence of neighbors (regardless of the total density and identity of neighbors) suffered higher damage (mean = 28.5%) than *Solanum* individuals growing alone (mean = 15.35%, t = -4.08, d.f. = 10, P = 0.001). This suggests that neighboring plants confer susceptibility to damage, but the magnitude of susceptibility depended on neighborhood composition.

3.3 DISCUSSION

I found two different components of the neighborhood to be important for damage patterns: *Solanum* density and frequency of *Solidago*. The positive relationship between *Solanum* density and damage to *Solanum* may have been due to numerical response of specialist herbivores to resources (i.e., bottom up effects, Strong et al. 1984) and changes to herbivore behavior (e.g., resource concentration effects Root 1973). I also observed a hump-shaped relationship between *Solanum* damage and the frequency of *Solidago*. This hump-shaped relationship could suggest multiple mechanisms operating to influence plant damage. Damage by herbivores involves several, hierarchical processes which includes locating host plants within a sea of non-host plants, host-plant selection among neighboring plants, and tolerating plant defenses once damaged. Each of these processes could have different relationships with the density and frequency of plants within the neighborhood. These foraging strategies are not unique to this habitat type, therefore non-linear relationships could be common in other habitats as well.

The non-linear relationship between *Solanum* damage and the frequency of *Solidago*, could suggest alternative long-term outcomes for competition and coexistence. The non-linear relationship was observed because I tested a broad range of plant frequencies. Past studies use a narrow range of frequencies, making it difficult to determine how common non-linear relationships are in nature. Traditional AE studies use substitutive designs to compare monocultures with polycultures where the frequency of each species remains fixed (typically at 1/number of species). These types of studies ignore damage that might occur at other plant frequencies, missing opportunities to uncover non-linear patterns in damage.
Furthermore, substitutive designs cannot determine whether differences in damage are due to changes in focal plant densities, neighbor plant densities, or changes in their frequencies since density and frequency of plants are changing simultaneously. Because I used a response surface design, I was able to separate the effects of plant density and frequency and found different relationships of damage with these two components of the neighborhood. Elucidating the relationship between damage with plant frequency and density can allow models to be fitted to experimental data to assess the long-term consequences of AE for plant competition and coexistence.

If changes in densities or in the frequency of neighbors occur across growing seasons, then variation in damage may occur with time. Shifts in damage could feed back to influence neighborhood composition, making AE a dynamic phenomenon. *Solidago* is a dominant species of old-field systems and forms dense monospecific stands five to 20 years following establishment (Hartnett and Bazzaz 1985). In the absence of disturbance, neighborhoods in this study became dominated by *Solidago* with time (Kim et al. *in revision*). As succession proceeds and as fields become more dominated by *Solidago*, damage to *Solanum* may increase, which could accelerate competitive exclusion of *Solanum* by *Solidago*. However, as neighborhoods become further dominated by *Solidago*, damage to *Solanum* would decreases which could slow rates of competitive exclusion and allow *Solanum* plants to persist. This non-linear relationship between *Solanum* damage and the frequency of *Solidago* may explain how some individuals of *Solanum* can persist in dense monocultures of *Solidago* (T.Kim pers. obs). In another study I investigate mechanisms for why damage to *Solanum* changes with neighborhood composition. Results suggest that multiple mechanisms are influenced by neighborhood composition including variation in host plant quality and foraging strategies of insect herbivores.

Understanding which components of the neighborhood influence damage has obvious conservation implications and applications for agriculture. If management goals are to reduce insect load and damage to target plants (e.g. crops, re-introduced native plants), then knowing which components of the neighborhood influence damage is needed. If non-linear patterns are common, then land managers may consider different land-use practices to reduce insect loads and damage. In natural systems, the relationship between damage and neighborhood composition could be incorporated into population models to gain a better understanding of the importance of herbivory for plant population dynamics.
Figure 3.1: Leaf tissue damage on *Solanum carolinense* and *Solidago altissima*. Thick horizontal lines indicate medians and whiskers encompass 1.5 times the interquartile range from the boxes. Leaf damage was averaged across plants in each $1m^2$ quadrat and all 13 density treatments are included in the box plots. Asterisks indicate significant differences in damage ($P < 0.05$) between plant species.
Figure 3.2: Effect of *Solidago* frequency on *Solanum* leaf tissue loss (mean percent leaf area removed per plant) at four different total plant densities per $1m^2$ quadrat. Black, filled circles indicate treatments with only one *Solanum* individual per quadrat.
Table 3.1: Effects of *Solanum* density and frequency of *Solidago* on mean leaf tissue damage. $R^2 = 0.25$, $F = 5.175$, df $= 3,35$, $P = 0.004$.

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>Df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>9352.1</td>
<td>1</td>
<td>102.29</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Frequency of <em>Solidago</em> (polynomial)</td>
<td>1005.1</td>
<td>2</td>
<td>5.49</td>
<td>0.0083</td>
</tr>
<tr>
<td>Density of <em>Solanum</em></td>
<td>607.9</td>
<td>1</td>
<td>6.64</td>
<td>0.0142</td>
</tr>
<tr>
<td>Residuals</td>
<td>3199.9</td>
<td>35</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
CHAPTER FOUR

THE EFFECT OF NEIGHBORHOOD COMPOSITION ON MECHANISMS OF ASSOCIATIONAL RESISTANCE AND SUSCEPTIBILITY

It has long been recognized that neighboring plants can influence plant performance (Harper 1977, Silander and Pacala 1985), and that neighbor effects can be mediated by consumers (Holt 1977). Neighboring plants can decrease or increase herbivore loads or damage to a focal plant, and these effects are known as associational resistance and susceptibility, respectively (Tahvanainen and Root 1972). The topic of associational effects (AE) has a rich history in applied fields such as agriculture and forestry (Letourneau et al. 2011), a recent interest in AE has emerged in ecology in efforts to understand the long-term consequences of context-dependent herbivory for plant competition and coexistence (Agrawal et al. 2006, Barbosa et al. 2009, Orrock et al. 2010, Hughes 2012, Underwood et al. in review). This requires identifying which components of the neighborhood (e.g. size of neighborhoods, identity of neighbors) influence damage and understanding how those neighborhood features influence the mechanisms generating those neighbor effects. Using this knowledge, mathematical models can be used to predict how or when neighboring plants influence damage to individual plants, and how feedbacks between consumers and plants scale up to ultimately influence plant population and community dynamics (Underwood et al. in review).

Numerous hypotheses have been proposed to explain how neighboring plants influence damage (reviewed by Barbosa et al. 2009). Neighbor effects can be mediated through herbivore traits such as feeding rates and behavior, and/or plant traits such as plant nutritional quality and morphology. For example, at large spatial scales, neighbors can interfere with an herbivore’s ability to locate host plants by emitting volatile chemicals or visually masking host plants (Marquis et al. 2002, Schroeder and Hilker 2008). Neighbors can also attract predators with food or/and shelter which could have consumptive or non-consumptive effects on herbivore load and damage (Morrison et al. 2004). At finer spatial scales, neighboring plants can affect the abiotic environment such as temperature, light, and relative humidity; these changes to the microclimate can influence herbivore feeding rates, development times and their distributions (Bach 1984,
Variation in microclimate can also influence plant growth patterns; for example shading by neighbors can alter leaf or plant morphology which could make focal plants more or less “apparent” (sensu Feeny 1976, Wise et al. 2010a) to insect herbivores. If resources are limited and the production of plant defenses is costly, neighboring competitors can also constrain the production of plant defenses (Bach 1984, Cipollini and Bergelson 2001, 2002, Agrawal 2004), making plants more vulnerable to herbivores. On the other hand, plant neighbors can have positive effects on plant defenses where neighbors emit volatile chemicals (after being damaged) that induce or prime the production of plant defenses for the focal plant, or are passively absorbed and re-emitted by the focal plant. Evidence for this has been mounting within species (Kost and Heil 2006, Shiojiri and Karban 2006) and between species (Karban 2001, Himanen et al. 2010) but seems to be limited to plants in very close proximity of one another.

While a large literature tests for the existence of neighbor effects, and examines possible mechanisms behind those effects, it is unclear exactly how the neighborhood influences damage and the associated mechanisms. We know that different neighborhood types (e.g. high or low diversity neighborhoods) can confer resistance or susceptibility; we don’t know which components of the neighborhood are responsible for these changes in damage. Neighborhoods can influence damage through variation in the density of the focal plant, through the relative density (or frequency) of the focal plants, or through the total density of plants in the neighborhood. Previous studies examining neighbor effects have used experimental designs that cannot separate the effects of plant density and plant frequency on damage (additive designs, Rand 1999, Hambäck et al. 2000), (substitutive designs, Letourneau 1995, Orians and Bjorkman 2009), and have thus classified all neighbor effects as associational. Because damage due to the density or frequency of plants in the neighborhood can arise through different mechanisms and could have different consequences for plant communities, it is important to differentiate the ways in which neighbors influence damage. Therefore, I define associational effects (i.e. frequency dependent effects) as the effects of different types of neighbors (e.g. different species, different genotypes) on damage or insect load a focal plant. Neighbor effects on damage and insect load due to changes in the focal plant density (e.g. resource concentration or dilution effects) will be referred to as density-dependent effects of neighbors.
Using a response surface experimental design where I manipulated the densities and frequencies of plants, I examined how the neighborhood composition (i.e. plant density and frequency) affected damage to a perennial plant, *Solanum carolinense* in the presence of a heterospecific neighbor, *Solidago altissima* (hereafter referred to by genera). I also examined how neighborhood composition affected four mechanisms known to influence damage (predator abundance, microclimate (including ambient temperature, light intensity, and soil moisture), plant quality, and herbivore foraging strategy). To my knowledge, no study has effectively addressed how the multiple mechanisms suspected to generate damage might change with the density and frequency of heterospecific neighbors. While these relationships have not been studied explicitly, there are reasons to believe that all mechanisms for damage should be sensitive to plant density and frequency. Because different mechanisms may predominate at certain densities or interact with one another, examining multiple mechanisms simultaneously will allow for a better understanding of how neighboring plants influence damage patterns.

### 4.1 METHODS

**4.1.1 Basic experimental design**

In 2011, I conducted a series of response surface experiments where I manipulated the densities of *Solanum* and *Solidago* to examine the effects of neighborhood composition on *Solanum* damage, herbivore load, and four mechanisms suspected to generate AE. Each response surface contained 17 density treatments with 1, 4, 8, or 16 individual plants at varying combinations of *Solanum* and *Solidago* frequency (Fig. 4.1). Densities of *Solanum* and *Solidago* spanned the range of naturally occurring densities in surrounding areas (1.57 to 25.19 plants per m$^2$), and each density combination (i.e., each point in Fig. 4.1) was replicated three times. Plants were prepared in May following the plant preparation protocol in the Introduction. In June, plants were then placed into plastic kiddie pools (91.4 cm diameter x 30.4 cm height, with added drainage holes) in random arrangements. The use of kiddie pools minimized disturbance associated with weeding, and ensured competition between *Solanum* and *Solidago*. The experimental unit was a neighborhood (i.e., each kiddie pool). For most analyses (unless otherwise indicated), the effects of total density, *Solanum* density, *Solidago* density, and frequency of *Solidago* on the measured response variables were analyzed using a series of
generalized linear models (GLMs) in R 2.12 (R Development Core Team 2010). An AIC based step-wise elimination process was used to select the best fit model. I examined four mechanisms as follows.

