

DIRECT AND INDIRECT BENEFITS OF HERBIVORY FOR PLANTS

A Dissertation

by

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## ABSTRACT

Herbivory is not always detrimental to plants. In some cases, herbivory can lead to overcompensation, whereby plants produce greater fitness or growth following damage. In order to improve ecologists understanding of overcompensation for insect herbivory I conducted a literature review and meta-analysis of the evidence for overcompensation. The meta-analysis explored the effects of plant, herbivore, and experiment characteristics on plant overcompensatory expression. In addition, I investigated how the timing of herbivory by cotton fleahopper, *Pseudatomoscelis seriatus* (Hemiptera: Miridae), affects the ability of cotton, *Gossypium hirsutum* (Malvaceae), to overcompensate. I infested cotton with fleahoppers during the first, second, third, and fourth week of squaring and monitored their effects on cotton growth and yield during two growing seasons. I also investigated the ability of the cotton fleahopper to be a pollinator of cotton. I determined fleahopper flower visiting frequency, their pollen load, their dispersal ability while carrying a pollen analog, and their pollination efficiency. Finally, herbivory can also be indirectly beneficial to plants if herbivores induce defense which deter a more damaging herbivore. I used greenhouse assays and RT-qPCR analysis to determine whether the cotton fleahopper can induced defense genes which decrease the performance of Lepidopteran pests.

I found evidence the literature that overcompensation for insect herbivory is more prevalent than previously thought. Over 25 plant species overcompensated with increased fitness, while over 45 plant species overcompensated with increased growth.

Overcompensation for insect herbivory has many economic, ecological, and evolutionary implications. I also found that cotton compensated for fleahopper herbivory, regardless of timing of herbivory. Fleahoppers also increased the branching of cotton. In addition, I found that fleahoppers are not efficient pollinators of cotton, despite being frequent flower visitors and carrying around 25 pollen grains on their body. Fleahoppers, however, could be pollinators of their wild host plants with smaller or composite flowers. Finally, data regarding indirect benefits of fleahopper herbivore were inconclusive. The qPCR analysis was incomplete and the greenhouse studies sample size was too small to detect effects of fleahopper herbivory on Lepidopteran performance. This study adds to ecologists' understanding of how herbivory is not always detrimental to plants.

## DEDICATION

I dedicate my dissertation to my family. Home is where the heart is. Thank you for your love and support.

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## NOMENCLATURE

ACO5	1-Aminocyclopropane-1-Carboxylicacid Oxidase-5
Bt	<i>Bacillus thuringiensis</i>
Chi	Chitinase
EIN4	Pressure
ET	Economic Threshold
ETOH	Ethanol
K	Potassium
LTL1	Li-tolerant lipase 1
1-MCP	1-Methylcyclopropene
P	Phosphorus
PCR	Polymerase Chain Reaction
PI	Proteinase Inhibitor
POD	Peroxidase
PPO	Polyphenol Oxidase
N	Nitrogen
NAWF	Nodes Above White Flower
RT-qPCR	Real Time Quantitative Polymerase Chain Reaction
UV	Ultra Violet

## TABLE OF CONTENTS

	Page
ABSTRACT .....	ii
DEDICATION .....	iv
ACKNOWLEDGEMENTS .....	v
NOMENCLATURE .....	vi
TABLE OF CONTENTS .....	vii
LIST OF FIGURES .....	ix
LIST OF TABLES .....	xi
CHAPTER I INTRODUCTION .....	1
Mutualisms .....	1
Direct benefits of herbivory .....	2
Indirect benefits of herbivory .....	3
Applied significance of beneficial plant-herbivore interactions .....	4
Ecological effects of overcompensation .....	6
Direct and indirect benefits of herbivory for cotton.....	6
Dissertation aims .....	9
CHAPTER II OVERCOMPENSATION FOR INSECT HERBIVORY: A REVIEW OF THE EVIDENCE .....	10
Introduction .....	10
Methods .....	14
Results .....	17
Discussion .....	23
CHAPTER III THE TIMING OF COTTON FLEAHOPPER HERBIVORY AND COTTON'S COMPENSATORY RESPONSE .....	34
Introduction .....	34
Methods .....	36
Results .....	40
Discussion .....	53

CHAPTER IV INVESTIGATION INTO THE POLLINATION EFFICIENCY OF A PLANT BUG (HEMIPTERA: MIRIDAE).....	59
Introduction .....	59
Methods.....	62
Results .....	66
Discussion .....	69
CHAPTER V PLANT-MEDIATED INTERACTIONS BETWEEN COTTON FLEAHOPPERS AND LEPIDOPTERAN PESTS .....	73
Introduction .....	73
Methods.....	77
Results .....	83
Discussion .....	85
CHAPTER VI CONCLUSIONS .....	90
LITERATURE CITED .....	95
APPENDIX 1 .....	117
APPENDIX 2 .....	127



## LIST OF FIGURES

	Page
Figure 1 Overall effect sizes for reproductive and vegetative overcompensation .....	18
Figure 2 Effect of plant characteristics on reproductive overcompensation.....	19
Figure 3 Effect of plant characteristics on vegetative overcompensation.....	20
Figure 4 Effect of herbivore characteristics on reproductive overcompensation.....	21
Figure 5 Effect of herbivore characteristics on vegetative overcompensation .....	22
Figure 6 Effect of experimental set up on reproductive overcompensation .....	24
Figure 7 Effect of experimental set up on vegetative overcompensation .....	24
Figure 8 Average lint kg/hectare (A, B), number of bolls (C, D), and retention of first position fruits (E, F) per plant at harvest in an open plot experiment in 2011 .....	41
Figure 9 Average number of nodes (A, B), vegetative branches (C, D), and fruiting branches (E, F) per plant at harvest in an open plot experiment in 2011.. .....	44
Figure 10 Average number of bolls per plant over time in an open plot experiment in 2011 produced by control plants and plants infested with fleahoppers during the first (A), second (B), third (C) and fourth (D) week of squaring..	46
Figure 11 Average lint kg/hectare (A, B), number of bolls (C, D), and retention of first position fruits (E, F) per plant at harvest in a field cage experiment in 2013.....	49
Figure 12 Average number of nodes (A, B), vegetative branches (C, D), and fruiting branches (E, F) per plant at harvest in field cage experiment in 2013.....	52
Figure 13 Photographs of a cotton fleahopper under a dissecting microscope (A) foraging on a cotton stigma and (B) carrying cotton pollen grains .....	67
Figure 14 Number of seeds per fruit among pollination treatments .....	68
Figure 15 Seed mass per fruit among pollination treatments.....	68
Figure 16 Lint weight per fruit among pollination treatments.. .....	69
Figure 17 Retention of caterpillars on fleahopper induced plants in a field experiment	83

Figure 18	Number of fruits (squares, flowers, green bolls and open bolls) per plant on fleahopper induced plants at the end of the growing season.....	84
Figure 19	Proportion of first position fruits retained on fleahopper induced plants in a field experiment.....	84
Figure 20	Branches on fleahopper induced plants in a field experiment .....	85
Figure 21	Leaf area damaged by caterpillars on fleahopper induced plants in a greenhouse experiment over three days of feeding .....	86
Figure 22.	Percent leaf area damaged by caterpillars on fleahopper induced plants in a greenhouse experiment over three days of feeding .....	86
Figure 23.	Weight gain by caterpillars on fleahopper induced plants in a greenhouse experiment over three days of feeding .....	87

## LIST OF TABLES

	Page
Table 1 Effects of fleahoppers and fleahopper timing of herbivory on harvest measures ( $\pm$ standard error) in an open plot experiment in 2011 .....	42
Table 2 Treatment effects of fleahoppers and fleahopper timing of herbivory on lint production ( $\pm$ standard error) by fruiting position and seed weight in number in an open plot experiment in 2011 .....	43
Table 3 Treatment effects of fleahoppers and fleahopper timing of herbivory on lint production ( $\pm$ standard error) by fruiting position and seed weight in number in an open plot experiment in 2011 .....	45
Table 4 Treatment effects of fleahoppers and fleahopper timing of herbivory on harvest measures in a field cage experiment in 2013 .....	48
Table 5 Effects of fleahoppers and fleahopper timing of herbivory on lint quality measures in a field cage experiment in 2013 .....	50
Table 6 Effects of fleahoppers and fleahopper timing of herbivory on lint production by position ( $\pm$ standard error) in a field cage experiment in 2013 .....	51
Table 7 Primer sequences for qPCR analysis.....	82
Table 8 Information from studies included in the meta-analysis .....	118
Table 9 Studies with evidence of overcompensation but not included in the meta-analysis .....	128

# CHAPTER I

## INTRODUCTION

### **Mutualisms**

Mutualisms between plants and insects are widespread and have immense ecological consequences to their communities (Janzen 1966, Bronstein 1994). Mutualisms are reciprocally beneficial interactions in which cooperation improves the fitness of both partners. Classically, plant-insect mutualisms fall into one of three main archetypes: pollination, seed dispersal, or protection. These mutualisms all function as an exchange of rewards for service between the organisms (Bronstein et al. 2006). In pollination and seed dispersal mutualisms for instance, plants exchange food substances like nectar or fruit flesh for seed and pollen dispersal. It is estimated that at least 90% of angiosperms are dependent on animal pollinators (Buchmann and Nabhan 1997) and that ants, in particular, play larger role for dispersing seeds for tropical plant species (Giladi 2006). Ants also act as defenders in plant protection mutualisms. In these mutualisms, plants provide food resources, and sometimes shelter for ants in exchange for an active defense against herbivores. There are at least 100 tropical plant genera that participate in ant-plant protection mutualisms (Davidson 1993). Overall, investigations into these ubiquitous and apparent mutualisms have increased our knowledge about the evolutionary ecology of plant insect interactions (Bronstein 1994, Bruno et al. 2003, Rudgers et al. 2003, Savage and Peterson 2007, Styrsky and Eubanks 2007). There is still much to learn, however, about less apparent and understudied mutually beneficial

plant-insect interactions — those between plants that exchange food resources to herbivores for various direct and indirect benefits to their metabolism, growth, and/or fitness.

### **Direct benefits of herbivory**

Herbivores can directly benefit their host plants if their damage stimulates an overcompensatory response, whereby damaged plants have higher fitness or growth compared to an undamaged plants. Plants undergo morphological and physiological changes, such as increased branching, increased photosynthesis, and modified metabolite storage after herbivory in order to overcompensate (Prins and Verkaar 1992, Tiffin 2000). The seminal study on overcompensation by Paige and Whitham (1987) documented excess regrowth by Scarlet Gilia, *Ipomopsis aggregate* (Polemoniaceae), following ungulate grazing. Although deer and elk damaged over 90% of the Scarlet Gila's aboveground mass, damage led to increased fitness by releasing the plant from apical dominance. Without apical dominance, damaged plants produced multiple flowering stems, while ungrazed plants only produced one flowering stem. Consequently, damaged Scarlet Gilia had 2.5 times greater fitness than their ungrazed counterparts. Subsequent studies of other vertebrate-plant interactions have demonstrated that overcompensation to vertebrate herbivory occurs in many diverse plant species (Lennartsson et al. 1998, Loeser et al. 2004, Nolet 2004, Van der Graaf et al. 2005, Yeh et al. 2012).

Overcompensation following insect herbivory, on the other hand, has been considered rare or non-existent by some authors (Agrawal 2000, Herrera and Pellmyr

2002, Díaz et al. 2004). There are, however, several examples of overcompensation for insect herbivory in both managed and unmanaged ecosystems. Wild radish plants, *Raphanus raphanistrum* (Brassicaceae), for instance, produced 136% more seeds following defoliation by the white cabbage worm caterpillars, *Pieris rapae* (Lepidoptera: Pieridae) (Agrawal et al. 1999) and potatoes, *Solanum tuberosum* (Solanaceae), produced larger tubers following Guatemalan potato moth, *Tecia solanivora* (Lepidoptera: Gelechiidae), herbivory (Poveda et al. 2010). In addition, recent research suggests that insects can select for increased regrowth capacity (Agrawal and Fishbein 2008, Hakes and Cronin 2011, Jogesh et al. 2014), increased seed production (Wise et al. 2013), and increased probability of flowering (König et al. 2014)(König et al. 2014), which are all potential mechanisms of overcompensation. Finally, mathematical models predict that overcompensation should evolve in plant populations with a high risk of herbivory (Vail 1992, Tuomi et al. 1994, Nilsson et al. 1996): a condition that insect herbivores certainly create. We hypothesize, therefore, that overcompensation for insect herbivory may be far more prevalent than previously assumed.

### **Indirect benefits of herbivory**

Insects can also indirectly benefit their host plants by inducing defenses against other, more damaging herbivores. Induced defenses are morphological and physiological changes after damage which can reduce or deter future herbivory (Karban and Baldwin 1997, Taiz and Zeiger 2010). Kessler and Baldwin (2004) called this effect an herbivore-induced plant vaccination. They found, for instance, that plant bugs, *Tupiocorus notatus* (Hemiptera: Miridae), vaccinated wild tobacco, *Nicotiana rustica*

(Solanaceae), against hornworms, *Manduca quinquemaculata* and *M. sexta* (Lepidoptera: Sphingidae) (Kessler and Baldwin 2004). Hornworms developed slower and gained less weight while feeding on plants previously damaged by the plant bugs. As a result, plant bug herbivory increased wild tobacco fitness when both plant bugs and caterpillars were present. *T. notus* herbivory alone did not affect wild tobacco fitness, but hornworm herbivory would have been harmful. Similarly, wild radish benefits from vaccination induced by *P. rapae* herbivory. Folivory by *P. rapae* larvae increased the concentration of glucosinolates in leaf tissues and the number of trichomes on leaf surfaces (Agrawal 1998). Unlike induced plants, intact wild radish was frequently damaged by naturally occurring insect herbivores like earwigs, aphids, grasshoppers, flea beetles and lepidopteran larvae (Agrawal 1998, 1999). As a result, the fitness of induced radish plants was 60% greater than uninduced plants (Agrawal 1998).

### **Applied significance of beneficial plant-herbivore interactions**

Investigations into the indirect and direct benefits of herbivory in agro-ecosystems can improve integrated pest management practices. Integrated pest management involves mixed use of chemical, biological, and cultural control methods to keep herbivore populations below economic injury thresholds. Understanding when and how plants may overcompensate, or gain indirect defenses from herbivores, will allow agriculturalists to calculate accurate thresholds for pests and produce maximum yields (Harris 1974). In particular, more pest management strategies are needed to reduce pesticide use. Pesticide use comes with many risks, such as selection for pesticide resistance among harmful insects, suppression of natural enemies and biocontrol agents,

pollution of the natural environment, health risks for humans, and high application costs (Bardner and Fletcher 1974, Pimentel et al. 1992, Wilson et al. 2003, Deguine et al. 2008).