4.1.2 Leaf damage and numerical responses of herbivores and predators
To address how neighborhood composition influenced damage to *Solanum* and herbivore and predator communities, I placed the pools in an abandoned agricultural field at the North Florida Research and Education Center to allow natural colonization of insect herbivores and predators (Quincy, FL; 30.58° N, 84.58° W). Pools were arranged in rings (eight to nine pools per ring) with two meters separating each pool. A total of six rings were randomly placed in a 50m x 75m field and each ring was separated by 10-15 m. The vegetation between pools was largely composed of grasses (e.g., *Paspalum urvillei*, *Digitaria ciliaris*) with some herbaceous annuals and perennials (e.g., *Rubus trivalis*, *Sida spinosa*). *Solanum* and *Solidago* were not observed in this particular field during the experiment but both species occur naturally in adjacent areas. *Solanum* and *Solidago* within the pools were visually surveyed for herbivores and predators between June and August. Each plant was surveyed every three to four days at different times during the day throughout this period to fully capture the herbivore and predator communities. Herbivores and predators were lightly dusted with luminous powder using a paint brush or bulb syringe (BioQuip Products) after counting to avoid re-counting the same individuals during surveys. Powder was re-applied when markings become faint. Leaf tissue damage to *Solanum* was surveyed at the end of the growing season (September). Separate GLMs (using Poisson distributions for count data) were used for each response variable (cumulative predator abundance, cumulative herbivore abundance (and their ratio), predator species richness, and *Solanum* leaf damage). *Solanum* leaf damage was square-root transformed to meet the assumptions of normality of residuals in GLM.

4.1.3 Microclimate effects
To determine the effects of neighborhood composition on microclimate, three environmental variables were measured: ambient temperature, light intensity, and soil moisture. Temperature and light data loggers (HOBO Pendant®) measured light intensity (kilolumens/ m²) and temperature (degrees Celsius), and data loggers were placed in the pools used for the experiment
outlined above. Data loggers were placed next to randomly selected *Solanum* plants to measure light intensity or under *Solanum* leaves to measure temperature. Soil moisture was measured by collecting soil core samples in July and August after heavy rainfall. Soil samples were weighed wet, oven-dried at 60 degree Celsius for 1 week, and re-weighed. Moisture content was calculated as (wet mass-dry mass)/dry mass. Separate GLMs were performed on mean ambient temperature, light intensity, and soil moisture content.

### 4.1.4 Constitutive and induced plant resistance

To determine how neighbors affect plant quality, I measured constitutive (CR) and induced (IR) resistance of *Solanum* to *L. juncta*, a specialist, chrysomelid beetle. A second response surface experiment using the same plant preparation protocol outlined in the Introduction was created in June. A total of seven density combinations made up each response surface (Fig. 1), and plants were allowed to compete for 6 weeks before CR and IR were measured. Because *Solanum* genotypes are known to differ in defense and growth (D. McNutt pers. comm.), each response surface set was entirely composed of a single *Solanum* genotype to ensure equal genetic effects across density combinations. *Solidago* clones were drawn from a random pool of 10 clones collected around north Florida. Four *Solanum* genotypes were used and each response surface set (with its unique *Solanum* genotype) was replicated twice (one set for CR analysis and the other set for IR analysis), resulting in a total of eight response surface sets (four genotypes x two sets per genotype). The unit of observation was plant neighborhood. For this experiment neighborhoods were scaled down to 45.7 cm diameter pots which were ¼ the volume of kiddie pools. The numbers of plants per pot varied from one to four individuals, representing density of 6.49 to 25.97 individuals per m\(^2\). The use of smaller pot sizes was necessary to conduct the experiment in a greenhouse (Florida State University Mission Road Research Facilities greenhouse, FL; 30.52°N, 84.4°W). There was limited greenhouse space to keep the pools indoors, and pools kept in the field would have required insecticide or netting to prevent colonization of herbivores which would have compromised the quality of leaves for bioassays.

Resistance was measured as the relative growth rate (RGR) of *L. juncta* larvae in laboratory bioassays. To measure IR, two fully expanded leaves near the top of the plant on a randomly selected *Solanum* plant from each neighborhood in the IR response surface set were damaged at 30% using one to three *L. juncta* larvae. Thirty percent leaf damage was sufficient to
induce resistance in *Solanum* in previous studies (D. McNutt pers. comm.). Insects were confined to leaves with mesh bags. Damage took less than 1 day after which herbivores and bags were removed. After three days, the two most recently expanded leaves on the same plant were collected for bioassays with two 2nd-3rd *L. juncta* larvae per plant. Larvae were weighed after three hours of starvation to eliminate food in digestive tracts, and each herbivore was offered one leaf in a 74 ml plastic soufflé cups (Dart Conex®) lined with damp filter paper. After 48 hours of feeding, *Solanum* leaves were removed. Beetles were starved for another three hours and weighed again. The RGR was calculated as the ln (final mass / initial mass). To measure CR, the two most recently expanded leaves were removed from a randomly selected *Solanum* plant in each neighborhood in the CR response surface set. Leaves were offered to two different 2nd-3rd *L. juncta* larvae and their relative growth rates were measured. To control for bag effects on leaf quality for IR plants, two leaves on these CR (or control) plants were bagged at the same time insects were bagged onto IR plants above. CR was measured as simply 1- RGR of herbivores fed CR plants. IR was measured as the 1-(RGR of herbivores fed IR plants – RGR of herbivores fed CR plants). Separate GLMs were performed on CR and IR and models included plant genotype as a fixed effect.

### 4.1.5 Herbivore foraging strategies

Plants, irrespective of their quality, can avoid detection and escape herbivory by hiding among neighboring plants. Because of this, the presence or absence of an herbivore within a neighborhood does not necessarily indicate preference (this would require perfect knowledge of all available neighborhoods according to the ideal free distribution (Fretwell and Lucas Jr 1970)). Rather, selected plants may be more “apparent” (*sensu* Feeny 1976) and thus easier to find. In May 2012, I conducted behavior experiments using *L. juncta* adults and a subset of nine neighborhoods (Fig. 4.1) to determine whether plants in different neighborhood types varied in apparency. I focused on adults because long-distance movement and host plant selection are typically performed by adults; larvae typically feed on plants where eggs were laid (T. Kim and D. McNutt pers. obs.). The same protocol was used to prepare a random mix of plant genotypes (see Introduction) but individual plants remained in separate 530ml pots for a total of two months (rather than five weeks) and pots were brought together to form neighborhoods just prior to data collection. This was done to avoid confounding effects of plant apparency and plant
quality, which would be a concern if competition between plants influenced plant size and quality. Paired neighborhoods were placed at opposite ends of an arena (2.5m x 1.25m x 0.75m in size, PVC framed and enclosed with screening) with one *L. juncta* adult placed in the middle. The locations of *L. juncta* after 24 hours were recorded and preferences determined as the neighborhood where the beetle was found, or neighborhoods with signs of *L. juncta* damage and eggs. Based on preliminary behavior observations, a period of 24 hours was used because it was long enough to allow beetles to acclimate to their new environments, but short enough that host-plant selection was likely based on apparency rather than on genetic differences in plant quality assessed through multiple sampling bouts of the two different neighborhood types (damage in both neighborhood options was never observed).

To examine how different components of the neighborhood influenced beetle preference, comparisons were broken up into three steps; each step testing one aspect of the neighborhood. To examine how plant frequency influenced choice, I used a subset of neighborhood types where total plant densities were held constant at four or 16 plants (low and high total densities, respectively) and the frequency of *Solanum* and *Solidago* varied (a substitutive design at two total densities, Appendix Ga). This allowed me to determine whether frequency was important but cannot distinguish whether it is the frequency of *Solanum* or *Solidago* that is important for damage because both are changing simultaneously. To overcome this, another set of comparisons were made where densities of *Solanum* remained fixed at one, four, and eight individuals and paired with diculture neighborhoods with an equal density of *Solanum* but *Solidago* densities varied at fifteen, twelve, and eight individuals, respectively (an additive design at three total densities, Appendix Gb). Finally, because paired neighborhoods in these additive comparisons also varied in size (thus confounding total density and frequency of *Solidago*), a third set of pair-wise comparisons were made between monocultures of varying sizes (one, four, 16 individuals, Appendix Gc) to determine if neighborhood size alone influence preference. A total of 12 paired neighborhood comparisons were made and each paired combination was replicated 10 times using different beetles with each replicate. Preference was recorded among paired treatments and 12 separate chi-square tests determined whether preference differed from random selection.
4.2 RESULTS

4.2.1 Associational effects
Leaf damage varied with plant species (Fig. 4.2); *Solanum* received more damage than *Solidago* (mean damage = 10% versus 4%, respectively) which was expected based on previous results (Kim and Underwood, in prep). Unlike the previous study where a hump-shaped relationship was observed between damage and frequency of *Solidago*, in this study a positive relationship between the frequency of *Solidago* and *Solanum* damage was observed ($F_{1,49} = 46.56$, $P < 0.001$, Fig. 4.3). Mean damage varied from 4.0% in monoculture of *Solanum* where the frequency of *Solidago* was zero and 18.8% in neighborhoods where the frequency of *Solidago* was >50%. The frequency of *Solidago* ($F_{1,46} = 12.6$, $P < 0.001$) had a positive relationship with the abundance of herbivores (Appendix Ic). The herbivore community was largely composed of generalists (two-lined spittle bugs, *Prosapia bicincta*, grasshoppers *Melanoplus* and *Aptenopedes* spp, and weevils (*Sitonia* sp)) making up 49% of the surveyed herbivores. Specialists such as *L. juncta* (false potato beetle) and *Epitrix fuscula* (eggplant flea beetle) made up < 3% of the surveyed herbivores. In general, *Solanum* plants grown in the presence of neighbors (irrespective of identity and composition) had higher herbivore loads and damage than *Solanum* plants with no neighbors (Fig. 4.3).