There are several examples of direct benefits derived from insect herbivory for crop plants (Harris 1974). Plant bug, *Nesidiocoris tenuis* (Hemiptera: Miridae), herbivory, for example, led to a 15% increase in tomato, *Solanum lycopersicus* (Solanaceae), fruit mass (Sánchez and Lacasa 2008), while galling by African rice gall midge, *Orseolia oryzivora* (Diptera: Cecidomyiidae) increased rice, *Oryza sativa* (Poaceae), yield by 12% (Omoloye et al. 2002). In addition, upland cotton, *Gossypium hirsutum* (Malvaceae), can overcompensate for cotton fleahopper, *Pseudatomoscelis seriatus* (Hemiptera: Miridae), herbivory (Ring et al. 1993). Ring et al (1993), found that fleahopper infested plants can produce upwards of 21% greater yield than uninfested plants.

Herbivores can also provide indirect benefits to crops. Wielgoss et al. (2012), for instance, found that plant bug, *Helopeltis sulawesi* (Hemiptera: Miridae), deters oviposition by cocoa pod borer, *Conopomorpha cramerella* (Lepidoptera: Gracillariidae) on cacao trees, *Theobroma cacao* (Malvaceae). The cocoa pod borer is a major cacao pest, and so, when both the plant bug and pod borer are present the plant bug facilitates increased yields by inducing resistance against the pod borer. Remarkably, models predicted that optimal yield could be achieved when 50% of cacao pods are damaged by *H. sulawesi*. Economic thresholds for *H. sulawesi*, therefore, may need an adjustment to



account for the yield benefits incurred by the induction of defenses that resist *C. cramerella*.

### **Ecological effects of overcompensation**

Following insect herbivory, many changes occur to host plant morphology and physiology (Karban and Baldwin 1997). Overcompensatory changes can not only affect plant growth and fitness, but also affect the dynamics of herbivore communities (Stinchcombe 2002, Craig 2010). A series of field studies by Utsumi and colleagues are a seminal example. They found that overcompensatory regrowth in willow species, *Salix spp.* (Salicaceae), following wood-boring by *Endoclita excrescens* (Lepidoptera: Hepialidae) larvae can select for feeding preference of a leaf beetle, *Plagioderia versicolora* (Coleoptera: Chrysomelidae) (Utsumi et al. 2009a). In this system, wood boring larvae caused willows to increase their number of lateral shoots (Utsumi and Ohgushi 2007). New lateral shoots were significantly longer, had more nitrogenous leaves than undamaged willows, and attracted high densities of *P. versicolora* (Utsumi and Ohgushi 2007, 2008). *P. versicolora* feeding on leaves on regrowth shoots also had significantly greater mass and fecundity than *P. versicolora* feeding on leaves from primary growth (Utsumi and Ohgushi 2008). Therefore, insect performance may be positively affected by plant overcompensatory regrowth at multiple trophic levels (Ohgushi 2012).

### **Direct and indirect benefits of herbivory for cotton**

As discussed, herbivores can directly or indirectly benefit their host plants and these benefits can have both economic and ecological implications. The interaction

between cotton, *G. hirsutum* (Malvaceae), and an insect herbivore, the cotton fleahopper, *P. seriatus* (Hemiptera: Miridae) is an ideal system to investigate the benefits of herbivory to host plants.

*G. hirsutum*, (Malvaceae) is a well-described shrub of immense economic importance as a cash fiber crop for the state of Texas and many countries worldwide. Approximately 5.5 million acres of cotton were planted in Texas in 2010, making Texas the top cotton producer in the United States (Williams 2012). It is a perennial plant with indeterminate growth, meaning that cotton can develop both vegetative structures (leaves and stems) at the same time as it develops reproductive structures (flowers, fruit, and seeds). Growth rates are dependent on environmental conditions, but plants typically begin producing flower buds on the 5 or 6<sup>th</sup> branch on the mainstem, approximately 30 days after seeding germination (Oosterhuis and Jernstedt 1999). Then, another 25 days may pass before the initial flower opening (Oosterhuis and Jernstedt 1999). After anthesis, a green boll (fruit) develops for about 6 weeks, before it opens to expose fibers at maturity (Oosterhuis and Jernstedt 1999).

*P. seriatus* are abundant, native, piercing-sucking mirid plant bugs, with a large host range of mostly herbaceous plants (Esquivel and Esquivel 2009). They normally infest cotton during the early season of its growth, and both adults and nymphs preferentially feed on developing cotton flower buds (called “squares” on cotton plants). Their feeding causes flower bud abscission, which is evidenced by blackened buds, or fruiting scars that remain after the buds abscise (Stewart and Sterling 1989). In recent years, fleahopper pest status has been increasing, Plant bugs are no longer suppressed

by pesticides used to control boll weevils and are not affected by *Bt* toxins in transgenic cotton (Deguine et al. 2008, Wilson et al. 2013). As a result, the cotton fleahopper has become the most expensive pest to control in Texan growing regions where it is estimated to cost \$10 million annually (Williams 2012). Current threshold for these insects ranges from 10-15 cotton fleahoppers per 100 cotton plant terminals in the Texas Blacklands (i.e.; central Texas locations like College Station, TX) and there are typically one to four applications of insecticides to target cotton fleahoppers in that region (Sansone et al. 2009).

Numerous agricultural trials, however, do not support the need for such extensive cotton fleahopper control. Instead, they demonstrate that moderate amounts of early season bud abscissions may benefit cotton production. Cultivars SP37H and STV213, for instance, overcompensated for 44 fleahoppers per 100 plants and 10 fleahoppers per 100 plants respectively (Ring et al. 1993). In addition, Stewart et al. (Stewart et al. 2001) documented increased yield following 100% square removal during the second week of squaring. Similarly, both Lei and Gaff (Lei and Gaff 2003) and Ungar et al. (1987) also found that early square removal led to overcompensation in yield. In order to improve pest management strategies for cotton fleahoppers, and reduced pesticide use against them, a better understanding of what conditions facilitate cotton overcompensation (or compensation) for early season damage, such as the damage caused by cotton fleahopper.

## Dissertation aims

In my dissertation, I reviewed the literature to estimate the prevalence of overcompensation to insect herbivory and conducted a meta-analysis to explore the effects of plant growth form, evolutionary history, herbivore-feeding guild, and other factors on the expression of overcompensation. My goal was to raise awareness of the evolutionary and ecological implications of overcompensation for insect herbivory and to develop testable hypotheses about when and where we expect to see overcompensation from insect herbivory.

In addition, I used field, greenhouse, and lab studies to investigate the direct and indirect benefits of *P. seriatus* herbivory for cotton. First, I determined the effects of timing of herbivory on cotton overcompensatory responses. Then, I determined the ability of cotton fleahopper to benefit cotton indirectly by inducing chemical defenses that could negatively affect other, more damaging herbivores like Lepidopteran larvae. Finally, after observing that cotton fleahoppers were frequent visitors of cotton flowers, I investigated their pollination efficiency.

By studying both the direct and indirect benefits of herbivory in an agro-ecosystem, I hope to contribute to deficiencies of both applied and basic ecological research. Agriculturalists can benefit from understanding that plant-herbivore interactions are dynamic and not always antagonistic.

CHAPTER II  
OVERCOMPENSATION FOR INSECT HERBIVORY: A REVIEW OF THE  
EVIDENCE

**Introduction**

Ecologists have studied thousands of plant -herbivore interactions in order to gain a better understanding of how herbivores impact plant growth and fitness (Turcotte et al. 2014). Herbivory is most often detrimental to plants (Crawley 1989, Bigger and Marvier 1998, Massad 2013), but plants can also tolerate injury (McNaughton 1983, Fornoni 2011). Tolerance, or compensation, is a plant defense strategy to maintain growth and fitness following damage (Painter 1958). Plants undergo morphological and physiological changes, such as increased branching, increased photosynthesis, and modified metabolite storage after herbivory to mitigate injury (Prins and Verkaar 1992, Tiffin 2000). In some cases, these changes can result in overcompensation whereby damaged plants have higher fitness than undamaged plants (Agrawal 2000). The classic example of this phenomenon was documented by Paige and Whitham (1987) who found that ungulate herbivory increased Scarlet Gilia, *Ipomopsis aggregata* (Polemoniaceae), seed production by 2.4 fold. Deer and elk removed Scarlet Gilia's apical meristem, released the plant from apical dominance, and caused the plant to produce more flowering stems than if left ungrazed.

Paige and Whitham (1987)'s conclusion that there may be evolutionary advantages for plants to be eaten sparked an extensive debate concerning

overcompensation (Agrawal 2000). Belsky (1986) and Belsky et al. (1993) immediately argued that overcompensation had only been observed under artificial conditions such as high resource availability, ideal temperatures, and no subsequent herbivory. As a result, they asserted that early research (see Dyer 1975, McNaughton 1979, and Paige and Whitham 1987) failed to demonstrate that overcompensation takes place in nature. They argued that compensatory regrowth was a general plant response to hostile environments (i.e., fire, trampling, frost, etc.) and not a co-evolved relationship between plants and herbivores (see also Bergelson and Crawley 1992a, 1992b). Further work by Paige addressed these concerns. Paige documented overcompensation for ungulate herbivory in ten additional Scarlet Gilia populations across Arizona and Colorado (Paige 1999), found that Scarlet Gilia overcompensated even when re-browsed (Paige 1992a), and demonstrated that fire, frost, and trampling rarely resulted in overcompensation (Paige 1992b). Subsequent studies of other vertebrate-plant interactions including work with cattle (Loeser et al. 2004), sheep (Liu et al. 2012), horses (Lennartsson et al. 1997), blackbirds (Dyer 1975), swans (Nolet 2004), geese (Van der Graaf et al. 2005), and voles (Yeh et al. 2012) demonstrated that overcompensation to vertebrate herbivory occurs in many diverse plant species.

Despite the growing awareness that overcompensation can result from vertebrate herbivory, overcompensation for insect herbivory has been assumed to be rare or non-existent by some authors (Agrawal 2000, Strauss and Zangerl 2002, Díaz et al. 2004, but see Trumble et al. 1993). This may be because grazing vertebrate herbivores typically remove more plant biomass than insect herbivores, producing more conspicuous or

obvious plant damage (Kotanen and Rosenthal 2000). Vertebrate herbivores may also be more likely to damage the meristem of plants and release apical dominance than insect herbivores. In addition, while some insect herbivores are folivores, many insect herbivores do not have chewing mouthparts and feed on specific plant tissues by mining, piercing plant cells, or sucking up plant liquids. Overall, insect herbivory may be harder to detect or difficult to quantify than vertebrate herbivory. Nevertheless, we hypothesize that overcompensation for insect herbivory is far more prevalent than previously assumed. Recent research suggests that insects can select for increased regrowth capacity (Agrawal and Fishbein 2008, Hakes and Cronin 2011), increased seed production (Wise et al. 2013), and increased probability of flowering (König et al. 2014), which are all potential mechanisms of overcompensation. Moreover, mathematical models predict that overcompensation should evolve in plant populations with high risk of herbivory (Vail 1992, Tuomi et al. 1994, Nilsson et al. 1996): a condition that insect herbivores certainly create.

Most discussions of overcompensation have focused on the change in plant fitness associated with herbivory. However, overcompensatory plant regrowth may have broad ecological effects even if overcompensatory plant regrowth is not correlated with an increase in plant fitness. For example, wood boring by swift moth larvae, *Endoclita excrescens* (Lepidoptera: Hepialidae), increased the number of lateral shoots produced by willow trees, *Salix spp.* (Salicaceae), and caused a multi-level trophic cascade among other insects (Utsumi and Ohgushi 2007, 2009). Wood boring caterpillars induced the growth of new lateral shoots and bored willows attracted higher densities and species

richness of other insect herbivores and predators (Utsumi et al. 2009b, Utsumi and Ohgushi 2009). Ohgushi (2012) predicted that overcompensatory plant regrowth following herbivory is widespread and that it causes broad ecological effects in many systems. The accuracy of Ohgushi's (2012) predication, however, remains to be seen because the overall prevalence of overcompensatory plant regrowth is unknown.

We reviewed the literature and conducted a meta-analysis to estimate the prevalence of overcompensation to insect herbivory and to explore the effects of plant growth form, evolutionary history, herbivore feeding guild, and other factors on the expression of overcompensation. Our goal was to increase understanding of the evolutionary and ecological implications of overcompensation for insect herbivory and to develop testable hypotheses about when and where we expect to see overcompensation from insect herbivory. Many questions regarding plant compensatory responses, including fitness overcompensation and overcompensatory plant regrowth, are unresolved (Whitham et al. 1991, Agrawal 2000). For example, it has been suggested that woody plants have a greater capacity to compensate than herbaceous plants because woody plants have more meristems that could be activated following damage to increase branching (Haukioja and Koricheva 2000). Additionally, it has been hypothesized that intense herbivory in tropical regions should select for higher compensation in plants growing at lower latitudes than plants growing in higher latitudes (Więski and Pennings 2014). Finally, many hypotheses emphasize resource availability as an important predictor of compensation (Wise and Abrahamson 2007), but Hawkes and Sullivan (2001)'s meta-analysis revealed that how resources influenced plant



compensation depended on other intrinsic plant characteristics (e.g., monocot or dicot, woody or herbaceous). Overall, we present evidence that plants can respond to insect herbivory with overcompensation. Moreover, we found that these plant responses are not restricted to certain taxa or ecosystems, and that a variety of conditions cause variation in plant overcompensatory responses.

## **Methods**

### *Literature search*

Studies documenting overcompensation for insect herbivory were identified with key word searches using the *Web of Science* and Google Scholar with the terms overcompensation, tolerance, compensation, plant, herbivore, and insects. The references within studies and their citations were also searched. To be included in the meta-analysis the study must have met the following criteria: (1) plant growth or reproduction following insect herbivory or simulated insect herbivory was significantly increased (at  $\alpha=.05$ ) compared to controls which were free of damage, (2) data were collected from independent plants, (3) plant responses were provided as plant fitness parameters, such as number and biomass of fruits, flowers or seeds, or plant growth parameters, such as the biomass, length, area, or number of plant organs such as branches, stems, roots or leaves, and (4) means, variances (SE or SD) and sample sizes were reported for both experimental and control plants. When necessary, means and variances were estimated from published figures using the software, Grabit XP (Datatrend Software, Inc). The literature search was ended in July 2014.

### *Meta-analysis*

We used the effect size Hedge's  $d$  to measure the strength of overcompensatory responses by plants. Hedge's  $d$  calculated by subtracting the sample mean of the control group (undamaged plants) from the sample mean of the experimental group (damaged plants) and dividing by their pooled standard deviation weighted by sample size (Rosenberg *et al.* 2000). We calculated Hedge's  $d$  using MetaWin 2.0 software (Rosenburg et al. 2000). Since we only collected data that showed overcompensation (i.e., the experimental group performed better than the control group) all effect sizes were positive. Typically, an effect size greater than 0.8 is considered a large effect, an effect size around 0.5 is considered a moderate effect, while an effect size of 0.2 is considered a small effect (Cohen 1988). Effect sizes were reported with 95% confidence intervals.

### *Categorical analysis*

In order to compare how different plant traits, insect traits, and experimental conditions influence the magnitude of overcompensatory responses expressed by plants, we categorized studies for various experimental variables for use in a categorical meta-analysis. A categorical meta-analysis is analogous to the statistical comparison of groups in an ANOVA except that effect sizes are compared across chosen categories instead of sample means. Categories included were (1) plant traits: taxonomy (species and family), functional group (monocot or dicot), life form (woody, graminoid, herbaceous or vine), and longevity (annual, perennial, biennial), (2) herbivore traits: taxonomy (order and family), feeding guild (chewing, cell-content feeding, phloem

feeding, mining, stem boring or gall forming), feeding site (leaves, stems, apical meristems, flowerbuds, flowers or fruits) and damage intensity (low, medium or high) and (3) experiment characteristics: site (field, garden, greenhouse, or environmental chamber), management (agricultural or uncultivated), latitude (tropical or temperate) and damage source (insect herbivory or simulated insect herbivory).

Damage intensity was categorized primarily using the description given by each author as to what a normal level of insect damage could be expected on plants in the field. When the experimenters used a damage level within their defined normal range, damage intensity was classified as “medium”, if the damage level was below their defined normal range it was classified as “low”, and if it was higher than their defined normal intensity it was categorized as “high”. Alternatively if no reference was made to a normal level of damage, 1-33% tissue damage was classified as low damage, 33-66% tissue damage was classified as medium damage, and 66-100% tissue damage was classified as high damage. Finally, when authors intentionally tested the effect of different damage intensities on plant compensation, the authors original classifications of what constitutes low, medium or high damage were maintained in the meta-analysis. In order to prevent pseudo-replication in our meta-analysis, whereby experimental samples are compared to the same control sample, we chose to include only the observations made at the medium damage level in all categorical analyses other than the analysis of damage intensity. Additionally, when studies had a repeated measures of growth or fitness parameters across time, we chose to include only the observation from the last data collection.

Categorical analyses were completed using random effects models using MetaWin 2.0 software (Rosenburg et al. 2000). Comparisons between categories were calculated using a between group homogeneity statistic,  $Q_B$ , tested against a  $\chi^2$  distribution with n-1 degrees of freedom, where n equals the number of observations (Rosenberg *et al.* 2000). The null hypothesis for each categorical analysis states that the overcompensatory effect is independent of the response variable.

## Results

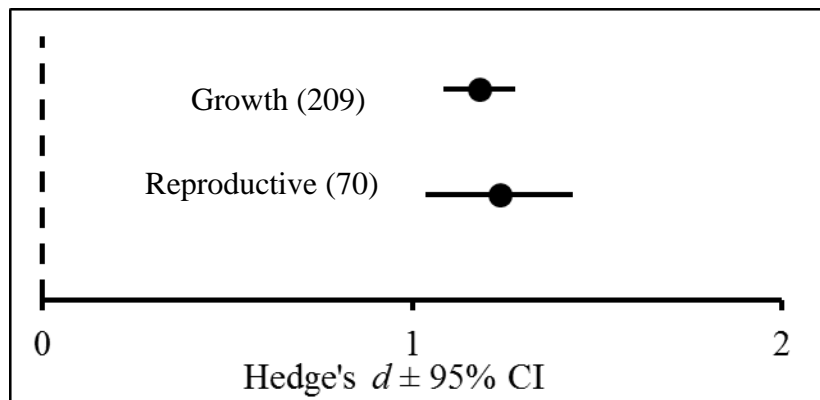
### *Summary of the database*

In total, we calculated 70 effect sizes from 17 publications documenting fitness overcompensation and 209 effect sizes from 50 publications documenting vegetative overcompensation published from 1976 to 2014 (Appendix 1). Thirty-three studies with evidence for overcompensation or vegetative overcompensation were excluded from our meta-analysis because they had missing statistics needed for the meta-analysis (Appendix 2). Effect sizes were greater than 1.0 for both fitness and vegetative overcompensation (Figure 1).

### *Effects of plant characteristics*

Overcompensation varied greatly among plant families for both reproductive ( $Q_B=51.2179$ ,  $df= 6$ ,  $P =0.001$  Figure 2) and vegetative ( $Q_B =45.2869$ ,  $df=13$ ,  $P =0.001$  Figure 3) responses. Plant life form, however, only had a significant effect on the degree of reproductive overcompensation ( $Q_B =24.7607$ ,  $df= 2$ ,  $P =0.004$ ; Figure 2); woody plants overcompensated approximately 40% more than herbaceous plants. Vegetative overcompensation, conversely, was similar for all growth forms ( $Q_B =3.5135$ ,  $df=3$ ,  $P =$

0.294; Figure 3). In addition, dicots overcompensated to greater degree than monocots, in terms of reproduction ( $Q_B = 9.8438$ ,  $df = 1$ ,  $P = 0.015$ ; Figure 2) but not in terms of vegetative growth ( $Q_B = 3.3532$ ,  $df = 1$ ,  $P = 0.070$ ; Figure 3). Finally, whether a plant was an annual, perennial, or biennial had no effect on plant fitness ( $Q_B = 5.4294$ ,  $df = 2$ ,  $P = 0.103$ ; Figure 2) or vegetative ( $Q_B = 1.9358$ ,  $df = 2$ ,  $P = 0.411$ ; Figure 3) overcompensation.

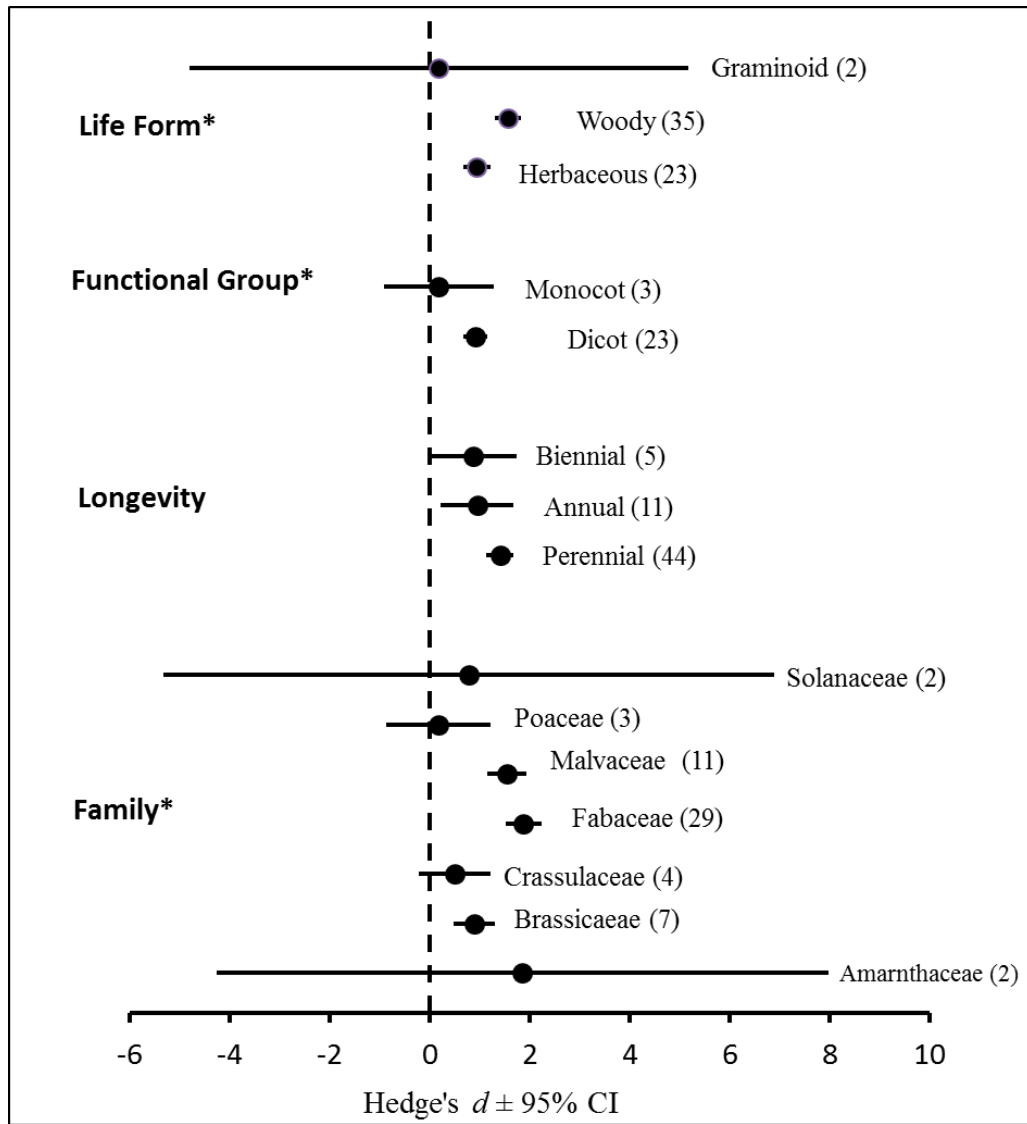


**Figure 1. Overall effect sizes for reproductive and vegetative overcompensation.** Horizontal lines represent 95% confidence intervals and sample sizes are shown in parenthesis.

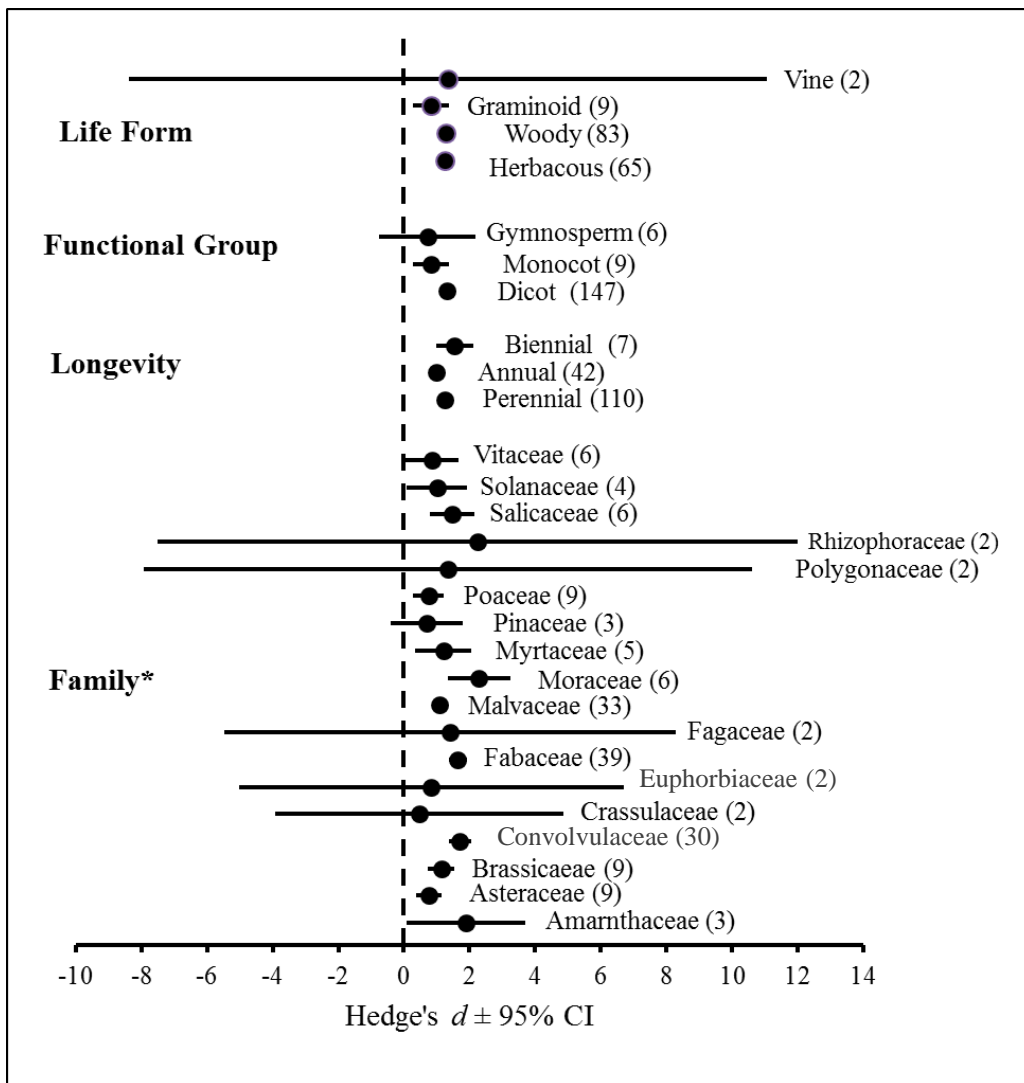
#### *Effects of herbivore characteristics*

Insect order and family were not significant sources of variation for plant reproductive overcompensation ( $Q_B = 3.6605$ ,  $df = 4$ ,  $P = 0.495$  and  $Q_B = 22.3381$ ,  $df = 6$ ,  $P = 0.060$ , respectively; Figure 4). In contrast, while insect order was not significant source of variation for vegetative overcompensatory responses ( $Q_B = 7.4576$ ,  $df = 2$ ,  $P = 0.059$ ;

Figure 5), insect family was a significant factor ( $Q_B = 32.6807$ ,  $df = 10$ ,  $P = 0.004$ ; Figure 5). For example, Chrysomelidae (Coleoptera) induced very large effects ( $d = 1.6627$

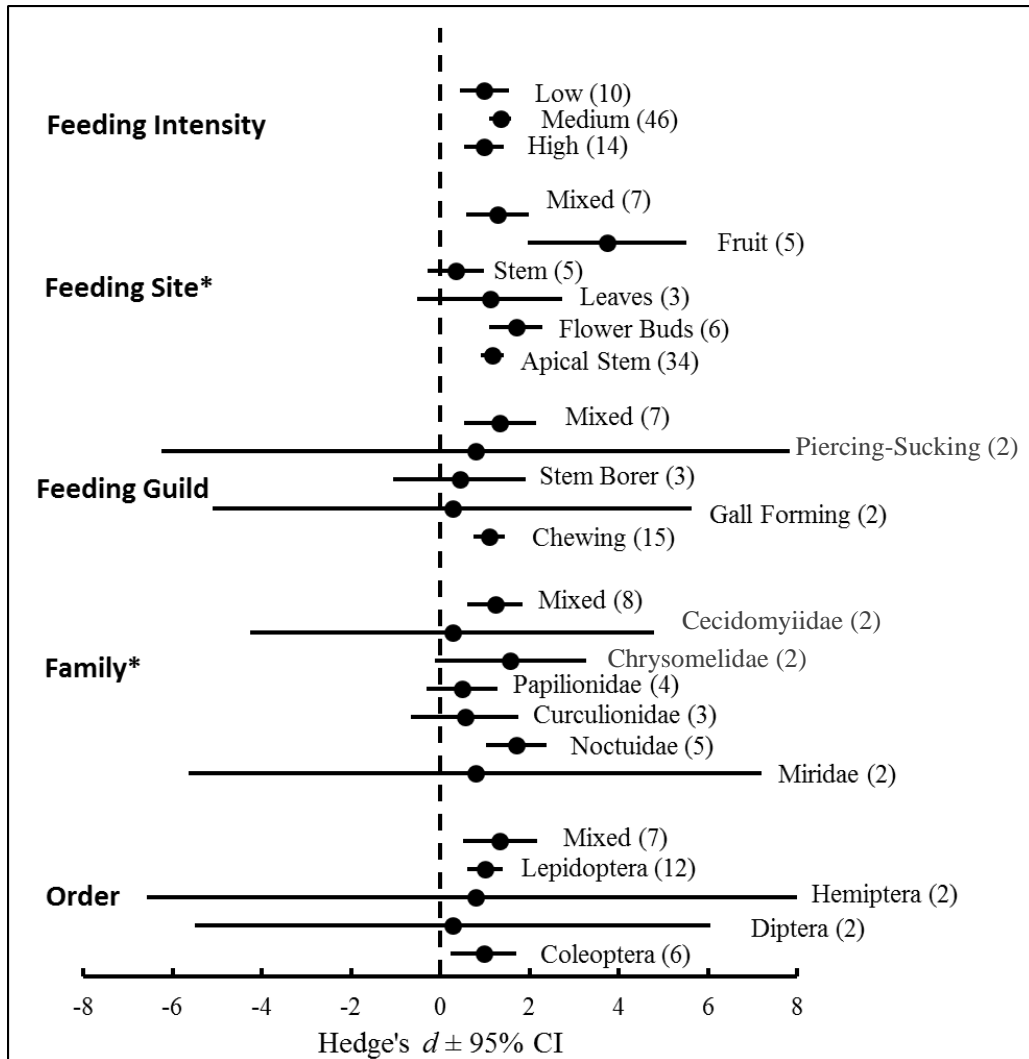


**Figure 2. Effect of plant characteristics on reproductive overcompensation.** Horizontal lines represent 95% confidence intervals and samples sizes are shown in parenthesis. Asterisks indicate significant between class heterogeneity ( $Q_B$ ).