4.2.2 Predator community
The frequency of *Solidago* positively influenced the predator communities within the neighborhoods, which were largely composed of spiders (e.g. green lynx spiders (*Peucetia viridians*), and yellow sac spiders (*Cheiracanthium inclusum*)) and predatory stinkbugs (e.g. *Euthyrhynchus floridanus* and *Stiretrus anchorago*). Predator abundance ($F_{1,45} = 9.12$, $P = 0.004$) and richness ($F_{1,47} = 13.79$, $P < 0.001$) increased with the frequency of *Solidago*. There was a significant interaction between the effects of *Solidago* frequency and density of *Solanum* on predator richness ($F_{1,47} = 4.6$, $P = 0.03$) and abundance ($F_{1,45} = 11.08$, $P = 0.001$); the effects of *Solidago* frequency was stronger at high *Solanum* densities (Appendix Ia and b). The ratio between predator and herbivores did not differ with the frequency of *Solidago* ($F_{1,41} = 0.719$, $P = 0.40$).
4.2.3 Microclimate
The density of *Solidago* had negative effects on mean light intensity (\(F_{1,48} = 6.50, P = 0.013\), Appendix Ja) and ambient temperature (\(F_{1,49} = 15.015, P < 0.001\), Appendix Jb). The mean temperature and light intensity in monocultures of *Solanum* were 31.7°C and 26.1 kilolumens / \(m^2\) respectively, compared to neighborhoods with high densities of *Solidago* (28.1°C and 17.2 kilolumens / \(m^2\) respectively). Soil moisture, on the other hand, decreased with the frequency of *Solidago* (\(F_{1,43} = 64.74, P < 0.001\), Appendix Jc). The mean soil water content was 90% in *Solanum* monocultures but 33.2% in neighborhoods with high densities of *Solidago*. There was also a significant interaction between the effects of *Solidago* frequency and density of *Solanum* on soil moisture (\(F_{1,43} = 15.5, P < 0.001\)); the negative effects of *Solidago* frequency was stronger at low *Solanum* densities.

4.2.4 Plant resistance
Neighborhood composition did not influence constitutive resistance (model: \(F_{7,20} = 1.47, P = 0.231\), Appendix Ha) but did influence induced resistance (model: \(F_{7,20} = 2.95, P = 0.027\), Appendix Hb). A genotype x density interaction was observed (\(F_{3,20} = 4.312, P = 0.016\), Fig. 4.4); three of the four genotypes exhibited a negative relationship between density and IR indicating that plants in high density neighborhoods were poorly defended compared to plants with fewer neighbors. For one genotype (genotype 111), plants growing at low densities were poorly defended compared to plants growing with neighbors (Fig. 4.4).

4.2.5 Herbivore foraging behavior
In neighborhoods with a high fixed density (sixteen individuals), *L. juncta* adults preferred monocultures over dicultures (\(\chi^2 = 3.6, \text{d.f.} = 1, P = 0.057\), Fig. 4.5b). On the other hand, in low density neighborhoods (four individuals), herbivores did not seem to prefer one neighborhood type over the other (Fig. 4.5a). To determine whether preference for dicultures was due to higher *Solanum* densities or lower *Solidago* densities, additive comparisons were made between monoculture where the densities of *Solanum* remained fixed at one, four, and eight individuals, versus diculture neighborhoods had an equal number of *Solanum* but included fifteen, twelve, and eight *Solidago* individuals, respectively. *L. juncta* preferred neighborhoods with less *Solidago* (\(\chi^2 = 3.6, \text{d.f.} = 1, P = 0.057\), Fig. 4.5c). To determine if preference for neighborhoods
in Fig. 5c was purely due to differences in neighborhood sizes, monocultures of varying sizes were compared. *L. juncta* did not show preference for neighborhoods based on sizes (Fig. 4.5d). Altogether, these results suggest that *L. juncta* avoided neighborhood with *Solidago* but only when *Solidago* densities were high.

4.3 DISCUSSION

Neighborhood composition has long been recognized as an important predictor for plant performance (Silander and Pacala 1985), and neighborhood effects can be mediated by changes in herbivore damage. Decades of research, particularly in agriculture, have demonstrated that different neighborhoods can influence damage to plants and insect load (reviewed by Barbosa et al. 2009), yet little progress has been made to identify which components of the neighborhood influence damage and associated mechanisms (but see Karban 2007). If we are to understand the long-term consequences of damage for plant communities, we need to understand how these components (i.e., the density and frequency of plants) influence damage as these density- and frequency-dependent processes could have different long-term implications for communities. In this study, herbivore damage and insect load were positively affected by the frequency of *Solidago* and not through changes in plant densities, making neighbor effects truly associational. Because a response surface design was used, I was able to separate the effects of these two important components of the neighborhood on damage, a process that previous studies are not able to do.

4.3.1 Frequency-dependent mechanisms in damage

I defined neighbor effects as associational if damage or mechanisms known to generate damage were frequency dependent. In this study, all four mechanisms suspected to influence damage were affected by neighborhood composition; some mechanisms were affected by *Solidago* frequency, while others were affected by the total density or *Solidago* density alone (Table 1). The frequency of *Solidago* affected predator abundance and richness, soil moisture, and an herbivore’s foraging behavior. While any of these mechanisms could, in theory, lead to the frequency-dependent damage patterns observed on *Solanum*, some mechanisms (e.g. soil
moisture and foraging behavior) have stronger support over others (e.g. predators) in this system. I discuss each frequency-dependent mechanism below.

First, predator abundance increased with the frequency of *Solidago*. Many of the predators surveyed within the neighbors, such as green-lynx spider and stink bugs, used tall plants such as *Solidago* as perches for ambushing prey (T. Kim, pers obs). Predation pressure (herbivore to predator ratio), however, did not vary with the frequency of *Solidago*. So while the enemies’ hypothesis (Root 1973) suggests that damage may be low in certain neighborhood types because the presence of predators suppresses herbivore damage through consumptive or non-consumptive effects, the lack of variation in predation pressure in this study makes predators an unlikely mechanism for generating frequency-dependent damage in *Solanum*.

Second, the frequency of *Solidago* influenced the behavior of *L. juncta*, a specialist herbivore on *Solanum*. *L. juncta* selected *Solanum* plants in neighborhoods with proportionally less *Solidago*, suggesting that *Solanum* in these particular neighborhoods were more apparent that *Solanum* surrounded by a high frequency of *Solidago*. *Solidago* could mask *Solanum* visually (Strong et al. 1984, Wise et al. 2010b), or through scent (Schroeder and Hilker 2008). However, the negative effect of *Solidago* frequency on host-finding by *L. juncta* opposes the positive relationship between damage or insect load and the frequency of *Solidago* in the field. Most herbivores observed in the field experiment were generalists who were instead found in higher numbers in neighborhoods with a high frequency of *Solidago*. Some herbivores could select neighborhoods with proportionally more *Solidago* because they provided refuge (Orrock et al. 2010, Hughes 2012), or allow herbivores to complete their lifecycle (e.g. ovipositing on nearby plants in Agrawal 2004). Understanding exactly how *Solidago* influenced herbivores in the field would require further investigation, using a range of both specialized and generalized herbivores.

Lastly, soil moisture was also negatively affected by the frequency of *Solidago*. It is known that soil moisture can affect insect herbivores through changes in plant quality in some systems, for example reduced soil moisture can constrain the production of defenses (Yamawo et al. 2012). However, this indirect effect of moisture on damage likely did not operate in this study because I found no effect of *Solidago* frequency on resistance to *L. juncta*. Soil moisture also can directly influence herbivores by affecting pupation rates for insects that pupate in the soil (Edwards and Epp 1965, Lapointe and Shapiro 1999, Ellis et al. 2004). Many insects
surveyed in my experiments pupate in soil (e.g. beetles and grasshoppers) for between three weeks to three months (Chown and Nicolson 2004). Lower soil moisture in pools with high frequencies of *Solidago* could have positively influenced puation rates, thereby increasing herbivore abundance in the plots for herbivores with shorter pupal periods. Further work would be required to directly test this mechanism for multiple herbivore species.

### 4.3.2 Density-dependent mechanisms of damage

Other components of the neighborhood influenced mechanisms known to generate AE, such as variation in plant quality, light and temperature. In the greenhouse I found that plant quality was dependent on the density of plants within the neighborhood (irrespective to the identity of the plant) in particular *Solanum* resistance to *L. juncta* larvae decreased with increasing plant density. Although this negative relationship between plant quality and density is expected if competition for resources is high, I did not observe any relationship between damage and plant density in the field experiment, suggesting that changes in plant quality were not important in the field. This lack of effect in the field could be due to the fact that there were few *L. juncta* individuals in the field experiment, although they are often common on *Solanum* in adjacent areas. Herbivore species can vary in their responses to plant quality (Awmack and Leather 2002, T. Kim *unpublished data*), so *Solanum* resistance to *L. juncta* would not necessarily be expected to predict resistance to other herbivore species.

Light intensity and ambient temperature were affected by *Solidago* density. Both of these microclimate variables can influence damage and insect load directly through effects on feeding times and duration, or indirectly through plant quality (Chown and Nicolson 2004). Higher metabolic and development rates are typically associated with higher temperatures in insects (Irlich et al. 2009). Therefore, I predicted damage to be highest in *Solanum* monocultures because mean ambient temperatures were high. I observed the opposite pattern of higher damage in neighborhoods with slightly cooler temperatures (those with more *Solidago*). Compensation in damage may have occurred if plant quality had been affected by microclimate (Chown and Nicolson 2004) but because there was no significant *Solidago* density effect on plant quality in the plant resistance study above, it is unlikely that light intensity and ambient temperature alone are influencing damage in the field.
4.3.3 Long-term consequences of context-dependent herbivory

In this study, I found that some mechanisms known to generate damage were dependent on the density of plants while other mechanisms were associational (i.e. frequency dependent). I examined the relationships between each of these mechanisms and neighborhood composition separately but in nature, multiple mechanisms could be operating simultaneously and interact to influence damage and herbivore load damage. Host plant selection and subsequent damage by herbivores is a culmination of various, often hierarchical, mechanisms, therefore, it is possible that many (or all) of the mechanisms examined in this study influenced damage. To determine the relationship between damage and the various mechanisms known to generate damage model simulations can be performed. Because the relationships between the various damage mechanisms and neighborhood composition (i.e. plant densities and frequencies) are known, predictions about which neighborhoods are more or less vulnerable to damage can be made, and the relative importance of each of the damage mechanisms evaluated. Furthermore, models can be used to predict how damage in turn influences plant competition and coexistence. In a previous study (Kim et al. in review), I found that competition between Solanum and Solidago was asymmetric with Solidago populations quickly outcompeting Solanum with time. In this same study, I observed a hump-shaped relationship between the frequency of Solidago and Solanum damage (Kim and Underwood, in prep); Solanum in monocultures and high Solidago frequency neighborhoods suffered less damage than plants in neighborhoods with intermediate frequencies of Solidago. This would suggest that as competition proceeds and as neighborhoods become more occupied by Solidago, damage to Solanum would increase. However as neighborhoods become overrun by Solidago, Solanum could escape herbivory, which could allow Solanum to persist. In this current study, herbivore pressure on Solanum increased with the frequency of Solidago. This positive relationship suggests that as competition proceeds, damage to Solanum increase which could feedback to accelerate competitive exclusion of Solanum by Solidago. Variation in damage patterns with Solidago frequency could explain why some Solidago fields are completely void of other plant species, while other fields have some individuals persisting in the understory.