**Figure 3. Effect of plant characteristics on vegetative overcompensation.** Horizontal lines represent 95% confidence intervals and samples sizes are shown in parenthesis. Asterisks indicate significant between class heterogeneity ( $Q_B$ ).

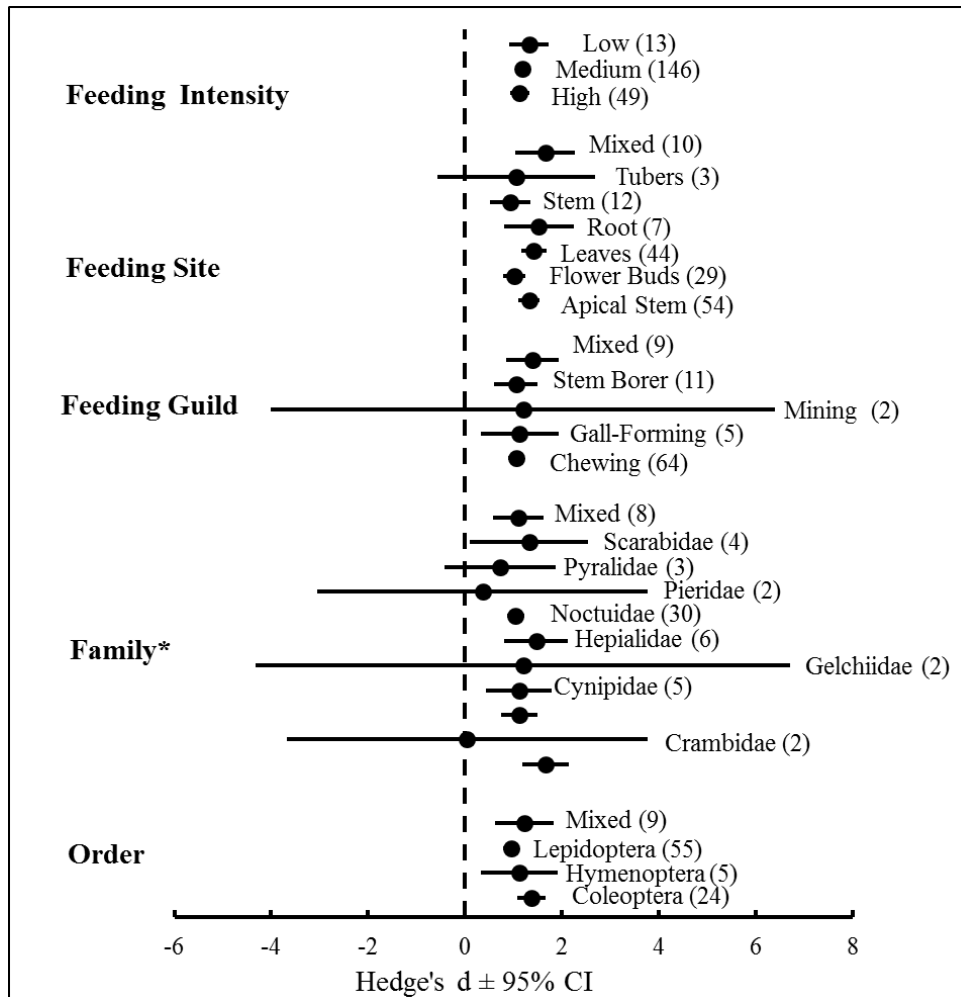
(1.1830-2.1424)), but Crambidae (Lepidoptera) induced very small effects ( $d= 0.0413$  (-3.6860-3.7685)). Herbivore feeding guild did not influence plant reproductive overcompensation ( $Q_B=7.2061$ ,  $df= 4$ ,  $P= 0.213$ ; Figure 4), or vegetative



**Figure 4. Effect of herbivore characteristics on reproductive overcompensation.** Horizontal lines represent 95% confidence intervals and samples sizes are shown in parenthesis. Asterisks indicate significant between class heterogeneity ( $Q_B$ )

overcompensation ( $Q_B=1.9860$   $df=4$ ,  $P=0.708$ ; Figure 5). Herbivore feeding site, however, influenced reproductive overcompensatory plant response ( $Q_B=34.2301$   $df=5$ ,  $P=0.001$ ; Figure 4). Damaged to fruits, or flower buds, for instance, produced extremely high overcompensatory responses ( $d=3.7458$  (1.19668-5.5247); Figure 4), while damage





**Figure 5. Effect of herbivore characteristics on vegetative overcompensation.** Horizontal lines represent 95% confidence intervals and samples sizes are shown in parenthesis. Asterisks indicate significant between class heterogeneity ( $Q_B$ ).

to stems produced small effects ( $d=0.3543$  (-0.2771-0.9858)). This was not the case for vegetative overcompensation as the effect of herbivore feeding site was only marginally significant ( $Q_B=12.8040$   $df=6$ ,  $P=0.054$ ; Figure 5). Finally, herbivore feeding intensity was not a source of variation for either reproductive ( $Q_B=2.7052$   $df=2$ ,  $P=0.313$ ; Figure 4) or vegetative ( $Q_B=0.65328$   $df=2$ ,  $P=0.612$ ; Figure 5) overcompensation.

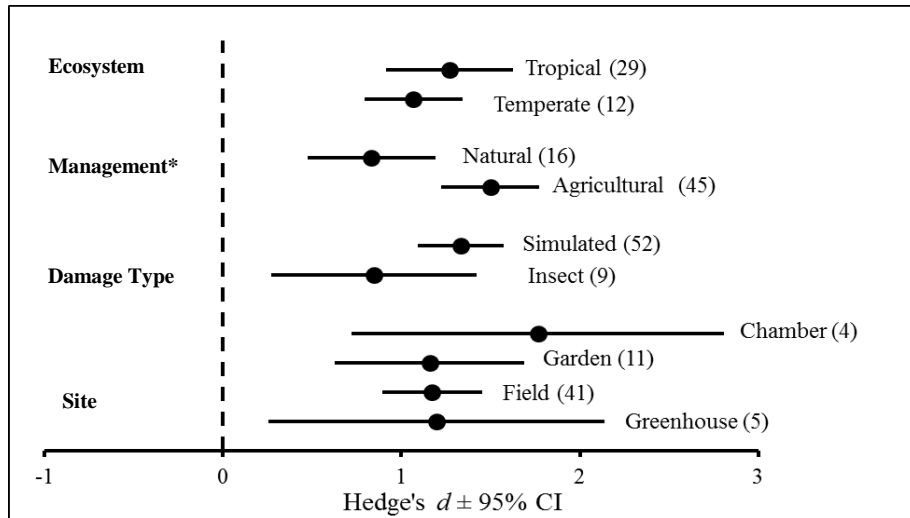
### *Effects of methodology*

Experiment site did not influence reproductive overcompensatory responses ( $Q_B = 2.9349$   $df = 3$ ,  $P = 0.429$ ; Figure 6) or vegetative responses ( $Q_B = 6.9824$   $df = 4$ ,  $P = 0.136$ ; Figure 7). Fitness overcompensation, however, was two-fold higher in agricultural systems than in uncultivated systems ( $Q_B = 9.4727$ ,  $df = 1$ ,  $P = 0.002$ ; Figure 6).

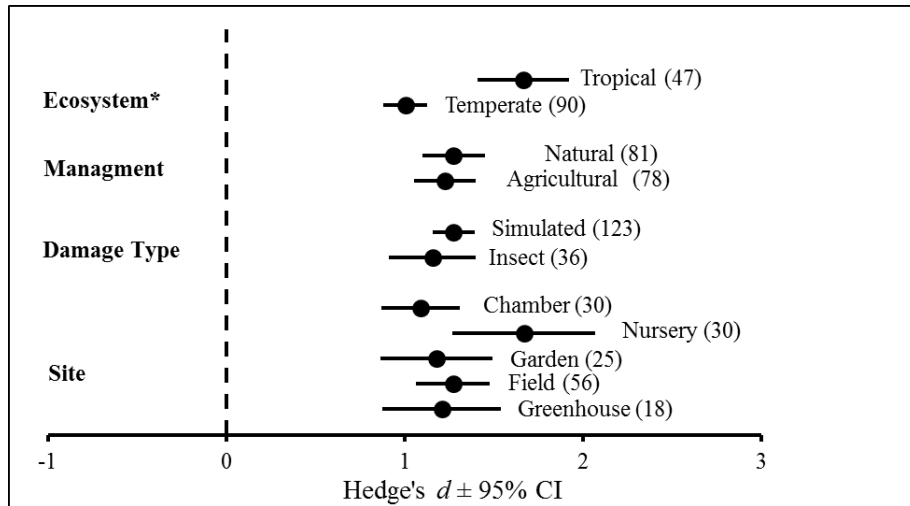
Vegetative overcompensation, nevertheless, was consistent across these systems ( $Q_B = 0.1586$ ,  $df = 1$ ,  $P = 0.672$ ; Figure 7). In addition, simulated insect damage caused no differences in overcompensatory and vegetative responses compared to damage caused by insects ( $Q_B = 3.0998$   $df = 1$ ,  $P = 0.108$ ; Figure 2-6 and  $Q_B = 0.7451$   $df = 1$ ,  $P = 0.3830$ ; Figure 7, respectively). Reproductive overcompensation ( $Q_B = 1.3107$   $df = 1$ ,  $P = 0.274$ ; Figure 6) did not vary across latitudes, but tropical areas seem to facilitate higher vegetative overcompensatory responses than temperate areas ( $Q_B = 21.5954$   $df = 1$ ,  $P = 0.001$ ; Figure 7).

### **Discussion**

Our literature review revealed overcompensation for insect herbivory is more prevalent than previously thought (Appendices 1 and 2). We found that insect herbivores increased fitness in at least 20 plant species (16 families) and stimulated vegetative overcompensation in at least 48 plant species (25 families). These taxa represented the breadth of plant diversity: monocots, dicots, gymnosperms, annuals, perennials, as well as woody and herbaceous species all overcompensated via increased fitness or growth.



**Figure 6. Effect of experimental set up on reproductive overcompensation.** Horizontal lines represent 95% confidence intervals and samples sizes are shown in parenthesis. Asterisks indicate significant between class heterogeneity ( $Q_B$ ).



**Figure 7. Effect of experimental set up on vegetative overcompensation.** Horizontal lines represent 95% confidence intervals and samples sizes are shown in parenthesis. Asterisks indicate significant between class heterogeneity ( $Q_B$ ).

There seems to be no limitations to the types of plants which can overcompensate.

Additionally, we found that at least 25 insect species representing 8 families and 5 orders induced overcompensation in their host plants and at least 33 insect species, representing 20 insect families and 5 orders induced vegetative overcompensation. These insects include chewing, boring, sucking, piercing, and galling herbivores.

Moreover, we found that insects can have a substantial positive impact on plant fitness and growth: effect sizes were on average greater than 1.1 (Figure 1). In terms of increased fitness, herbivory by leaf beetles, *Agasicles hygrophila* (Coleoptera: Chrysomelidae), for example, increased the number of alligator weed, *Aternanthera philozeroides* (Amaranthaceae), reproductive buds by 112% (Lu et al. 2010). In addition, stem boring weevil larvae, *Ceutorhynchus roberti* (Coleoptera: Curculionidae) increased the number of *Alliaria petiolate* (Brassicaceae) inflorescences by 50% (Gerber et al. 2008). Vegetative responses were also strong. Weevils, *Oxyops vitiosa* (Coleoptera: Curculionidae) increased branching in *Melaleuca quinquenervia* (Myrtaceae) by 100% (Pratt and Rayamajhi 2005), and the Guatemalan potato moth, *Tecia solanivora* (Lepidoptera: Gelechiidae), increased potato, *Solanum tuberosum* (Solanaceae) tuber mass by 100% (Poveda et al. 2010).

#### *Effects of plant characteristics*

Haukioja and Koricheva (2000) hypothesized that woody plants may have a greater capacity to compensate than herbaceous plants because they have more meristems available for activation which would increase branching following damage. We found, however, that woody plants overcompensated to a greater degree than

herbaceous plants in terms of increased fitness, but not in increased vegetative regrowth (Figures 2 and 3). Reproductive overcompensation of woody plants may be strengthened by their ability to store resources that can be allocated to reproduction following insect herbivory (Haukioja and Koricheva 2000). The long life span and indeterminate growth form of many shrubs and trees probably plays an important role in this response. For example, cotton, *Gossypium hirsutum* (Malvaceae), can overcompensate for early season damage to flower buds (Stewart et al. 2001). Cotton is a woody plant with indeterminate growth which routinely produces more fruits than it can support and, as a consequence, will naturally shed about 20% of its fruits (Guinn 1982). When insects cause early season fruit loss, cotton can invest more into vegetative structures, such as leaves and roots (Sadras 1996a). As a consequence later in the growing season, cotton can use the stored resources and the greater photosynthetic capacity of its increased vegetative biomass to support more or heavier fruits (Sadras 1995).

We also observed that reproductive overcompensation was greater in dicots than monocots. Notably, we found only two studies which observed reproductive overcompensation in monocots and both of them were studies of cultivated rice (e.g., Omoloye et al. 2002, Lv et al. 2010). We do not know if reproductive overcompensation for insect herbivory is really less common in monocots than dicots or if appropriate studies have not been published. Many studies of compensation in monocots only quantify changes in biomass and not reproduction. For example, Crutchfield and Potter (1995) found that root-feeding Japanese beetle grubs, *Popillia japonica* (Coleoptera:

Scarabidae) increased the aboveground biomass of four turfgrass species and Alward and Joern (1993) found that foliar grazing by grasshoppers, *Ageneotettix deorum* (Orthoptera: Acrididae), increased the biomass of grass, *Bouteloua gracilis* (Poaceae).

#### *Effects of plant-herbivore characteristics*

Insects that feed on reproductive plant parts induced the greatest levels of reproductive overcompensation (Figure 4). If we consider insects as “nature’s pruners” then this result is not surprising. Fruit set is resource-limited, and so, fruit shed caused by insects can reduce assimilate competition among fruits on the same branch or plant (Stephenson 1981, Obeso 2002). Consequently, remaining, undamaged, or newly developed fruits can become larger than if no fruit was shed (Sadras 1995). Plant bug, *Nesidiocorus tenuis* (Hemiptera: Miridae), damage to tomato, *Solanum esculentum* (Solanaceae), induced fruit abortion, but the remaining fruits were larger than fruits of plants without plant bug herbivory (Sánchez and Lacasa 2008).

Surprisingly, herbivore feeding guild (i.e., chewing, piercing-sucking etc.) was not a significant source of variation for reproductive or vegetative overcompensation. Chewing herbivores were by far the most prevalent insect herbivore in our database, followed by stem boring insects, but overcompensation by other guilds was rare. Nevertheless, no particular feeding guild significantly altered the level of overcompensation compared to the others. Leaf beetles (Coleoptera: Chrysomelidae), however, tended to have the largest effect on vegetative overcompensation among herbivore families. Leaf beetle, *Galerucella californiensis*, defoliation, for example,

increased the number of shoots produced by *Lythrum Salicaria* (Lythraceae) over 1000% (Schat and Blossey 2005).

#### *Damage intensity*

Unexpectedly, damage intensity did not affect the intensity of overcompensation (Figures 4 and 5). Some authors have suggested that plants are better able to compensate for low levels of herbivory, because high herbivory rates may overpower the plants ability to recover (Stowe et al. 2000), but we did not find support for this prediction. Instead, we found that some plants can overcompensate for spectacular levels of insect damage. Dominguez and Dirzo (1994), for example, found that *Erythroxylum havanense* (Erythroxylaceae) produced larger seeds following complete defoliation and Sevillano et al.(2010) found that *Melaleuca quinquenervia* (Myrtaceae) overcompensated for 15-25 phloem feeding psyllids (Hemiptera: Psyllidae) per branch; this is a high number for these herbivores on these plants.

#### *Effects of ecosystem*

We found evidence that vegetative overcompensation for insect herbivory was stronger in the tropics than in temperate areas (Figure 7). Although ecologists have acknowledged high levels of plant resistance in lower latitudes for many years (Coley and Aide 1991, Dyer and Coley 2002, Stamp 2003, Schemske et al. 2009, Rasmann and Agrawal 2011), plant tolerance across a latitudinal gradient has only recently been addressed (Więski and Pennings 2014). Consistent with our findings, Wieski and Pennings (2014) suggested that plants growing at lower latitudes will have higher tolerance than plants higher latitudes, due to selection by heavy herbivory in tropical

regions. In the only test of this hypothesis, they measured new leaf production of defoliated woody shrub, *Iva frutescences* (Asteraceae), populations along the Atlantic Coast ranging from subtropical Florida to temperate Maine. In contrast to their prediction, they found no evidence for higher regrowth capacity of *I. frutescences* populations in the subtropical climates. To account for these findings, Wiecki and Pennings (2014) suggested that the different selection pressures—freezing temperatures at high latitudes and high herbivory rates at low latitudes—might equalize regrowth capacity among plants in the two climates. A comparison of the physiological and morphological mechanisms which facilitate compensation and overcompensation in temperate and tropical regions would help ecologists clarify these discrepancies.

We also found that fitness overcompensation was greater in agricultural systems than in natural systems (Figure 6). This result suggests that perhaps high resource availability and lower intraspecific plant competition contributes to stronger overcompensatory responses, as predicted under the compensatory continuum hypothesis (CCH) (Maschinski and Whitham 1989, Whitham et al. 1991). Huhta (2000) found, for example, that *Erysimum strictum* (Brassicaceae) increased seed production following apical meristem damage, but only under the addition of fertilizer. Alternatively, this result could be a byproduct of breeding crops with high allocation rates to reproductive organs or reduced risk from plant pathogens.

#### *Ecological consequences of overcompensation*

Although our review shows that overcompensatory regrowth is widespread (Appendix 1 and 2) only a handful of studies have investigated the community wide



effects of this plant response (Ohgushi 2012). Ohgushi (2012) suggested that trophic cascades, such as increased herbivore and predator abundance on overcompensating plants, are common and ubiquitous in terrestrial systems. Utsumi and Ohgushi (2007, 2009) provided a seminal example of this phenomenon in their descriptions of a bottom up trophic cascade caused by insect stem borers feeding on willow trees that we previously described. They found that the high nutritional quality of the newly sprouted plant tissues was preferred by herbivores over the older shoots (Utsumi and Ohgushi 2009).

Similarly, Craig et al. (1986) predicted that new regrowth was triggered by herbivores specifically to benefit their offspring (i.e., the resource regulation hypothesis; Craig 2010). This hypothesis was formed following observations that arroyo willow, *S. lasiolepis* (Salicaceae), resprouting caused by stem galling sawfly larvae *Euura lasiolepis* (Hymenoptera: Tenthredinidae), benefits the subsequent sawfly generation (Craig et al. 1986). The younger, longer, and faster growing new branches were thought to be more nutritious for larvae than older branches (Craig 2010). Similar outcomes have been observed following apical damage by moth larvae, *Zeiraphera canadensis* (Lepidoptera: Tortricidae), on white spruce, *Picea glauca* (Pinaceae) (Carroll and Quiring 2003), and by stem girdling beetles, *Oncideres rhodosticta* (Coleoptera: Cerambycidae), feeding on mesquite, *Prosopis glandulosa* (Fabaceae) (Duval and Whitford 2008). Notably, the applied significance of these outcomes are understudied, but needs more attention (Muller-Scharer and Steinger 2004); recent research suggests vegetative regrowth by invasive plants can influence the success of biological control

agents (Quiram 2013, Tipping et al. 2015). Biological control agents can encourage vegetative growth of these unwanted plants.

#### *Genetics and mechanisms*

Work to determine the genetic, physiological, and morphological mechanisms which underlie overcompensation (e.g., increased branching, increased metabolism, and increased photosynthesis) is just beginning (Scholes et al. 2013, Dalrymple 2014, Scholes and Paige 2014). Scholes and Paige (2011) tested the novel hypothesis that increased chromosomal number via endoreduplication (e.g., genome replication without mitosis) facilitates overcompensation for apical meristem damage. They found that endoreduplication triggered by apical meristem removal is correlated with increased DNA content in *Arabidopsis thaliana* (Brassicaceae) (Scholes and Paige 2011, 2014). In a follow-up study, Siddappaji et al (2013) identified the gene *G6PDH1* as having a significant role in the *Arabidopsis* overcompensation; *G6PDH1* encodes a regulatory enzyme in the oxidative pentose-phosphate pathway (OPPP) which is responsible for converting glucose to ribose-5-phosphate and ultimately leads to nucleotide synthesis (Scholes et al. 2013). *G6PDH1* up-regulation, therefore, is consistent with increased DNA content in overcompensating *Arabidopsis* (Siddappaji et al. 2013). This work could revolutionize agriculture if analogous genes could be located and up-regulated in crop plants (Siddappaji et al. 2013).

#### *Evolution of overcompensation*

With such large positive effects of herbivory on plant fitness, it is easy to hypothesize that overcompensation should be adaptive for plants (Crawley 1987, van der

Meijden 1990, Hakes and Cronin 2011). Lennartsson et al. (1997) provided support for this hypothesis when they found that not only could the grassland plant, *Gentianella campestris* (Gentianaceae), overcompensate for ungulate browsing, but that historically grazed populations were more likely to overcompensate than historically ungrazed populations. In light of evidence for evolutionary adaptation for overcompensation, several authors suggested that plants and herbivores can be mutualists (Paige 1992a, Agrawal 2000). Evidence that overcompensation is an adaptive trait following insect herbivory, however, remains scarce, despite a considerable amount of evidence that insect herbivory selects for compensation (but see Hakes and Cronin 2011). Boalt et al. (2010), for example, found that *Cardamine pratensis* (Brassicaceae) populations exposed to high rates of orange tip butterfly larvae, *Anthocharis cardamines* (Lepidoptera: Pieridae), herbivory are more tolerant than populations exposed to lower attack rates. Moreover, Wise and Abrahamson (2013)'s model predicted strong selection for tolerance by goldenrod *Solidago altissima* (Asteraceae) under attack by larger numbers of spittlebugs, *Philaenus spumarius* (Hemiptera: Cercopidae).

In order to confirm that insects can select for overcompensation ecologists need a better understanding of the costs (i.e., tradeoffs) and benefits of reproductive and vegetative overcompensation on the lifetime plant fitness. Some areas that need more research include how overcompensating plants interact with pollinators (Lay et al. 2011), whether there are trade-offs between male and female fitness for overcompensating plants (Strauss et al. 2003, Wise et al. 2008) and whether resistance is reduced in overcompensating plants (Poveda et al. 2012). In addition, ecologists evaluating

overcompensation need to demonstrate that it is genetically controlled and heritable in natural populations. We predict a high likelihood of finding this evidence in the future because many studies have already found genetic variation for compensation in plant populations (Shen and Bach 1997, Agrawal et al. 1999, Peacock et al. 2002, Hakes and Cronin 2011, Bustos-Segura et al. 2014) and others have found that tolerance is a heritable trait (Juenger and Bergelson 2000, Fornoni et al. 2003, Hakes and Cronin 2011).

### *Conclusion*

We set out to increase awareness and appreciation that overcompensation for insect occurs in both uncultivated and agricultural systems. This review highlights the prevalence of overcompensation and vegetative overcompensation for insect herbivory among many taxa in myriad ecosystems. We suggest that continued discussion of the ecological and evolutionary implications of overcompensation is necessary to improve hypothesis regarding plant defense against herbivores, regardless of whether overcompensation signifies a plant-herbivore mutualism (Edwards 2009) or an exceptional phenomenon (Olejniczak 2011). Our meta-analysis highlights the need for more research to understand the patterns, if any exist, that will allow us to predict overcompensatory responses. Finally, we stress that vegetative overcompensation can have significant effects on plant, herbivore, and predator communities, and a better understanding of the consequences of vegetative overcompensation for agro-ecosystems and weed management is needed.

CHAPTER III  
THE TIMING OF COTTON FLEAHOPPER HERBIVORY AND COTTON'S  
COMPENSATORY RESPONSE

**Introduction**

For over a century, cotton boll weevils and lepidopteran larvae were the primary cotton pests. Cotton producers relied heavily on pesticides to reduce their impact on yield. It was not until the implementation of the boll weevil eradication program in the 1970s and the development of transgenic *Bt* technology in the 1990s that cotton producers were able to reduce pesticide use for many years (Haney et al. 1996, Perlak et al. 2001, Pray et al. 2002). These advances, however, triggered the rise of plant bugs (Miridae: Hemiptera) as new primary cotton pests (Deguine et al. 2008, Wang et al. 2009, Musser et al. 2009a, Wilson et al. 2013). Mirids were no longer suppressed by pesticides used to control boll weevils and were not affected by *Bt* toxins in transgenic cotton (Deguine et al. 2008, Wilson et al. 2013). Consequently, mirid populations rebounded and, in some cases, increased to outbreak levels (Deguine et al. 2008, Lu et al. 2010b).

Mirids feed by penetrating plant cells and using salivary enzymes for extra-oral digestion of cell contents before sucking them out (Miles 1972). They damage cotton terminal meristems and cotton squares causing loss of apical dominance and square abscission (Parker et al. 2009). Large mirids, such as *Creontiades dilutus*, and *Lygus lineolaris*, can also damage bolls (Musser et al. 2009b, McColl et al. 2011). In an

attempt to limit the impact of mirids on yield, there has been a resurgence of pesticide use in recent years (Lu and Wu 2011, Krishna and Qaim 2012, Mensah et al. 2013). Consequently, there is a need for further development of integrated pest management (IPM) strategies for mirid control (Lu et al. 2008, Wilson et al. 2013)

IPM aims to keep pest populations below economic thresholds (ET) while minimizing risks from insecticide use (Kogan 1998, Castle and Naranjo 2009). Establishing ETs for mirids which are practical for growers, however, has been difficult because mirid densities do not always correlate with yield loss (Rosenheim et al. 2006, Whitehouse 2011, Wilson et al. 2013). This disparity is due in part to cotton's ability to tolerate early season square loss or apical damage (Sadras 1995, Wilson et al. 2003, Rosenheim et al. 2006). When damaged, cotton tolerates herbivory and it is able to maintain yields similar to undamaged plants (Trumble et al. 1993). Nevertheless, growers are hesitant to rely on tolerance to offset damage by herbivores because plant tolerance is not easy to predict and may only be evident at the end of the growing season (Spencer 1987, Mi et al. 1998, Rosenheim et al. 2006, Whitehouse 2011). In addition, the ability of plants to compensate is influenced by many conditions, such as nutrient availability, water availability, plant genotype, and timing of herbivory (Maschinski and Whitham 1989, Strauss and Agrawal 1999, Sadras and Felton 2010). In order for compensation to be effectively incorporated into ET calculations, the effects of these conditions on cotton compensation needs to be validated (Mi et al. 1998, Bednarz and Roberts 2001).

The objective of this study was to assess the effect of the timing of herbivory by

the cotton fleahopper *Pseudatomoscelis seriatus* (Hemiptera:Miridae), on the compensation ability of upland cotton, *Gossypium hirsutum*, (Malvaceae). In recent years, the cotton fleahopper has been a primary pest in Texas growing regions, with up to four pesticide applications applied yearly to suppress their populations (Parker 2009, Williams 2012, 2013). Tolerance for cotton fleahopper herbivory, however, has been regularly documented (Sansone et al. 2009b, Parajulee et al. 2011, Knutson et al. 2013). A more targeted spraying regime based on how the timing of herbivory impacts cotton's ability to compensate for herbivory may be able to decrease the number of pesticide applications used against cotton fleahoppers without loss of yield(Whitehouse 2011). Here, we document how fleahopper herbivory at a density higher than threshold levels currently accepted alters cotton's canopy structure, but causes no yield loss, regardless of the timing of herbivory.

## **Methods**

### *Field plot study*

We performed a field plot experiment at the Texas A&M Field Laboratory in Burleson County, TX in 2011. Cotton cultivar 'Deltapine 174RF' was planted on April 18, 2011 in a conventionally managed 0.3 hectare field. We treated the field with Round-Up herbicide to eliminate weeds and fertilized with 14.69kg of nitrogen/hectare with a time-release formula. Furrow irrigation was applied biweekly and insecticide was not used during this experiment. We randomly assigned eighty 1.5m long plots along 15 rows one treatment combination from eight combinations in a 4x2 factorial design.

Treatments included timing of herbivory during the 1st, 2nd, 3rd, or 4th week of squaring and fleahopper infestation, present or absent (control).