Distinguishing context-dependent herbivory as frequency- or density-dependent has important implications for both applied and basic ecology. From an applied perspective, insect pest management in agriculture or forestry requires correct planting strategies to minimize insect
load, damage, and insect spread. If damage was truly dependent on the density of the focal plant alone, then planting non-target plants to minimize damage would be unnecessary. However, if damage was indeed frequency-dependent, then considering the density of non-targets would be an essential component of pest management as well. From a basic ecology perspective, understanding the long-term consequences of damage for plant communities would require knowing how damage varies with plant density and frequency. Because damage can arise via frequency- and density- dependent mechanisms, the long-term outcome of these different mechanisms can yield different results. Furthermore, if neighborhood composition affects AE and its associated mechanisms, then the strength of AE and the importance of AE mechanisms may shift during plant competition as plant densities and frequencies change. Therefore, understanding how AE changes with the neighborhood composition is critical for evaluating dynamic feedbacks between herbivores and plants. Ignoring these feedbacks can lead to conflicting interpretations of the importance of herbivore effects on plant population and community dynamics.
Figure 4.1: Response surface designs for three experiments. Densities of *Solanum* and *Solidago* for field experiment (small black, filled circles) and herbivore foraging experiment (black, open circles). Values represent the number of plants per 91.4 cm diameter kiddie pools. Grey, filled circles represent equivalent densities of *Solanum* and *Solidago* for constitutive and induced resistance experiments in smaller pot sizes (45.7 cm diameter).
Figure 4.2: Percent leaf damage of *Solanum* and *Solidago*. Thick horizontal lines indicate medians and whiskers encompass 1.5 times the interquartile range from the boxes. Leaf damage was averaged for plants in each 1m² quadrat. Asterisks indicate significant differences (P < 0.05) between species (*t*= 4.738 df= 1, 88, *P* < 0.001).
Figure 4.3: The effect of *Solidago* frequency on *Solanum* leaf damage. Damage data were square-root transformed for analyses but untransformed data shown here. Black line represents line of best fit. Open black circles represent mean damage in neighborhoods with only one *Solanum*. $R^2 = 0.48$, $F = 46.56$, df = 1,49, $P < 0.001$. 
Figure 4.4: Effects of neighborhood composition on induced resistance measured using the relative growth rates of *Leptinotarsa juncta* beetle larvae. $R^2 = 0.33$, $F = 3.72$, df = 7,20, $P = 0.027$. A significant plant genotype by density interaction was observed ($F = 4.312$, df = 3,20, $P = 0.016$).
Figure 4.5: Preference of adult *Leptinotarsa juncta* beetles for different neighborhood types. X-axes are comparisons between paired neighborhoods represented as neighborhood “1” vs neighborhood “2”. Neighborhood composition represented as X, Y coordinates in response surface (X = density of *Solanum*, Y = density of *Solidago*, Table 1). Y-axes are preference for a neighborhood type after 10 trials. Grey bars represent neighborhood “1”; white bars represent neighborhood “2”. Panels A and B show neighborhood comparisons where total densities are fixed at four or sixteen individuals, respectively, but varied in the frequency of *Solanum* and *Solidago* (substitutive comparisons). Panel C shows neighborhood comparisons where the density of *Solanum* is fixed but densities of *Solidago* varied (additive comparison). Panel D shows monocultures of *Solanum*, but plant densities (or neighborhood size) varied. Dashed lines represent random selection. Asterisks indicate significant differences from random selection at P=0.057 ($X^2 = 3.6$; d.f. = 1).
Table 4.1. Summary of neighborhood effects on mechanisms suspected to generate associational effects.

<table>
<thead>
<tr>
<th>AE Mechanisms</th>
<th>Neighborhood matters?</th>
<th>If so, dependent on…</th>
<th>Density (total, (Solanum, or Solidago))</th>
<th>Frequency of (Solidago) (i.e. an associational effect)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Predator community</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abundance</td>
<td>Yes</td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td>Richness</td>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Microclimate</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil moisture content</td>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Light intensity</td>
<td>Yes</td>
<td></td>
<td></td>
<td>Solidago</td>
</tr>
<tr>
<td>Ambient temperature</td>
<td>Yes</td>
<td></td>
<td></td>
<td>Solidago</td>
</tr>
<tr>
<td><strong>Plant resistance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constitutive</td>
<td>No</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Induced</td>
<td>Yes</td>
<td></td>
<td></td>
<td>Total</td>
</tr>
<tr>
<td><strong>Herbivore foraging strategy</strong></td>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
CHAPTER FIVE

LATITUDINAL VARIATION IN PLANT DAMAGE AND PALATABILITY OF TWO OLD-FIELD PLANT SPECIES

A longstanding theory in biogeography is that species interactions, including herbivory, competition and predation, are stronger in southern latitudes compared to those in the north (reviewed by Schemske et al. 2009). Latitudinal gradients in herbivory were first evaluated in two influential review papers (Coley and Aide 1991, Coley and Barone 1996) where authors reported higher leaf damage in broad-leaved tropical plants compared to plants in temperate regions (10% versus 7% damage, respectively). The latitudinal gradients (LG) hypothesis predicts that because herbivore abundances and diet specialization are generally greater in the tropics, then the diversity and levels of plant defenses (both physical and chemical) should be higher in the tropics as well. Since the publication of these seminal papers, several experimental studies have evaluated the existence of LG in herbivory and plant defenses in a number of different habitats. In a meta-analysis (Moles et al. 2011a) only 14 of 38 studies found higher herbivory in lower latitudes (e.g., salt marshes in North America and Europe, Pennings et al. 2001, Pennings et al. 2007), but in many other systems, no pattern (e.g., Acacia shrubs in Eucalpt forests in Australia, Andrew and Hughes 2005), or the reverse patterns were observed (e.g., hardwood trees in North American forests, Adams and Zhang 2009). In a recent, global study by Moles et al. (2011b), researchers from 14 countries surveyed plants across various systems (including rainforests, deserts, tundra, savanna, and temperate forests) using standardized protocols and phylogenetic contrasts to determine whether latitudinal patterns exist in 14 plant traits known to confer resistance. For only six of the 14 traits measured, low-latitude species had higher levels than high-latitude species; six traits showed no relationship with latitude and two traits had negative relationships. Two decades following the publications of Coley and Aide (1991) and Coley and Barone (1996), support for this once widely accepted pattern in herbivory and plant defenses is waning and now considered limited to only some habitat types (e.g. salt marshes) and some plant traits. There is now a call to move away from further describing LG in herbivory and plant defenses to re-evaluating why we should expect LG in plant defenses and
herbivory to exist by examining the evolutionary processes thought to cause latitudinal patterns (Johnson and Rasmann 2011).

One way to re-examine whether LG should exist is to consider the role of herbivores. The LG hypothesis suggests that differences in plant defenses should arise from differences in herbivore abundances but few LG studies actually measure herbivore abundance while measuring damage and plant defenses. It is often assumed that herbivore abundance in southern latitudes is higher than in northern latitudes but if no relationship exists, then a lack of LG herbivory and plant defenses would not be surprising. Additionally, if we want to examine variation in selection pressures, then we need to understand at how variation in plant traits influences herbivore performance. Traits thought to confer resistance to herbivores (putative traits) are typically measured on plants, but not all these putative traits actually confer resistance (or do so equally) to herbivores (Carmona et al. 2011). For traits that do confer resistance, herbivore species are known to respond differently to each of those traits (Agrawal 2000), making it difficult to assess the effectiveness of those traits in reducing overall damage. Therefore, if different locations have different suites of herbivores with some plant traits effective at reducing damage from some herbivores over other traits, then our expectation for observing LG in herbivory is not straight-forward and simple as previously thought.

Those few studies that have looked for change in herbivore responses across latitude have focused on measuring behavioral responses such as the amount of plant material consumed or herbivore preference (Hay et al. 1994, Swihart et al. 1994, Pennings et al. 2001). The amount consumed, however, does not scale linearly to changes in herbivore performance. For example, compensation in feeding is common where herbivores feed more on low quality plants to overcome nutrient deficiencies, change the biochemical content in their guts, and not all consumed material becomes integrated into insect biomass (Jongsma and Bolter 1997, Chown and Nicolson 2004). Additionally, some plant defenses may have delayed effects such as digestibility reducers (e.g. tannins and proteinase inhibitors) which may not immediately influence the amount of plant material consumed, but can reduce the amount of nutrients absorbed by herbivores, possibly delaying herbivore growth and increasing susceptibility to predation (Coley and Barone 1996). Therefore consumption rates may not be a reliable indicator for herbivore performance. Similarly, herbivore preference may also be a poor indicator for performance. Preference for one plant option does not necessarily mean the other plant option is
poor quality food, or that the chosen plant will lead to higher performance. Instead bioassays using the relative growth rates of the herbivores should be used to determine how plants influence herbivore performance (Underwood et al. 2002). Measuring plant traits alone (as in previous studies) does not allow us to understand the ecological and evolutionary consequences of those traits for herbivores, especially if different traits may interact to influence herbivory.

In this study, I examined the relationship between latitude and herbivore abundance, plant nutrient content, and performance of herbivores feeding on two common old-field plant species (*Solanum carolinense* and *Solidago altissima*) spanning a broad geographic range (> 12 degree). Specifically, I asked (1) is there a LG in herbivore pressure (insect abundance)? (2) is there a LG in leaf damage? (3) do leaf nutrient content and herbivore performance vary with latitude? Because herbivores can respond differently to various cocktails of plant defenses, I assessed herbivore performance for both generalist and specialist herbivores known to feed on *Solanum* and *Solidago* to get a general overview of LG in herbivore responses.

### 5.1 METHODS

#### 5.1.1 Field survey

In 2008, 18 old-fields were surveyed at six latitudinal locations ranging from Florida to New York (> 12 degrees in latitude, Fig. 5.1). At each location, three early successional fields were chosen to survey (<5 years post disturbance). Field sizes were at least 50m x 50m in area, and separated by 2km. At each site, the local abundance of *Solanum* and *Solidago* were recorded using two 50m x 1m belt transects, separated by 20m. For twenty randomly selected *Solanum* and *Solidago* plants within transects, leaf damage (percent area removed) on all leaves was measured. I characterized the herbivore community in each field (as opposed to only those on my focal plants) by sweep-netting across the entire length of both belt transects. Field surveys were done between late July and early August which corresponds to the middle of the growing season (peak herbivore activity and plant growth) at each latitudinal location. Surveys started in Florida, ended in New York, and were completed within a two week period.
5.1.2 Plant quality

To measure plant quality, five surveyed plants were collected from the field and returned to Florida State University (Tallahassee, FL 30.43° N, 84.28° W) where nutritional content and effects on herbivore performance were measured. Plants were oven-dried for 1 week at 60 degrees Celsius after which dried plants were ground to a fine powder using a mortar and pestle. Plant powder was stored in a freezer at -18C degrees. Nutrient content, total percent nitrogen and carbon to nitrogen ratio were assessed using a CHN elemental analyzer at the National High Magnetic Field Laboratory (Tallahassee, FL).

To examine herbivore performance, no-choice bioassays were performed in the lab using specialist and generalist insects known to feed on *Solanum* and *Solidago*. I used plant powder from plants collected from each site to make a standard insect diet, by reconstituting powder into an agar mixture, following a protocol by Pennings et al. (2007). The diet consisted of 0.5g of plant powder and 10ml of agar solution (1%). Because a large amount of plant material was required for the diet, plant material from all individuals of each plant species at each field was combined. Therefore the performance of herbivores on *Solanum* and *Solidago* diets were assessed at the field level, and not the individual plant level. Generalist herbivores (American grasshopper (*Schistocerca americana*) and beet army worm (*Spodoptera exigua*)) were tested on *Solanum* and *Solidago* diets separately. Specialist herbivores were tested only on their respective host plants (false-potato beetle (*Leptinotarsa juncta*), and tobacco hornworm (*Manduca sexta*) tested on *Solanum* diet, Goldenrod beetle, (*Trirhabda virgata*) on *Solidago*). A control diet consisting of only agar and water was used to determine how agar influenced herbivore growth. Grasshoppers were obtained from a laboratory colony at the University of Florida (J. Capinera) and raised on lettuce and barley. Both caterpillar species were obtained from insect rearing facilities (Benzon Research for *Spodoptera* and Carolina Biological Supplies for *Manduca*) and fed on arterial diets (Southland Products Inc). *Leptinotarsa* were obtained from a laboratory colony at Florida State University (N. Underwood), and raised on *Solanum* foliage from plants collected in north FL. One month prior to the bioassays, beetles were fed live plants collected from the different latitudes and grown in the greenhouse to avoid bias. *Trirhabda* beetles were obtained from various fields in NY and VA. Adults were fed plants from various locations to avoid bias as well.
Performances of most herbivores (except the *Trirhabda* beetle) were assessed by the relative growth rates (RGR) of insect larvae. Seven to ten larvae of each insect species were used for the bioassays and were fed either *Solanum* or *Solidago* diet from each site. Prior to the start of the bioassays, larvae were starved for 3 hours to remove food content in their digestive tracts and each larva was weighed separately. Standardized pieces of diet (4cm³) were offered to each larva in 75-150 ml soufflé cups lined with moist filter paper. Herbivores fed on the diet for 3 days. After three days of feeding, the diet was removed, and the larvae starved for an additional 3 hours and weighed. The relative growth rates of larvae were determined as the ln (final mass of herbivores / initial mass of herbivores). To account for agar effects which varied amongst herbivores, the final RGR for each herbivore was calculated as the RGR (diet) – mean RGR (agar). For *Trirhabda* feeding on *Solidago* diet, adult females were used because larvae were not available. Because the growth rate of adult insects varies little, I characterized performance as the number of eggs laid per clutch after feeding on diet for 3 days.

5.1.3 Statistics
The experimental unit was each field so damage in the field, nutrient content, and bioassay results were averaged across individuals at each field for each plant species. Even though sampling was done at a similar time in the season at all sites, response variables were also standardized by dividing by growing degree days because the longevity of leaves could influence damage and nutrient content, thus confounding leaf age with latitude (Coley and Barone 1996). Degree days were calculated as the number of days between the start of the growing seasons and the time of survey (in July/Aug). The start of the growing season was defined as the week where mean temperature was greater than 21 degrees Celsius (NOAA National Climatic Data Center http://www.ncdc.noaa.gov/cdo-web/search). By standardizing damage and nutrient content by the growing degree days, I was able to assess the amount of damage incurred and nutrient content produced per day (hereafter referred to as “standardized damage and nutrient content”). The cumulative amount of damage and nutrient content were those measured at the time of the surveys.

Because not all herbivores were available at the same time and the large number of total bioassays to be performed, bioassays were carried out in 5 temporal blocks. In four of the blocks, bioassays using *Leptinotarsa, Manduca, Spodoptera*, and *Schistocerca* were done

56
between February-June 2009. Bioassays using *Trirhabda* adults were performed in the final temporal block in September 2011. Due to the availability of insects, bioassays for only four of the six latitudinal locations were performed using grasshoppers for both *Solanum* and *Solidago*. Also, only three of the six locations were used for bioassays using *Trirhabda*. A total of 870 bioassays were performed (180 *Leptinotarsa*, 180 *Manduca*, 252 *Spodoptera*, 168 *Schistocerca* and 90 *Trirhabda*).

I conducted a series of GLMs in R 2.12 (R Development Core Team 2010) to examine relationships between latitude and the abundance of herbivores, plant damage, nutrient content (percent N and C:N), and the RGRs of each herbivore species. For GLMs examining latitudinal relationships with plant damage and herbivore abundance, plant abundance was included into the model as a covariate. For GLMs examining latitudinal relationships with RGRs of herbivores, temporal blocks were initially included as a fixed effect but was later dropped because they were not significant. The RGRs for each herbivore species from all temporal blocks were pooled and average per field. Some of the relationships with latitude appeared non-linear; therefore I included a quadratic latitude term into the model. An AIC based stepwise elimination process was used to select the best model.

### 5.2 RESULTS

#### 5.2.1 Damage
In general, *Solanum* received greater leaf damage (15.0%) than *Solidago* (7.1%, t = -4.078, df = 31, P < 0.001). A positive, nonlinear relationship was observed between latitude and cumulative (F$_{5,12}$ = 6.057, P = 0.005) and standardized (F$_{1,16}$ = 15.29, P = 0.001) *Solidago* damage; plants at lower latitudes had less damage than plants at higher latitudes (Fig. 5.2). A negative relationship with latitude was observed for cumulative damage to *Solanum* (F$_{1,16}$ = 6.832, P = 0.01), much of which was attributed to *Solanum* plants in NY that experienced very little damage. However, when damage was standardizing by growing degree days, that relationship disappeared and damage was consistent across latitude (F$_{1,16}$ = 0.042, P = 0.83).
5.2.2 Insect herbivore communities

Herbivores were largely composed of Hemipterans (77% of the abundance of herbivores). The abundance and richness of herbivores did not vary with latitude ($F_{3,14} = 1.12, P = 0.37; F_{3,14} = 2.986, P = 0.06$, respectively). However, the abundance of foliar-feeding insects varied positively with latitude ($F_{3,14} = 3.621, P = 0.04$); most of this pattern was driven by Coleoptera abundances (67% of leaf-feeding herbivores) with certain species becoming very abundant at higher latitudes (e.g. *Trirhabda virgata* and *Microrhapala vittata*). Latitude had positive but marginal effects on foliar-feeding insect species richness ($F_{2,15} = 3.13, P = 0.07$).

5.2.3 Nutrient content

*Solanum* contained higher percent nitrogen (mean 2.7%) than *Solidago* (mean 1.7%, $t = -8.17, df = 31, P < 0.001$). A negative relationship with latitude was observed for cumulative N in *Solidago* ($F_{1,16} = 4.5, P = 0.049$) and a marginally significant negative relationship for *Solanum* ($F_{1,16} = 3.11, P = 0.09$, Fig. 5.3). When standardized to growing degree days, positive relationships were observed with latitude for both *Solidago* ($F_{1,16} = 23.23, P < 0.001$) and *Solanum* ($F_{1,16} = 8.19, P < 0.001$). Positive C:N relationships were observed for both *Solanum* and *Solidago* for cumulative ($F_{1,16} = 3.94, P = 0.06, F_{1,16} = 7.148, P = 0.01$;) and standard C:N ($F_{1,16} = 24.69, P < 0.001; F_{1,16} = 21.56, P < 0.001$), indicating that northern latitude plants were less nutritious than southern plants. *Solidago* had a higher C:N than *Solanum* (25.6 and 17.1, respectively) suggesting that *Solidago* was a lower quality plant than *Solanum* for generalist herbivores.

5.2.4 Bioassays

Across all bioassays, generalist herbivores lost weight whereas specialists gained weight, suggesting that the specialists were better able to meet their needs on diet than generalists. Nevertheless, there was variation in performance among diets from different locations for some specialists and generalists. For *Solanum* specialists (Fig. 5.4), there was no relationship between latitude and the RGR of *Leptinotarsa*, ($F_{1,16} = 0.042, P = 0.839$) but a concave relationship with *Manduca* ($F_{2,16} = 3.775, P = 0.047$). For generalists feeding on *Solanum*, there was no relationship between latitude and the RGR of *Schistocerca* ($F_{1,16} = 0.49, P = 0.49$) but a convex relationship with latitude for *Spodoptera* ($F_{2,15} = 5.49, P = 0.01$). *Spodoptera* feeding on
northern and southern latitude plants had higher RGRs than those feeding on *Solanum* plants at mid-latitudes.

For generalist herbivores feeding on *Solidago* (Fig. 5), as on *Solanum* a convex relationship was observed with latitude for *Spodoptera* ($F_{2,15} = 5.892, P = 0.010$) but unlike *Solanum*, a positive relationship was observed between the RGR of *Schistocerca* and latitude ($F_{2,9} = 15.12, P = 0.001$), indicating that northern *Solidago* plants were more palatable to *Schistocerca*. For the specialist leaf feeding beetle, *Trirhabda*, a negative relationship was observed between the numbers eggs per clutch and latitude ($F_{1,7} = 6.577, P = 0.03$).

5.3 DISCUSSION

Latitudinal gradients in species interactions have long interested ecologists (Schemske et al. 2009), but recent studies in plant-herbivore systems have questioned the generality of LG in herbivory and plant defenses (Johnson and Rasmann 2011, Moles et al. 2011a, Moles et al. 2011b). Focus has now shifted to understanding why most recent empirical studies appear to contradict earlier observational studies and to re-evaluating our expectations for why LG in plant defenses and damage should exist (Johnson and Rasmann 2011). One area of research lacking data is our understanding of latitudinal variation in herbivore responses to plant traits. Previous studies have largely ignored variation in herbivore abundances across latitudinal gradients and how herbivore performance varies with plant traits. If relationships between herbivore abundances or performance exist then this may explain why some LG patterns in defenses and herbivory occur in some systems, while in others they do not. In this study, I examined how damage, herbivore load, and herbivore performance varied across a broad geographic range in old-field habitat.

I found that some aspects of my system matched the LG hypothesis and others did not. Damage, in general, did not vary with latitude but when plant species were examined separately, *Solanum* had the expected negative relationship with latitude while *Solidago* had the opposite relationship. Northern latitudes had a higher abundance and richness of foliar feeding insects (the opposite prediction of the LG hypothesis) and these differences in herbivore community composition could be responsible for LG in herbivore damage. A LG in nutrient content was also observed where higher latitude plants were less nutritious (i.e., higher C:N) than low latitude...
plants (expected direction according to LG hypothesis) but once differences in plant age (growing degree days) were accounted for, latitudinal patterns disappeared. In general, the performance of herbivores did not vary with latitude, but once herbivores were examined separately, some relationships were linear (positive and negative), some were non-linear and some showed no pattern with latitude. If latitudinal variation in herbivore communities and variation in responses by different herbivores is common in other systems, then the lack of a LG in herbivory and plant defenses is not surprising. These results reinforce the idea that the relationship between the expression of plant traits, herbivore responses, and the amount of damage is not as simple and straightforward as previously thought.

5.3.1 Herbivore responses are complex
In a recent study conducted across a broad geographic range (Moles et al. 2011b), latitudinal gradients in only six of 14 measured putative resistance traits were observed. Other studies preceding this large-scale study found similar patterns (e.g., Andrew and Hughes 2005, Adams et al. 2009), raising doubt about the generality of the LG hypothesis. Before completely rejecting the LG hypothesis, looking solely at plant traits can be misleading because some measured traits may not actually deter herbivores, some traits may interact to influence damage, and some traits (e.g. total tannins and total phenolics) are measured at too coarse a resolution to be meaningful.