We monitored all plants within each plot biweekly for the development of squares and treated the first five plants within each plot reaching squaring. Plants were enclosed at the terminal using cages constructed with 8oz Styrofoam cups cut to fit around the mainstem. The Styrofoam cup supported No-see-um Nylon Netting (BioQuip Products, Rancho Dominguez, CA) which enclosed the two uppermost nodes of the plant. Openings of the cage were closed off with Velcro. We collected adult fleahoppers from nearby fields of silverleaf nightshade, *Solanum elaeagnifolium*, and fed them organic green beans (*Phaseolus vulgaris*) for 1-3 days in the lab until use. One adult fleahopper was placed in each cage for 48 hours, while control cages were left empty. One fleahopper was used, which is higher than the average number of fleahoppers that is found in untreated cotton in this region, 0.1-0.275 fleahoppers per plant (Sansone et al. 2009b) and to the economic threshold for the cotton fleahopper in Burleson Co., which is 10-15 fleahoppers per 100 plants, or 0.1- 0.15 fleahopper per plant (Parker et al. 2009, Sansone et al. 2009b). Cages and fleahoppers were removed from all plants after 48 hours. We only used data from plants in each plot where the fleahopper was found alive inside the cage after the treatment to calculate the average response of plants in each plot.

After the plants began to flower in mid-July, we recorded the number of bolls, nodes, and nodes above the uppermost white flower (NAWF) once a week. NAWF is an in-season indicator of cotton maturity. When cotton plants reach five or fewer NAWF



the plant is considered to have produced the last flower that will develop into a harvestable fruit (Bourland et al. 1992). When the plants reached  $NAWF \leq 5$  we counted the number of nodes, and determined the retention of first position fruits, which are the most important fruits produced by cotton for yield (Kerby et al. 2010).

We harvested all plots over the course of one week (9/17/2011-9/25/2011) when 70% of bolls were open. We included harvest date as a block in our analysis and recorded the number of nodes, number of vegetative and fruiting branches, and the retention of fruits at the first position. Lint was ginned at the Cotton Improvement Laboratory (Texas A&M University, College Station TX) and we determined whole plant lint mass, and lint mass by fruiting position. Lint quality was analyzed at the Texas Tech Fiber and Biopolymer Research Institute (Texas Tech University, Lubbock, TX).

#### *Field cage study*

In 2013 we modified our previous experiment into a randomized complete block design using field cages to prevent undesired herbivory on plants from natural populations of herbivores. On April 17th 2013, ‘Deltapine 174RF’, was planted in a grow room (14/10 L:D, average: 33.5°C, 30%RH). On May 27th 2013, when the plants reached 4-6 leaves, they were transplanted into twenty 1.8m<sup>2</sup> field cages (Lumite Inc. Alto, Georgia) in the same field used in 2011. Eight plants were evenly spaced inside each cage and we randomly assigned one of the eight treatment combinations in our 4x2 factorial design. Treatments were: timing of herbivory (1st, 2nd, 3rd, and 4th week of squaring) and fleahopper infestation or no infestation (control). Irrigation was applied

once a week for three weeks, until the transplanted plants became acclimated to field conditions. Afterwards, irrigation was applied biweekly. Each plant served as a replicate, blocked by field cage. Some plants were lost when a few cages became infested with aphids early in the experiment, and final sample sizes ranged from n=17 plants to n=20 plants. We released Lady beetles, *Hippodamia convergens* (Coleoptera: Coccinellidae), inside all cages and they successfully controlled aphid populations for the rest of the season (Biocontrol Network LLC, Brentwood, TN).

Plants in this experiment were treated as described for the open plot experiment during the 1st, 2nd, 3rd, or 4th week of squaring. We infested plants with one adult field collected cotton fleahopper for 48 hours, and control cages were left empty for 48 hours. We checked all cages after 24 hours and replaced dead or missing fleahoppers. Fleahoppers were collected from nearby feral fields of silverleaf nightshade and maintained in the lab for 1-2 days on organic green beans until use.

We tracked the number of bolls, the number of nodes and NAWF once a week after the plants began to flower in mid-July. When the plants reached  $NAWF \leq 5$  we counted the number of nodes, and calculated the retention of first position fruits. We harvested these plants on Oct 11th, 2013 by pulling the plants from the ground, bagging them in large plastic bags, and storing them in a laboratory cold room. They were kept refrigerated until we harvested the bolls and collected the data, as described for the open plot experiment. Lint was ginned at the Cotton Improvement Laboratory (Texas A&M University, College Station TX) and we determined whole plant lint mass and lint mass

by fruiting position. Lint quality was analyzed at the Texas Tech Fiber and Biopolymer Research Institute (Texas Tech University, Lubbock, TX).

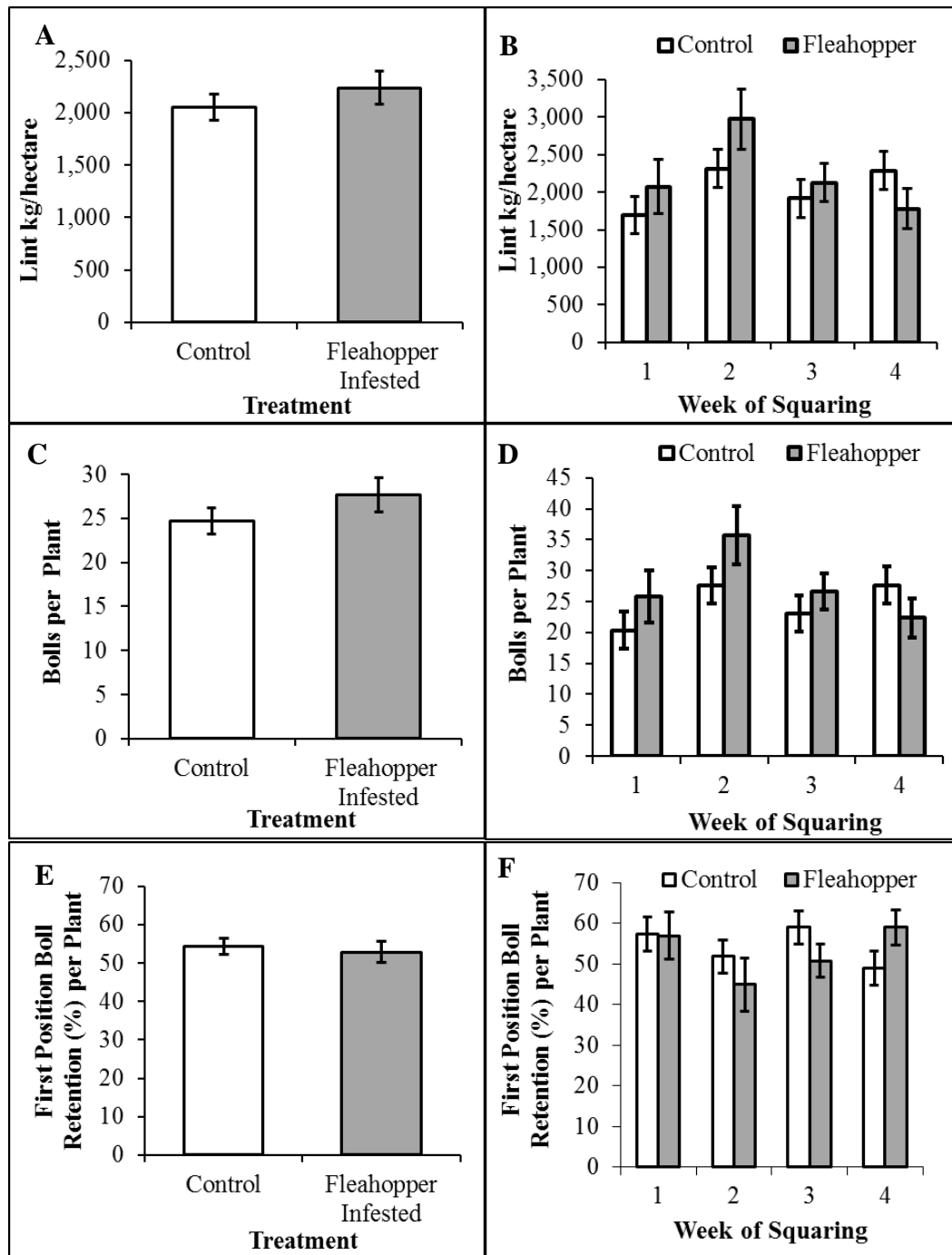
### *Data analysis*

Data were analyzed using a two-way ANOVA using PROC GLM (SAS Institute, version 9.3) where week of squaring and fleahopper infestation were treated as fixed effects. We used harvest date as a random effect for the open plot experiment and field cage location as a random effect for the field cage experiment. Means were separated by Fisher's least significant difference at  $\alpha = 0.05$  level. We used multivariate repeated-measures ANOVA to compare the number of bolls per plant during the in-season fruit production in 2011. Means for the repeated measures analysis were also separated by Fisher's least significant difference at  $\alpha = 0.05$  level.

## **Results**

### *Open plot field study*

Regardless of timing of herbivory, fleahopper herbivory had no effect on the amount of lint, number of bolls, or retention of first position fruits at harvest in our open plot experiment (Figure 8, Table 1). There were also no differences in lint yield among fruiting positions (Table 2), nor any increase in the number of fruiting sites (data not shown, *fleahopper*:  $F_{1,67}=0.465$ ,  $p=0.498$ , *fleahopper\*week*:  $F_{7,60}=2.277$ ,  $p=0.088$ ). Nevertheless, we found significant differences between the vegetative structures of fleahopper treated plants and control plants (Figure 9; Table 1). Fleahopper infestation marginally increased the average number of nodes per plant by 1.3 nodes (Figure 9A)



**Figure 8. Average lint kg/hectare (A, B), number of bolls (C, D), and retention of first position fruits (E, F) per plant at harvest in an open plot experiment in 2011. Figures 1A, 1C, and 1E are data from the fleahopper infestation effect, while Figures 1B, 1D, and 1F are data from the fleahopper by week of squaring interaction. Bars represent  $\pm$  standard error.**

**Table 1. Effects of fleahoppers and fleahopper timing of herbivory on harvest measures ( $\pm$  standard error) in an open plot experiment in 2011.**

<b>Harvest 2011</b>	<b>df 1</b>	<b>df 2</b>	<b>F</b>	<b>p</b>
<b>Lint (kg/h)</b>				
<i>Fleahopper</i>	1	67	0.805	0.373
<i>Fleahopper*Week</i>	7	60	1.548	0.213
<b>Bolls</b>				
<i>Fleahopper</i>	1	67	1.477	0.229
<i>Fleahopper*Week</i>	7	60	1.545	0.213
<b>First Position Bolls Retention (%)</b>				
<i>Fleahopper</i>	1	67	0.165	0.686
<i>Fleahopper*Week</i>	7	60	0.091	0.155
<b>Nodes</b>				
<i>Fleahopper</i>	1	67	3.260	0.076
<i>Fleahopper*Week</i>	7	60	0.950	0.422
<b>Vegetative Branches</b>				
<i>Fleahopper</i>	1	67	4.775	<b>0.033</b>
<i>Fleahopper*Week</i>	7	60	0.935	0.430
<b>Fruiting Branches</b>				
<i>Fleahopper</i>	1	67	3.961	<b>0.051</b>
<i>Fleahopper*Week</i>	7	60	1.450	0.237

and significantly increased the number of vegetative branches and fruiting branches by approximately one branch each (Figures 9C and 9E).

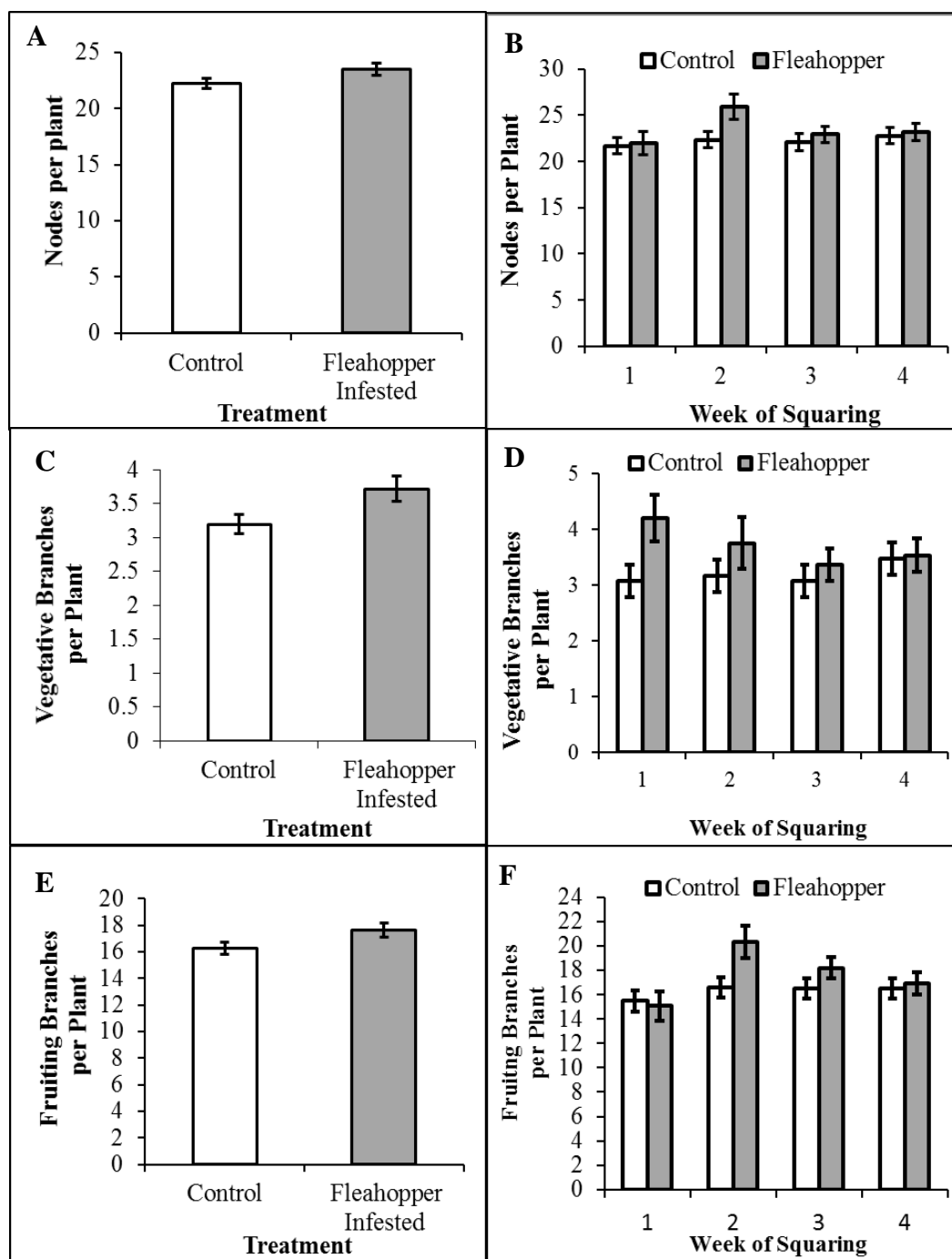
Fleahoppers negatively influenced several measures of lint quality, regardless of the timing of herbivory (Table 3). First of all, fleahopper herbivory increased lint micronaire to  $5.12 \pm 0.05$  units from  $4.97 \pm 0.05$  units produced by control plants. Both fleahopper infested plants and control plants, however, were just outside the acceptable range for processors for this quality measure ( 0.5 units - 4.9 units; Judith M. Bradow, n.d.). Secondly, fleahoppers infested plants had a lower lint strength than controls. Controls had “very strong” lint,  $30.68 \pm 0.26$  g/tex, while fleahopper infested plants had “strong” lint,  $29.85 \pm 0.26$  g/tex (USDA 2005). Finally, lint elongation was lowered