It is widely known that herbivore responses to plants are complex, depending on diet specialization, taxa, and different plants traits (Bernays and Graham 1988, Hay et al. 1994, Barbosa 1998). In this study, I found that relationships with latitude varied with diet specialization where generalists lost mass while feeding on Solanum and Solidago whereas specialists gained weight. The exact relationship with latitude varied with herbivores species. Some herbivores exhibited non-linear relationships with latitude (Spodoptera and Manduca) whereas other had positive (Schistocerca), negative (Trirhabda) or no relationship (Leptinotarsa). Variation in growth rates may have occurred because herbivores respond to various compounds in plants differently (Barbosa 1998, Pennings et al. 1998). Generalists are typically more sensitive to plant defenses whereas as specialists are better able to tolerate chemical defenses in plants (Karban and Agrawal 2002). Specialists can also vary in their responses to compounds in host plants. For example, proteinase inhibitors (PI) are considered general defenses against herbivore by slowing digestion, however different herbivores respond...
differently to the various forms of PI. Lepidoptera larvae, for example, are known to be more sensitive to trysin proteinase inhibitors (PI) whereas Coleoptera larvae are known to be more sensitive to cysteine PI (Michaud et al. 1995, Zavala et al. 2004). Plant defenses can also have synergistic effects. *Spodoptera exigua* is known to perform extremely poorly on plants with both trypsin PI and nicotine, but is able to compensate when feeding on plants expressing only one of these two chemical compounds (Steppuhn and Baldwin 2007). Because herbivore responses to plant defenses are complex, relying on many interacting factors, is it unclear how we should expect plant defense traits to vary with latitude.

### 5.3.2 Incorporating plant and herbivore phenology

In this study, I found that standardizing leaf age did affect relationships with latitude. Relationships which were once significant including *Solanum* damage and nutrient content became non-significant once plant age was accounted for, whereas other relationships (e.g., *Solidago* damage) become more significant. These results suggest that plant age may be important in our understanding and interpretation of LG in herbivory. One of the earlier messages by Coley and Aide (1991) and Coley and Barone (1996) was that leaf age or longevity should be accounted for when comparing levels of and variation in plant defenses. Because southern plants live longer than northern plants, it has been thought that southern leaves/plants are more apparent (*sensu* Feeny 1976) to herbivores and therefore selection for plant defenses should be stronger in the tropics than in temperate areas. In order to determine whether differences in damage are due purely due to plant age or due to variation in selection pressures, experiments teasing those two components apart are needed. Alternatively, sampling herbivores and plants across multiple points in the growing season (rather than single snapshots) may yield a better understanding of how differences plant and herbivore phenologies influence LG in herbivory and plant defenses.

### 5.3.3 Previous studies

One of the best studied systems of LG in herbivory and plant defenses comes from salt marsh systems. In this system, both observational and experimental studies have been performed, including common garden and reciprocal transplant experiments (Salgado and Pennings 2005, Pennings et al. 2009) and studies examining herbivore responses to variation in plant traits.
(Pennings et al. 2001, Ho et al. 2010). This system exhibits the predicted patterns of LG in damage and plant defenses and similar investment in other broad-ranging systems where LG patterns in herbivory and defenses do not exist (e.g. old field systems) should be performed. Some authors suggest that because salt marshes are homogeneous across a broad range in latitude and support simple trophic communities influenced by both top-down and bottom-up population regulation, this somehow encourages stronger selection for plant defenses in lower latitudes (Johnson and Rasmann 2011). Comparative studies would allow us to better understand why LG patterns are observed in some systems while in others, they do not.

5.3.4 Conclusions
In this study, I demonstrated that the latitudinal relationships in damage, plant nutrient content, herbivore abundance, and herbivore performance are complex, depending on leaf longevity, plant species, diet specialization, and herbivore species. Previous studies examining LG in herbivory or plant defenses have largely ignored variation in herbivore responses to plants, even though this information may be needed to better understand latitudinal variation in selection pressures on plants. To determine why LG in herbivory and plant defenses occur in some areas while in other they do not, a more thorough investigation of relationships between herbivore abundance, damage, and plant resistance is needed and how these relationships should vary with latitudes. Phylogenetically controlled comparative studies, more comprehensive analyses of plant resistance including tolerance, induced resistance and indirect defenses (e.g. predators), considering the role of environmental variation (e.g. resource availability), and examining the population-level responses of herbivores to variation in plant traits are promising areas of future research.
Figure 5.1: Locations of latitudinal surveys. Six latitudes were used for surveys including areas in and around Tallahassee, FL; Rome, GA; Oak Ridge, TN; Dublin, VA; Boyce, VA; and Ithaca, NY (bottom to top). Three sites per location were surveyed yielding 18 old-fields.
Figure 5.2: Latitudinal gradients in herbivory (% leaf damage) for *Solanum* (grey) and *Solidago* (black). A. Cumulative damage (damage assessed during time of survey) and B. standardized damage (damage standardized by growing degree days). Lines represent best fit lines from models.
Figure 5.3: Relationships between latitude and percent nutrient (cumulative and standardized, A,B respectively) and carbon to nitrogen ratios (cumulative and standardized, C,D, respectively)) for Solanum (grey) and Solidago (black). Solid lines represent best fit lines from models.
Figure 5.4: Relationships between latitude and the relative growth rates of Solanum specialists (*Manduca sexta*, *Leptinotarsa juncta*) and generalists (*Spodoptera exigua* and *Schistocerca americana*) feeding on Solanum diet.
Figure 5.5: Relationships between latitude and (A) the number of eggs per clutch for a *Solidago* specialist (*Trirhabda virgata*) (B) the relative growth rates of generalists *Spodoptera exigua* and (C) *Schistocerca americana*) feeding on *Solidago* diet.
CHAPTER SIX
CONCLUSION

Feedbacks or reciprocal interactions are an integral part of most ecological systems yet experimental studies examining plant-herbivore interactions often focus on unidirectional effects. Incorporating reciprocal effects of interactions can have important outcomes for communities. In this dissertation, I examined reciprocal interactions between two plant species, *Solanum carolinense* and *Solidago altissima* and their insect herbivores.

In chapter 2, I examined how herbivore influenced plant communities. Theory suggests that herbivores influence plants through changes in their competitive interaction, yet previous experimental studies focused on changes to per-capita competition, ignoring herbivore effects on demographic processes. By fitting competition models to experimental data, I found that herbivores influenced plants through both per-capita competition and changes in their intrinsic growth rates, which could have long-term consequences for coexistence.

In chapter 3, I examined how neighborhood composition (i.e. density and frequency of plants) influenced damage to *Solanum*. I found that the magnitude of herbivore damage to *Solanum* was a function of plant neighborhood composition, specifically a hump-shaped relationship between damage and the frequency of *Solidago* in the neighborhood was observed. As succession proceeds and as neighborhoods become dominated by *Solidago*, herbivore damage could feedback to influence *Solanum* abundance, accelerating rates of competitive exclusion.

In chapter 4, I examined how neighborhood composition influenced four mechanisms known to influence damage (predator abundance, herbivore foraging behavior, plant resistance, and microclimate). Some mechanisms (e.g. predator abundance, foraging behavior) were influenced by the frequency of *Solidago* while others (e.g. plant resistance, microclimate) were influenced by the total density or density of *Solidago*. These mechanisms could interact to influence damage.

In chapter 5, I investigated how interactions between plants and insect herbivores varied in across a broad latitudinal range. Theory suggests that plants in low latitudes should experience more damage and higher plant defenses than plants in high latitudes, because herbivore abundances (and selection pressures) are typically higher at low latitudes. I examined
how herbivore abundance, damage to *Solanum* and *Solidago*, and plant nutrient content varied with latitude. I also examined relationships between latitude and the performance of generalist and specialist herbivores. I found latitudinal relationships for most measured variables but the exact relationship was complex depending on leaf longevity, plant species, diet specialization, and herbivore species.

To understand community-level consequences of plant-herbivore interactions, we need to examine reciprocal interactions between plants and herbivores. This dissertation took an important first step in examining plant herbivore interactions from both perspectives, and characterized how plant density and frequency influences herbivory and plant competition. This information can be used to construct a more detailed mechanistic model describing the dynamic nature of plant-herbivore interactions to examine importance of herbivory in structuring plant communities.
Response surface experimental design with varying densities of *Solanum* and *Solidago* in 1m$^2$ quadrats. A total of 17 density combinations were used.
APPENDIX B

CHAPTER 2: Detailed description of statistical methods and ANOVA tables

To test the effects of spray treatment on plant damage and compare between *Solanum* and *Solidago*, we performed a type III ANOVA using SAS PROC GLM (SAS Institute 2010). Plant damage (response variable) was log-transformed to meet the assumptions of ANOVA. Spray treatment, plant species, and their interactions were fixed factors. Error df = 148. Data from 2007 used only.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Type III SS</th>
<th>Mean Square</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant species</td>
<td>1</td>
<td>16712.52</td>
<td>16712.52</td>
<td>252.40</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Spray treatment</td>
<td>1</td>
<td>7086.51</td>
<td>7086.51</td>
<td>107.02</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Plant species* Spray treatment</td>
<td>1</td>
<td>1314.95</td>
<td>1314.95</td>
<td>19.86</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

To test the effects of spray treatment on plant biomass and compare between *Solanum* and *Solidago*, we performed a type III ANOVA using SAS PROC GLM (SAS Institute 2010). Spray treatment, plant species, and their interactions were fixed factors. Error df = 152. Data from 2007 used only.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Type III SS</th>
<th>Mean Square</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant species</td>
<td>1</td>
<td>172440815.6</td>
<td>172440815.6</td>
<td>51.37</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Spray treatment</td>
<td>1</td>
<td>30538272.6</td>
<td>30538272.6</td>
<td>9.10</td>
<td>0.0030</td>
</tr>
<tr>
<td>Plant species * Spray treatment</td>
<td>1</td>
<td>540790.8</td>
<td>540790.8</td>
<td>0.16</td>
<td>0.6887</td>
</tr>
</tbody>
</table>
APPENDIX B (continued)

To test the effects of spray treatment, initial hetero- and conspecific planting density, and year on current plant density, I performed a repeated-measures ANOVA using SAS PROC MIXED (SAS Institute 2010). Spray treatment, initial heterospecific planting density, initial conspecific planting density, and their interactions were fixed factors. Year was a random effect. Three- and four-way interactions between year and predictors were never significant and dropped from the models. Analyses performed separately for Solanum (A) and Solidago (B).

A. Solanum

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>3</td>
<td>222</td>
<td>5.55</td>
<td>0.0011</td>
</tr>
<tr>
<td>Spray treatment</td>
<td>1</td>
<td>71</td>
<td>1.14</td>
<td>0.2884</td>
</tr>
<tr>
<td>Conspecific</td>
<td>1</td>
<td>71</td>
<td>115.65</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Heterospecific</td>
<td>1</td>
<td>71</td>
<td>0.00</td>
<td>0.9958</td>
</tr>
<tr>
<td>Year * spray treatment</td>
<td>3</td>
<td>222</td>
<td>1.05</td>
<td>0.3716</td>
</tr>
<tr>
<td>Conspecific * Year</td>
<td>3</td>
<td>222</td>
<td>20.76</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Heterospecific * Year</td>
<td>3</td>
<td>222</td>
<td>5.03</td>
<td>0.0022</td>
</tr>
<tr>
<td>Conspecific * spray</td>
<td>1</td>
<td>71</td>
<td>1.14</td>
<td>0.2887</td>
</tr>
<tr>
<td>Heterospecific * spray</td>
<td>1</td>
<td>71</td>
<td>0.16</td>
<td>0.6871</td>
</tr>
<tr>
<td>Heterospecific * Conspecific</td>
<td>1</td>
<td>71</td>
<td>2.69</td>
<td>0.1051</td>
</tr>
</tbody>
</table>

B. Solidago

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>3</td>
<td>222</td>
<td>24.69</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Spray treatment</td>
<td>1</td>
<td>71</td>
<td>0.08</td>
<td>0.7741</td>
</tr>
<tr>
<td>Heterospecific</td>
<td>1</td>
<td>71</td>
<td>0.33</td>
<td>0.5678</td>
</tr>
<tr>
<td>Conspecific</td>
<td>1</td>
<td>71</td>
<td>122.80</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Year * spray treatment</td>
<td>3</td>
<td>222</td>
<td>9.24</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Heterospecific * Year</td>
<td>3</td>
<td>222</td>
<td>5.45</td>
<td>0.0012</td>
</tr>
<tr>
<td>Conspecific * Year</td>
<td>3</td>
<td>222</td>
<td>42.24</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Heterospecific * spray</td>
<td>1</td>
<td>71</td>
<td>0.60</td>
<td>0.4428</td>
</tr>
<tr>
<td>Conspecific * spray</td>
<td>1</td>
<td>71</td>
<td>5.10</td>
<td>0.0271</td>
</tr>
<tr>
<td>Heterospecific * Conspecific</td>
<td>1</td>
<td>71</td>
<td>2.44</td>
<td>0.1224</td>
</tr>
</tbody>
</table>
APPENDIX B (continued)

To test the effects of the total initial planting density (low or high) and proportion of heterospecific neighbors (0 to 1) on current plant density, I performed a repeated-measures ANOVA using SAS PROC MIXED (SAS Institute 2010). Initial planting density and proportion of heterospecific neighbors, and their interactions were fixed factors. Year was a random effect. Three-way interactions between predictors were never significant and dropped from the models. Analyses performed separately for Solanum (A) and Solidago (B).

A. Solanum

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>2</td>
<td>90</td>
<td>10.35</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Planting density</td>
<td>1</td>
<td>44</td>
<td>66.64</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Proportion of heterospecifics</td>
<td>1</td>
<td>44</td>
<td>77.80</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Year * planting density</td>
<td>2</td>
<td>90</td>
<td>3.45</td>
<td>0.0359</td>
</tr>
<tr>
<td>Proportion of heterospecifics</td>
<td>1</td>
<td>44</td>
<td>21.86</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>* Planting density</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportion of heterospecifics</td>
<td>2</td>
<td>90</td>
<td>0.69</td>
<td>0.5044</td>
</tr>
<tr>
<td>* Year</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

B. Solidago

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>2</td>
<td>90</td>
<td>26.81</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Planting density</td>
<td>1</td>
<td>44</td>
<td>34.69</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Proportion of heterospecifics</td>
<td>1</td>
<td>44</td>
<td>12.79</td>
<td>0.0009</td>
</tr>
<tr>
<td>Year * planting density</td>
<td>2</td>
<td>90</td>
<td>9.32</td>
<td>0.0002</td>
</tr>
<tr>
<td>Proportion of heterospecifics</td>
<td>1</td>
<td>44</td>
<td>2.18</td>
<td>0.1473</td>
</tr>
<tr>
<td>* Planting density</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportion of heterospecifics</td>
<td>2</td>
<td>90</td>
<td>3.86</td>
<td>0.0247</td>
</tr>
<tr>
<td>* Year</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
APPENDIX C

CHAPTER 2: AIC weights (w) for five standard competition models

AIC weights (w) for five standard competition models using stem density recruitment data. Data from both sprayed and unsprayed treatments were pooled and recruitment data divided into three transition periods (2007-2008, 2008-2009, 2009-2010). Numbers in bold represent models with the highest support for each transition period. Mean weights across years were determined, and the models with the highest mean support are indicated with asterisks. These models were used for examining herbivore effects on model parameters (Table 1).

<table>
<thead>
<tr>
<th>Model</th>
<th>Basic form</th>
<th>Solanum (S)</th>
<th>Solidago (G)</th>
</tr>
</thead>
<tbody>
<tr>
<td>May (1974)</td>
<td>$X_{t+1} = X_t + X_t \lambda \frac{K - (X_t + \beta Y_t)}{K}$</td>
<td>0.17</td>
<td><strong>0.31</strong></td>
</tr>
<tr>
<td>Ricker (1954)</td>
<td>$X_{t+1} = X_t \lambda \exp(-c(X_t + \beta Y_t))$</td>
<td>0.22</td>
<td>0.30</td>
</tr>
<tr>
<td>Leslie (1958)</td>
<td>$X_{t+1} = \frac{X_t \lambda}{1 + (X_t + \beta Y_t)^b}$</td>
<td>0.08</td>
<td>0.04</td>
</tr>
<tr>
<td>Law and Watkinson (1987)</td>
<td>$X_{t+1} = \frac{X_t \lambda}{1 + c(X_t + \beta Y_t)}$</td>
<td><strong>0.33</strong></td>
<td>0.24</td>
</tr>
<tr>
<td>Hassell and Comins (1976)</td>
<td>$X_{t+1} = \frac{X_t \lambda}{1 + c(X_t + \beta Y_t)^b}$</td>
<td>0.21</td>
<td>0.11</td>
</tr>
</tbody>
</table>
APPENDIX D

CHAPTER 2: Recruitment data

Recruitment data for *Solanum* (right) and *Solidago* (left) in the absence (black) and presence (grey) of insect herbivores. Open symbols represent observed values. Filled symbols represent predicted values from the fit best models (Table 1) in (A) transition 1 (2007 – 2008); (B) transition 2 (2008-2009); and (C) transition 3 (2009-2010).
APPENDIX E

CHAPTER 2: Importance weights

Importance weights ($w^+$) of herbivore effects ($\gamma$) on $\lambda$, $\beta$, and $c$ using AICc weights ($w$) from the 16 candidate Law and Watkinson competition models (Table 1). Importance weights for Solanum (A) and Solidago (B) calculated for each transition year separately.

A) Solanum

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>$\gamma_\lambda$</td>
<td>0.107</td>
<td>0.100</td>
<td>0.442</td>
</tr>
<tr>
<td>$\gamma_\beta$</td>
<td>0.422</td>
<td>0.986</td>
<td>0.219</td>
</tr>
<tr>
<td>$\gamma_c$</td>
<td>0.191</td>
<td>0.105</td>
<td>0.440</td>
</tr>
<tr>
<td>$\gamma_\sigma$</td>
<td>0.766</td>
<td>0.627</td>
<td>0.220</td>
</tr>
</tbody>
</table>

B) Solidago

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>$\gamma_\lambda$</td>
<td>0.677</td>
<td>0.260</td>
<td>0.736</td>
</tr>
<tr>
<td>$\gamma_\beta$</td>
<td>0.256</td>
<td>0.347</td>
<td>0.434</td>
</tr>
<tr>
<td>$\gamma_c$</td>
<td>0.413</td>
<td>0.262</td>
<td>0.367</td>
</tr>
<tr>
<td>$\gamma_\sigma$</td>
<td>0.955</td>
<td>0.250</td>
<td>0.159</td>
</tr>
</tbody>
</table>
APPENDIX F

CHAPTER 3: Response surface design

Response surface experimental design with varying densities of *Solanum* and *Solidago* in 1m$^2$ quadrats. A total of 13 density combinations were used.
APPENDIX G

CHAPTER 4: Neighborhoods in pair-wise preference experiments

Neighborhoods represented by $X,Y$ ($X$ is *Solanum* densities, $Y$ is *Solidago* densities). Three types of comparisons were made to examine which component of the neighborhood influenced preference: (A) Frequency of *Solanum* and *Solidago* at fixed low and high densities (B) Frequency and density *Solidago* at fixed *Solanum* densities (C) neighborhood size effects in *Solanum* monocultures.

**A. Substitutive comparisons (fixed total density)**

<table>
<thead>
<tr>
<th>High density (16 individuals)</th>
<th>Low density (4 individuals)</th>
</tr>
</thead>
<tbody>
<tr>
<td>16,0 vs. 8,8</td>
<td>4,0 vs. 2,2</td>
</tr>
<tr>
<td>8,8 vs. 1,15</td>
<td>2,2 vs. 1,3</td>
</tr>
<tr>
<td>1,15 vs. 16,0</td>
<td>1,3 vs. 4,0</td>
</tr>
</tbody>
</table>

**B. Additive comparisons (fixed *Solanum* densities)**

<table>
<thead>
<tr>
<th>Mono-</th>
<th>Di-</th>
</tr>
</thead>
<tbody>
<tr>
<td>1,0</td>
<td>1,15</td>
</tr>
<tr>
<td>4,0</td>
<td>4,12</td>
</tr>
<tr>
<td>8,0</td>
<td>8,8</td>
</tr>
</tbody>
</table>

**C. Neighborhood size (monoculture of *Solanum* only)**

<table>
<thead>
<tr>
<th>Mono-</th>
<th>Di-</th>
</tr>
</thead>
<tbody>
<tr>
<td>1,0</td>
<td>4,0</td>
</tr>
<tr>
<td>4,0</td>
<td>16,0</td>
</tr>
<tr>
<td>16,0</td>
<td>1,0</td>
</tr>
</tbody>
</table>
APPENDIX H

CHAPTER 4: ANOVA tables for constitutive and induced resistance

ANOVA tables for neighborhood composition effects on (A) constitutive and (B) induced resistance of *Solanum* to a specialist beetle larvae, *Leptinotarsa juncta*.

<table>
<thead>
<tr>
<th>A) Constitutive resistance</th>
<th>Type III SS</th>
<th>Df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>0.233</td>
<td>1</td>
<td>8.12</td>
<td>0.009</td>
</tr>
<tr>
<td>Plant genotype</td>
<td>0.295</td>
<td>3</td>
<td>3.42</td>
<td>0.036</td>
</tr>
<tr>
<td>Density : Plant genotype</td>
<td>0.262</td>
<td>3</td>
<td>3.05</td>
<td>0.052</td>
</tr>
<tr>
<td>Residuals</td>
<td>0.573</td>
<td>20</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>B) Induced resistance</th>
<th>Type III SS</th>
<th>Df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>0.210</td>
<td>1</td>
<td>10.80</td>
<td>0.003</td>
</tr>
<tr>
<td>Plant genotype</td>
<td>0.364</td>
<td>3</td>
<td>6.24</td>
<td>0.003</td>
</tr>
<tr>
<td>Density : Plant genotype</td>
<td>0.251</td>
<td>3</td>
<td>4.31</td>
<td>0.016</td>
</tr>
<tr>
<td>Residuals</td>
<td>0.3893</td>
<td>20</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
APPENDIX I

CHAPTER 4: ANOVA tables for herbivore and predator communities

Effects of neighborhood composition on (A) predator abundance, (B) predator richness and (C) herbivore abundance.