**Table 2. Treatment effects of fleahoppers and fleahopper timing of herbivory on lint production ( $\pm$  standard error) by fruiting position and seed weight in number in an open plot experiment in 2011.**

<b>Average Lint (g) by Fruiting Position per Plant</b>			
<b>Week of Infestation</b>	<b>1st</b>	<b>2nd</b>	<b>Rest of Plant</b>
<b>Week 1</b>			
Control	13.76 $\pm$ 1.61	7.95 $\pm$ 1.24	22.13 $\pm$ 5.04
Fleahopper	14.47 $\pm$ 2.28	8.00 $\pm$ 1.75	27.80 $\pm$ 7.13
<b>Week 2</b>			
Control	15.51 $\pm$ 1.61	9.30 $\pm$ 1.24	31.62 $\pm$ 5.04
Fleahopper	17.42 $\pm$ 2.54	11.50 $\pm$ 1.95	43.08 $\pm$ 5.04
<b>Week 3</b>			
Control	15.50 $\pm$ 1.61	9.44 $\pm$ 1.24	22.11 $\pm$ 5.04
Fleahopper	14.36 $\pm$ 1.61	9.00 $\pm$ 1.24	29.59 $\pm$ 5.04
<b>Week 4</b>			
Control	13.71 $\pm$ 1.61	8.38 $\pm$ 1.24	33.57 $\pm$ 5.04
Fleahopper	13.54 $\pm$ 1.70	6.94 $\pm$ 1.30	22.55 $\pm$ 5.31
<b>Effects</b>			
Fleahopper	F <sub>1,67</sub> =0.061	F <sub>1,67</sub> =0.008	F <sub>1,67</sub> =0.686
	p= 0.805	p= 0.928	p= 0.411
Fleahopper*Week	F <sub>7,60</sub> =0.240	F <sub>7,60</sub> =0.526	F <sub>7,60</sub> =1.582
	p=0.868	p=0.667	p=0.189

from 8.61%  $\pm$  0.13% to 8.24%  $\pm$  0.13% by fleahopper herbivory. Both of these measurements, however, are considered “very high” (Cotton Inc., 2014). Fiber length and uniformity were unaffected by our treatments; all plants had “medium” to “long” fibers (range= 1.08  $\pm$  0.01 inches to 1.01  $\pm$  0.01 inches; Cotton Inc., 2014) and most plants had a “high” degree of uniformity (range= 82.00%  $\pm$  0.54%  $\pm$  to 82.97%  $\pm$  0.54%; USDA, 2005).

We found that fleahopper infestation marginally accelerated plant development. Fleahopper treated plants reached NAWF  $\leq$ 5 in 97  $\pm$  2 days after planting, about five



**Figure 9. Average number of nodes (A, B), vegetative branches (C, D), and fruiting branches (E, F) per plant at harvest in an open plot experiment in 2011.** Figures 1A, 1C and 1E are data from the treatment effect, while Figures 1B, 1D, and 1F are data from the treatment\*week interaction. Bars represent  $\pm$  standard error.

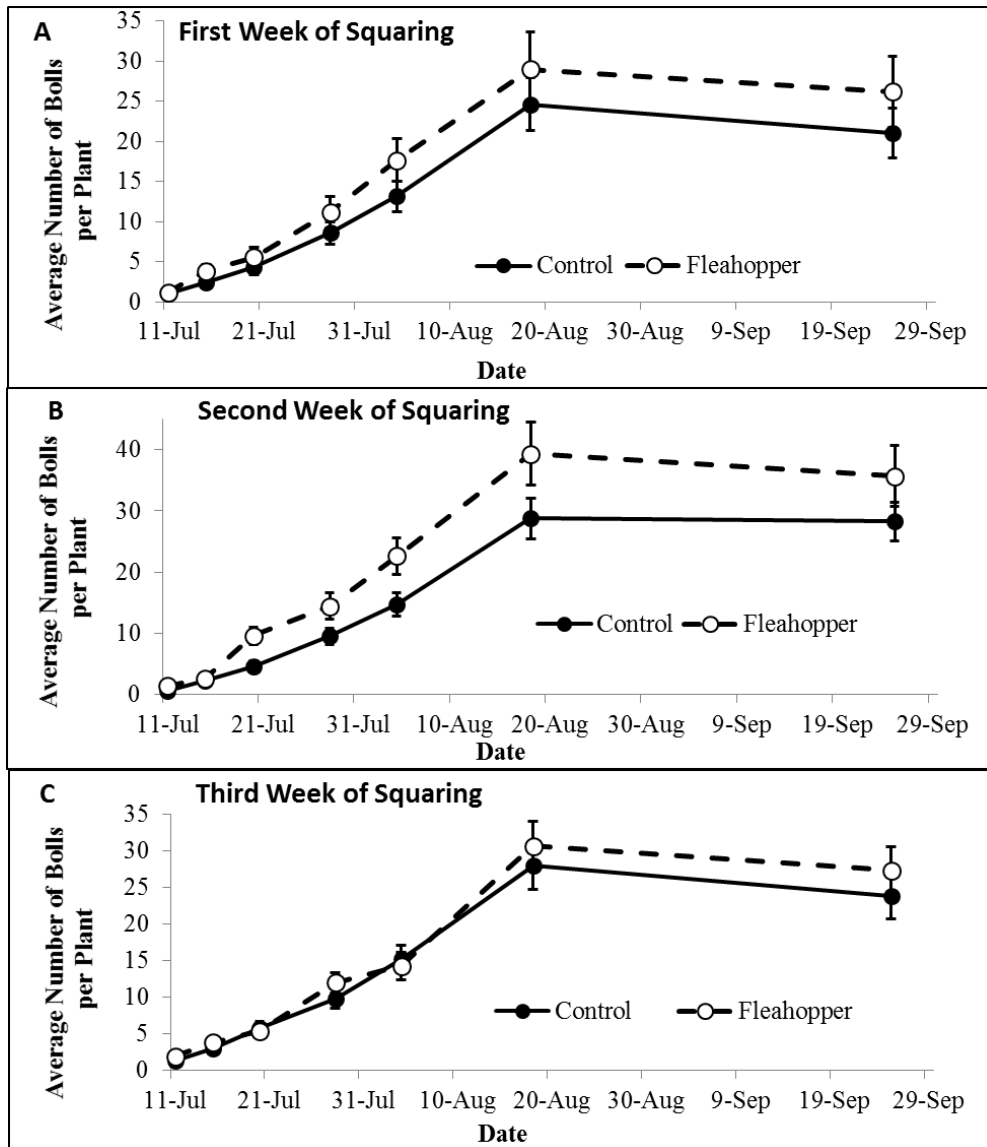
**Table 3. Treatment effects of fleahoppers and fleahopper timing of herbivory on lint production ( $\pm$  standard error) by fruiting position and seed weight in number in an open plot experiment in 2011.**

<b>Lint Quality 2011</b>	<b>df 1</b>	<b>df 2</b>	<b>F</b>	<b>p</b>
<b>Micronaire</b>				
<i>Fleahopper</i>	1	22	6.231	<b>0.023</b>
<i>Fleahopper*Week</i>	7	17	0.085	0.306
<b>Length</b>				
<i>Fleahopper</i>	1	22	0.058	0.813
<i>Fleahopper*Week</i>	7	17	2.029	0.150
<b>Uniformity</b>				
<i>Fleahopper</i>	1	22	0.549	0.469
<i>Fleahopper*Week</i>	7	17	1.633	0.221
<b>Strength</b>				
<i>Fleahopper</i>	1	22	4.871	<b>0.042</b>
<i>Fleahopper*Week</i>	7	17	1.852	0.179
<b>Elongation</b>				
<i>Fleahopper</i>	1	22	4.191	<b>0.057</b>
<i>Fleahopper*Week</i>	7	17	0.156	0.924

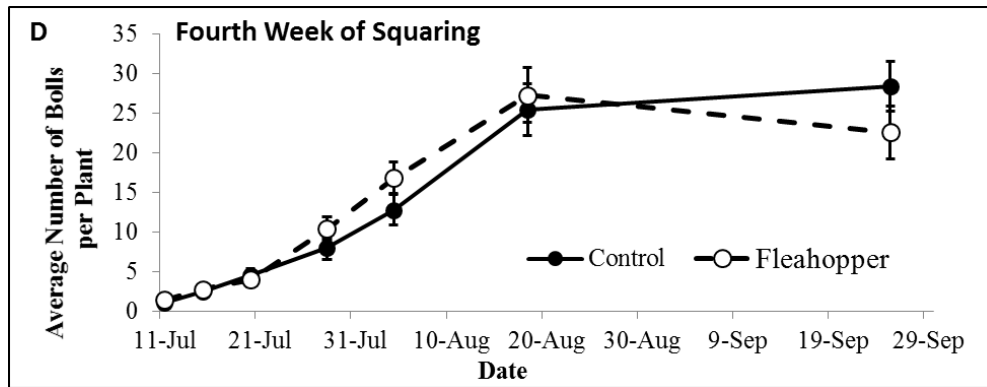
days sooner than control plants (*fleahopper*:  $F_{1,64}=3.443$ ,  $p=0.069$ ). Timing of herbivory, however, had no effect on the number of days to reach cutout (data not shown; *fleahopper\*week*:  $F_{7,57}=1.387$ ,  $p=0.226$ ). Despite a slightly accelerated rate of fruiting, neither the number of nodes (data not shown; *fleahopper*:  $F_{1,64} = 0.650$ ,  $p=0.423$ , *fleahopper\*week*:  $F_{7,56} = 0.679$ ,  $p=0.569$ ) nor the retention of first position fruits (data not shown; *fleahopper*:  $F_{1,64} = 0.735$ ,  $p=0.395$ , *fleahopper\*week*:  $F_{7,56}=0.870$ ,  $p=0.462$ ) differed between control and infested plants when NAWF  $\leq 5$ .

Timing of herbivory affected the number of bolls per plant during the mid-season fruiting period ( $F_{7,53}= 1.79$ ,  $p=0.031$ , wilks  $\Lambda = 0.588$ , partial  $\eta^2 = 0.046$ ; Figures 10 A-D). After we infested plants with fleahoppers during the second week of squaring, we





**Figure 10. Average number of bolls per plant over time in an open plot experiment in 2011 produced by control plants and plants infested with fleahoppers during the first (A), second (B), third (C) and fourth (D) week of squaring. The final date shows the number of bolls collected at harvest. Bars are  $\pm$  standard error. Significant differences ( $p < 0.05$ ) are indicated by an asterisk**



**Figure 10.** Continued.

observed an increased number of bolls over control plants on July 20<sup>th</sup> and again on August 4<sup>th</sup> (Figure 10B). Fleahoppers also marginally increased the number of bolls on July 28<sup>th</sup> ( $p=0.061$ ), but by the time we harvested, the effect was negligible ( $p=0.215$ ) (Figure 10B). There was also a trend for fleahopper infestation to precede an increase in the number of bolls per plant in plants infested during the first week of squaring (Figure 10A). There was, however, no indication of differential boll production in plants treated with fleahoppers during the 3<sup>rd</sup> and 4<sup>th</sup> week of squaring (Figures 10C and 10D).

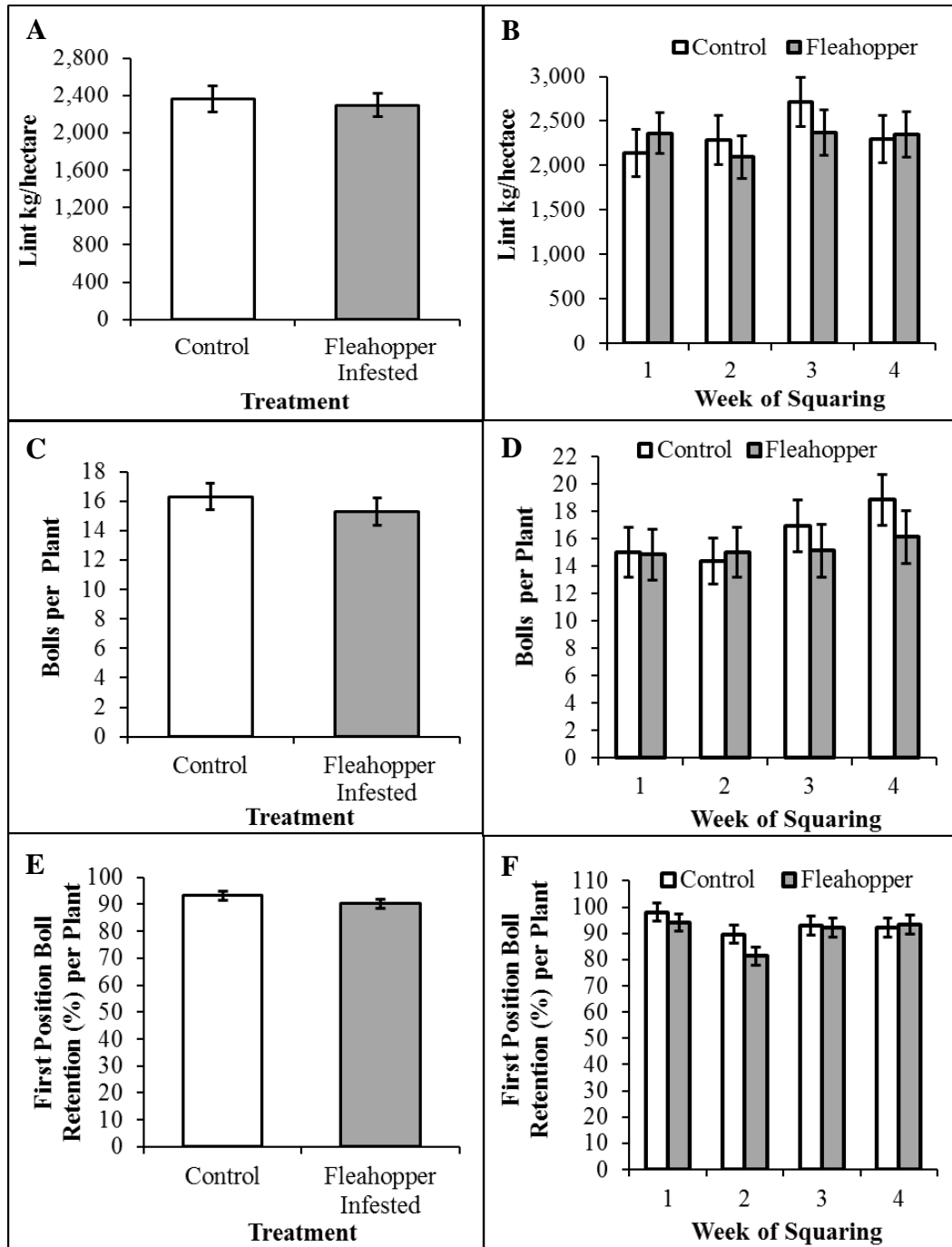
#### *Closed plot field study*

In 2013, fleahopper herbivory had no effect on the amount of lint, number of bolls, or retention of first position fruits at harvest regardless of timing of herbivory (Table 4, Figure 11). Likewise, the amount of lint harvested from the 1<sup>st</sup> and 2<sup>nd</sup> positions and the rest of the plant did not differ between treatments (Table 5), and fleahoppers did not cause variation in lint quality (Table 6). In addition, we found no