<table>
<thead>
<tr>
<th></th>
<th>Type III SS</th>
<th>Df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Predator abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency of Solidago</td>
<td>11.384</td>
<td>1</td>
<td>9.12</td>
<td>0.004</td>
</tr>
<tr>
<td>Density of Solanum</td>
<td>5.843</td>
<td>1</td>
<td>4.68</td>
<td>0.035</td>
</tr>
<tr>
<td>Density of Solidago</td>
<td>2.098</td>
<td>1</td>
<td>1.68</td>
<td>0.201</td>
</tr>
<tr>
<td>Frequency of Solidago: Density of Solanum</td>
<td>13.818</td>
<td>1</td>
<td>11.08</td>
<td>0.001</td>
</tr>
<tr>
<td>Density of Solanum: Density of Solidago</td>
<td>10.166</td>
<td>1</td>
<td>8.15</td>
<td>0.006</td>
</tr>
<tr>
<td>Residuals</td>
<td>56.114</td>
<td>45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. Predator richness</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency of Solidago</td>
<td>8.622</td>
<td>1</td>
<td>13.79</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Density of Solanum</td>
<td>0.027</td>
<td>1</td>
<td>0.04</td>
<td>0.833</td>
</tr>
<tr>
<td>Frequency of Solidago: Density of Solanum</td>
<td>2.871</td>
<td>1</td>
<td>4.59</td>
<td>0.037</td>
</tr>
<tr>
<td>Residuals</td>
<td>29.366</td>
<td>47</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. Herbivore abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frequency of Solidago</td>
<td>38.571</td>
<td>1</td>
<td>12.60</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Total density</td>
<td>1.258</td>
<td>1</td>
<td>0.41</td>
<td>0.524</td>
</tr>
<tr>
<td>Density of Solanum</td>
<td>11.244</td>
<td>1</td>
<td>3.67</td>
<td>0.061</td>
</tr>
<tr>
<td>Total density: Density of Solanum</td>
<td>5.831</td>
<td>1</td>
<td>1.90</td>
<td>0.174</td>
</tr>
<tr>
<td>Residuals</td>
<td>140.76</td>
<td>46</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
APPENDIX J

CHAPTER 4: ANOVA tables for microclimate

Effects of neighborhood composition on (A) mean light intensity, (B) mean ambient temperature, and (C) mean soil moisture content.

<table>
<thead>
<tr>
<th>A. Light intensity</th>
<th>Type III SS</th>
<th>Df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of <em>Solanum</em></td>
<td>496903</td>
<td>1</td>
<td>2.36</td>
<td>0.130</td>
</tr>
<tr>
<td>Density of <em>Solidago</em></td>
<td>1375670</td>
<td>1</td>
<td>6.54</td>
<td>0.013</td>
</tr>
<tr>
<td>Residuals</td>
<td>10089036</td>
<td>48</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>B. Temperature</th>
<th>Type III SS</th>
<th>Df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of <em>Solidago</em></td>
<td>41.252</td>
<td>1</td>
<td>15.01</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Residuals</td>
<td>134.618</td>
<td>49</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>C. Soil moisture</th>
<th>Type III SS</th>
<th>Df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>0.016</td>
<td>1</td>
<td>0.87</td>
<td>0.354</td>
</tr>
<tr>
<td>Frequency of <em>Solidago</em></td>
<td>0.996</td>
<td>1</td>
<td>52.82</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Density of <em>Solanum</em></td>
<td>0.018</td>
<td>1</td>
<td>0.96</td>
<td>0.331</td>
</tr>
<tr>
<td>Density: Frequency of <em>Solidago</em></td>
<td>0.016</td>
<td>1</td>
<td>0.86</td>
<td>0.356</td>
</tr>
<tr>
<td>Density: Density of <em>Solidago</em></td>
<td>0.041</td>
<td>1</td>
<td>2.19</td>
<td>0.145</td>
</tr>
<tr>
<td>Frequency of <em>Solidago</em>: Density of <em>Solanum</em></td>
<td>0.292</td>
<td>1</td>
<td>15.50</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Residuals</td>
<td>0.810</td>
<td>43</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
REFERENCES


Bolker, B. 2010. bbmle: Tools for general maximum likelihood estimation. R package version 0.9.5.1. Based on stats4 by the R Development Core Team http://CRAN.R-project.org/package=bbmle.


Johnson, M. T. J. and S. Rasmann. 2011. The latitudinal herbivory-defence hypothesis takes a
detour on the map. New Phytologist **191**:589-592.

Journal of Insect Physiology **43**:885-895.

Karban, R. 2001. Communication between sagebrush and wild tobacco in the field. Biochemical
Systematics and Ecology **29**:995-1005.

Karban, R. 2007. Associational resistance for mule's ears with sagebrush neighbors. Plant
Ecology **191**:295-303.

Systematics **33**:641-664.

Trends in Ecology & Evolution **17**:164-170.

Kim, T. N., N. Underwood, and B. I. Inouye. *in revision*. Insect herbivores change the outcome
of plant competition through effects on demographic processes. Ecology.

Kost, C. and M. Heil. 2006. Herbivore-induced plant volatiles induce an indirect defence in

Lapointe, S. L. and J. P. Shapiro. 1999. Effect of soil moisture on development of Diaprepes
abbreviatus (Coleoptera : Curculionidae). Florida Entomologist **82**:291-299.

plants on native communities. Ecology **86**:2990-2997.


Leslie, P. H. 1958. A stochastic model for studying the properties of certain biological systems
by numerical methods. Bionietrica **45**:16-31.

Letourneau, D. K. 1995. Associational susceptibility: Effects of cropping pattern and fertilizer on
Malawian bean fly levels. Ecological Applications **5**:823-829.

Escobar, V. Galindo, C. Gutierrez, S. D. Lopez, J. L. Mejia, A. M. A. Rangel, J. H. Rangel, L.


Underwood, N., P. A. Hambäck, and B. I. Inouye. in review. A conceptual framework for associational effects: when do neighbors matter and how would we know?


BIOGRAPHICAL SKETCH

EDUCATION

University of Wisconsin (Madison, Wisconsin)  2012-
Postdoctoral fellowship in Entomology
  Supervisor: Dr. Claudio Gratton

Florida State University (Tallahassee, Florida)  2006-2012
Doctor of Philosophy in Biological Science
  Dissertation title: Community-level consequences of plant-herbivore interactions
  Chair: Dr. Nora Underwood

University of Florida (Gainesville, Florida)  2003-2006
Master of Science in Zoology
  Thesis title: The spatial and temporal effects of fire on insect herbivore community structure
  Chair: Dr. Robert D Holt

McGill University (Montreal, Canada)  1995-1999
Bachelor of Science in Resource Conservation

RESEARCH AND PROFESSIONAL EXPERIENCE

Herbarium Curator (FSU Robert K. Godfrey Herbarium, Tallahassee, FL)  2010
  Maintained collections of plants and microalgae specimens, maintained digital imaging database, supervised undergraduate workers.

Research Assistant (San Diego State University, San Diego, CA)  2001-2003
  Led a project aimed at (1) understanding the effects of disturbance and plant invasion on the small mammal, bird, arthropod, and plant components of the coastal sage scrub food web and (2) developing an Index of Biological Integrity to help policy makers and researchers make decisions regarding land management issues.

Biological Research Assistant USGS-BRD, Volcanoes National Park, HI  2000
  Participated in studies aimed at understanding the effects of non-native arthropods and mammals on the abundance and distribution of native plant and insect species in the wet and dry forests of the Hawaii Volcanoes National Park.

PUBLICATIONS


**PRESENTATIONS (*/ UNDERGRADUATE AUTHOR*)**


Kim, T. N. and R.D. Holt. 2007. The direct and indirect effects of fire on insect herbivore communities. Poster at the Ecological Society of America Conference. San Jose, CA.
TEACHING EXPERIENCE

Florida State University:
- Conservation Biology Fall 2012
- General Ecology Spring 2012
- Insect Ecology Experimental Biology Lab Fall 2011
- Plant Biology Lab and Lecture Fall 2007–Spring 2010, Summer 2012
- Foraging Ecology Experimental Biology Lab Spring 2007
- Biological Science I Laboratory Fall 2006

University of Florida:
- Integrative Principles in Biology I Spring 2006
- Integrative Principles in Biology II-Lab Fall 2004, Fall 2005, Spring 2006
- General Ecology Spring 2005
- Integrative Principles in Biology I-Lab Fall 2003–Summer 2004

UNDERGRADUATE MENTORING

Arshad, A. The effects of plant quality and herbivore density on the distribution and foraging behaviors of herbivores (*Spodoptera exigua*). DIS student. Graduated FSU and working at Capital Regional Medical. Currently applying to medical school. 2011


Stanfield, J. Latitudinal variation in plant palatability and herbivore preference in two perennial plants, *Solanum carolinense* and *Solidago altissima*. Women in Mathematics, Science, and Engineering (WIMSE) student. Senior at Florida State University, FL. 2009

Huot, O. The effects of dispersed and concentrated herbivore damage on induced resistance in *Solanum carolinense*. Research Experience for Undergraduates (REU) student. Graduated from Cornell University and first-year grad student at Texas A&M. 2009


OUTREACH & PROFESSIONAL SERVICE

Curriculum committee for General Biology labs 2012
- Participated in the revision of General Biology II labs (BSC 2011L-FSU).

Website creator for undergraduate research opportunities 2008–2012
- Created and maintains a departmental website advertising research opportunities (paid & unpaid) for undergraduates (FSU).
Lead symposium organizer and moderator at the Ecological Society of America Annual Conference (Pittsburgh, PA) 2010

Co-organizer of an organized oral session at the Ecological Society of America Annual Conference (Pittsburgh, PA) 2010

Middle-school instructor in marine and wetland ecology 2009
Saturday-at-the-Sea (FSU)

Treasurer for Ecology and Evolution graduate student group 2009
Department of Biological Science (FSU)

Union representative for Graduate Assistants United labor union 2009
Department of Biological Science (FSU)

GRANTS, FELLOWSHIPS, & AWARDS

- Doctoral Dissertation Improvement Grant (NSF) $13,116 2011
- Florida State University Outstanding Teaching Assistant Award (FSU) $500 2010
- Dissertation Research Grant from the Graduate School (FSU) $750 2009
- Robert K. Godfrey Endowment Award in Botany (FSU) $750, $1000 2008, 2009
- Frances M. Peacock Scholarship (Cornell Lab of Ornithology & Garden Club of America) $4000 2005
- Grinter Fellowship (UF) $9000 2003-2006
- Florida Native Plant Society Endowment Award $1000 2004
- Graduate student research fund from Department of Zoology (UF) $500 2004

PROFESSIONAL SOCIETY MEMBERSHIPS

- Ecological Society of America, Sigma-Xi, The Society for Integrative and Comparative Biology, Florida Native Plant Society

JOURNAL REVIEWS

- Ecological Entomology, Ecology