**Table 4. Treatment effects of fleahoppers and fleahopper timing of herbivory on harvest measures in a field cage experiment in 2013.**

<b>Harvest 2013</b>	<b>df 1</b>	<b>df 2</b>	<b>F</b>	<b>p</b>
<b>Lint (kg/h)</b>				
<i>Fleahopper</i>	1	125	0.130	0.720
<i>Fleahopper*Week</i>	7	119	0.472	0.703
<b>Bolls</b>				
<i>Fleahopper</i>	1	139	0.050	0.823
<i>Fleahopper*Week</i>	7	132	1.511	0.254
<b>First Position Bolls Retention (%)</b>				
<i>Fleahopper</i>	1	138	0.141	0.240
<i>Fleahopper*Week</i>	7	132	0.201	0.892
<b>Nodes</b>				
<i>Fleahopper</i>	1	138	0.225	0.636
<i>Fleahopper*Week</i>	7	132	1.489	0.223
<b>Vegetative Branches</b>				
<i>Fleahopper</i>	1	137	1.726	0.191
<i>Fleahopper*Week</i>	7	130	3.421	<b>0.020</b>
<b>Fruiting Branches</b>				
<i>Fleahopper</i>	1	137	0.490	0.485
<i>Fleahopper*Week</i>	7	130	0.731	0.536

difference in the number of nodes (Table 4, Figures 12A and 12B), or in the number of fruiting sites (*fleahopper*:  $F_{1,137}=1.603$ ,  $P=0.318$ , *fleahopper\*week*:  $F_{7,137}=0.929$ ,  $P=0.429$ ) between treatments. We did find, however, a significant effect of the timing of herbivory on the number of vegetative branches per plant at harvest (Table 4, Figure 12D). Plants infested with fleahoppers during the first week of squaring had significantly more vegetative branches than control plants. In contrast, there were no difference in the number of fruiting branches between treatment and control plants, regardless of timing of herbivory (Table 4, Figures 12E and 12F).



**Figure 11. Average lint kg/hectare (A, B), number of bolls (C, D), and retention of first position fruits (E, F) per plant at harvest in a field cage experiment in 2013. Figures 11A, 11C and 11E are data from the flea hopper effect, while Figures 11B, 11D, and 11F are data from the flea hopper\*week interaction**

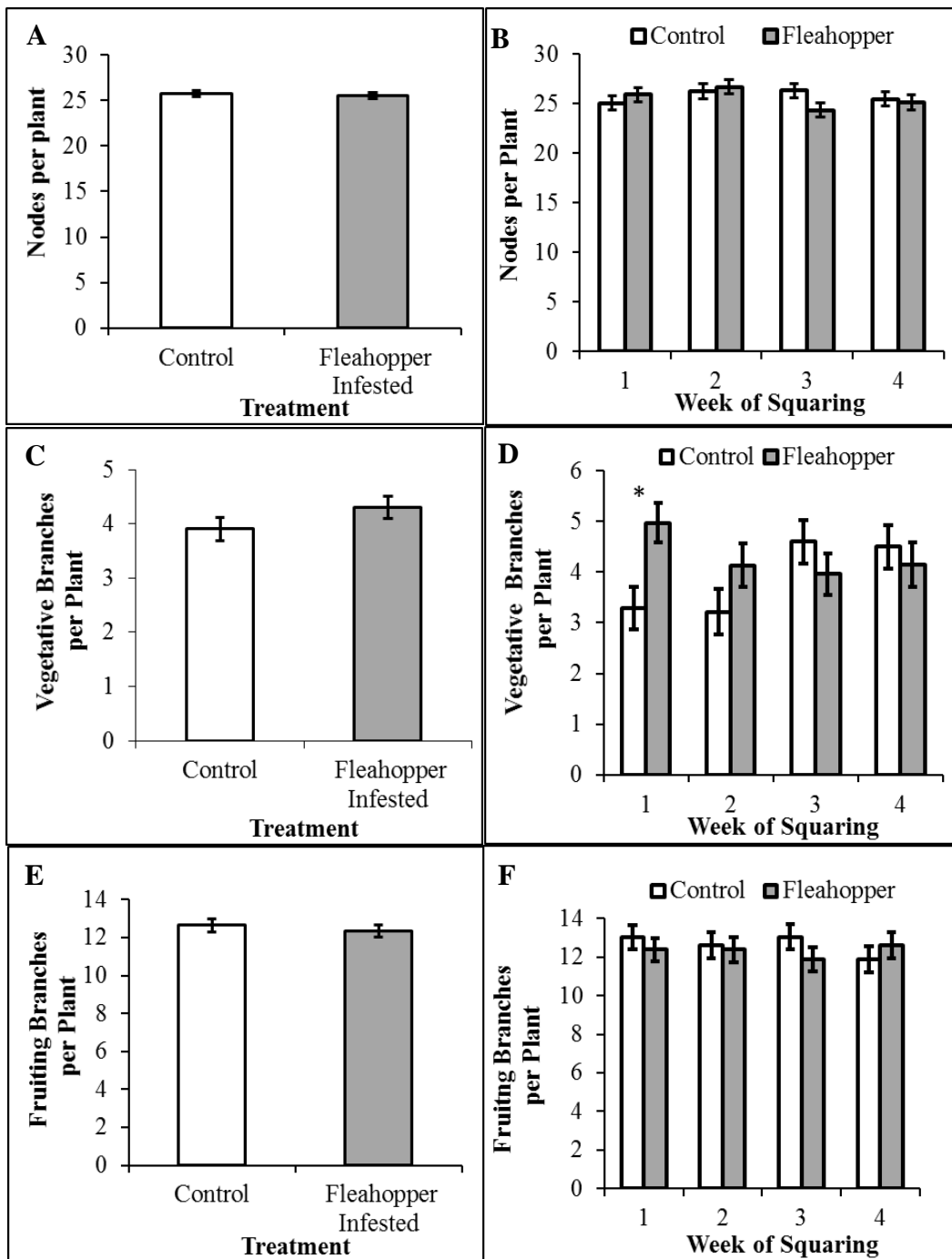
**Table 5. Effects of fleahoppers and fleahopper timing of herbivory on lint quality measures in a field cage experiment in 2013.**

<b>Lint Quality 2013</b>	<b>df 1</b>	<b>df 2</b>	<b>F</b>	<b>p</b>
<b>Micronaire</b>				
<i>Fleahopper</i>	1	22	0.000	1.000
<i>Fleahopper*Week</i>	7	17	0.146	0.673
<b>Length</b>				
<i>Fleahopper</i>	1	22	8.914	0.096
<i>Fleahopper*Week</i>	7	17	0.0026	0.118
<b>Uniformity</b>				
<i>Fleahopper</i>	1	22	3.661	0.196
<i>Fleahopper*Week</i>	7	17	1.6601	0.397
<b>Strength</b>				
<i>Fleahopper</i>	1	22	0.039	0.862
<i>Fleahopper*Week</i>	7	17	1.150	0.496
<b>Elongation</b>				
<i>Fleahopper</i>	1	22	9.697	0.091
<i>Fleahopper*Week</i>	7	1617	12.802	0.073

As in 2011, timing of herbivory had no effect on our measures of in season plant development. All plants matured at the same rate, showing no difference in the number of days to reach cutout (data not shown; *fleahopper\*week*:  $F_{7,37}=0.232$ ,  $p=0.873$ ) regardless of fleahopper infestation (data not shown; *fleahopper*:  $F_{1,44}=0.002$ ,  $p=0.969$ ). In addition, the number of nodes and the retention of first position fruits at cutout did not differ between treatments (*fleahopper*:  $F_{1,111} = 0.587$ ,  $p=0.445$ , *fleahopper\*week*:  $F_{7,105} = 1.857$ ,  $p= 0.143$ ; and *fleahopper*:  $F_{1,116} = 1.437$ ,  $p=0.234$ , *fleahopper\*week*:  $F_{7,110} = 0.673$ ,  $p= 0.571$  respectively). Blocking by field cage had a significant effect on all in season measures of plant development.

**Table 6. Effects of fleahoppers and fleahopper timing of herbivory on lint production by position ( $\pm$ standard error) in a field cage experiment in 2013.**

	<b>Lint (g) by Fruiting Position per Plant</b>		
<b>Week of Infestation</b>	<b>1st</b>	<b>2nd</b>	<b>Rest of Plant</b>
<b>Week 1</b>			
Control	20.71 $\pm$ 1.78	11.97 $\pm$ 1.49	21.36 $\pm$ 4.59
Fleahopper	20.77 $\pm$ 1.62	13.44 $\pm$ 1.31	25.50 $\pm$ 4.05
<b>Week 2</b>			
Control	20.77 $\pm$ 1.86	14.21 $\pm$ 1.56	21.90 $\pm$ 4.43
Fleahopper	19.64 $\pm$ 1.61	11.54 $\pm$ 1.35	23.16 $\pm$ 4.29
<b>Week 3</b>			
Control	22.27 $\pm$ 1.85	15.28 $\pm$ 1.55	29.88 $\pm$ 4.76
Fleahopper	20.83 $\pm$ 1.72	13.67 $\pm$ 1.45	22.68 $\pm$ 4.16
<b>Week 4</b>			
Control	19.59 $\pm$ 1.79	13.19 $\pm$ 1.50	25.03 $\pm$ 4.05
Fleahopper	18.95 $\pm$ 1.72	11.77 $\pm$ 1.50	28.90 $\pm$ 4.43
<b>Effects</b>			
Fleahopper	F <sub>1,124</sub> = 0.405 p= 0.526	F <sub>1,124</sub> = 0.061 p= 0.805	F <sub>1,122</sub> = 0.028 p= 0.868
Fleahopper*Week	F <sub>7,118</sub> = 0.071 p= 0.975	F <sub>7,118</sub> =0.240 p=0.667	F <sub>7,116</sub> = 0.717 p= 0.544



**Figure 12. Average number of nodes (A, B), vegetative branches (C, D), and fruiting branches (E, F) per plant at harvest in field cage experiment in 2013. Figures 12A, 12C and 12E are data from the treatment effect, while Figures 12B, 12D, and 12F are data from the treatment\*week interaction. Bars are  $\pm$ standard error.**

## Discussion

The purpose of this study was to determine how the timing of cotton fleahopper herbivory affects cotton compensatory ability in the Texas Blacklands. Contrary to our initial expectations, we found that that timing of fleahopper herbivory did not influence cotton yield. This result was unexpected given previous research showing that timing of manual square removal can cause variation in cotton's compensatory response (Kletter and Wallach 1982, Ungar et al. 1987, Sadras 1995, Stewart et al. 2001, Lei and Gaff 2003). Stewart et al. (2001), for instance, documented increased yield (i.e., overcompensation) following 100% square removal during the second week of squaring, but yield loss following 100% square removal during the fourth week of squaring. Similarly, both Lei and Gaff (2003) and Ungar et al. (1987) found that early square removal led to overcompensation in yield, while later square removal led to similar yield as control plants (i.e., compensation). Nevertheless, our results show that cotton can tolerate moderate cotton fleahopper infestations during the first four weeks of squaring. Fleahopper infested plants in both our open plot and field cage experiments produced similar yield as uninfested plants, with little effect on lint quality. Our data, therefore, reaffirm other studies which frequently demonstrate the compensatory capabilities of cotton.

We found in our open plot experiment that fleahopper herbivory altered cotton's architecture by increasing the number of nodes and the number of branches per plant (Figures 9A, 9C, and 9E). Given the short exposure to herbivory in our experiments, we credit these architectural changes to cotton's response to apical meristem damage, and



not to square loss. Damage to apical meristems releases cotton from apical dominance and activates dormant axillary buds which increases branching (Heilman and Namken 1981, Wilson 1982, Aarssen 1995, Lei and Gaff 2003). Release from apical dominance is a well described compensatory mechanism for many plant species and can trigger overcompensation (Paige and Whitham 1987, Sadras and Fitt 1997, Tiffin 2000). We did not, however, document changes in vegetative growth in our field cage experiment (but see Figure 12D). Instead, we observed that plant growth was likely affected by the field cages we used. Plants in field cages had abnormally long internode lengths and were very tall, reaching the top of the cages early in the experiment compared to plants growing outside cages (L. Garcia personal observation). Due to these effects, we suggest that future investigations should avoid using field cages that cover the entire plant.

There are several ways that changes in increased branching can bring about compensation. In some cases, increased branching can lead to increased number of fruiting sites. More fruiting sites provide additional opportunities for cotton to maintain its fruit load following damage (e.g., Lei and Gaff, 2003). However, we observed only a marginal increase in number of fruiting sites on fleahopper infested plants in either experiment, and so, this may not be the only compensatory mechanism which occurred in our experiment. Longer branches can also cause an increase in the number of fruiting sites. It is possible that although our fleahopper infested plants had more branches, control plants had longer branches, allowing them to produce similar numbers of fruiting sites.

It has also been suggested that increased investment into vegetative structures, such as increased branching, can increase cotton's photosynthetic potential. In turn, a better ability to acquire resources could increase cotton's fruit carrying capacity (Brook et al. 1992, Sadras 1995). Indeed, Sadras (1996a, 1996b) observed morphological changes, such as increased leaf area, increased verticality of branches, and increased internode lengths in damaged cotton which corresponded with increased radiation use efficiency. Similarly, Holeman and Oosterhuis (1999) found that square loss can increase cotton's CO<sub>2</sub> exchange rate. Our data set does not allow us to offer any suggestions about the photosynthetic capacity of our plants. We suggest, however, that future research continues to investigate these hypotheses because data on the photosynthetic responses of cotton to insect herbivory is very limited.

It is important to emphasize that cotton's various compensatory responses described above (i.e., increased branching, increased number of fruiting sites, and increased photosynthesis) are likely not mutually exclusive. They might all play a role in the variation in results across cotton compensation studies, including our own. Being able to accurately describe the conditions which facilitate cotton compensation (or overcompensation) remains difficult due to myriad abiotic and biotic conditions cotton experiences during the growing season that cannot always be controlled (Barman and Parajulee 2013). We predict that our results would change, for instance, if we also varied fleahopper densities. Parajulee et al. 2011, for example, found that cotton compensated for low (1 per plant) and high (4 per plant) fleahopper nymph densities, but overcompensated for moderate (2 per plant) fleahopper nymph densities. In addition,

our finding that early season square loss and/or meristem damage slightly accelerated cotton maturation contradicts other authors who found that damage delayed fruiting (Stewart et al. 2001, Barman and Parajulee 2013). Delayed fruiting is a considerable concern for growers because it can limit cotton's compensation capacity if bolls do not have enough time mature for harvest before poor weather conditions develop (Sadras 1996a). Overall, we recommend that researchers continue to clarify cotton's compensatory responses under various conditions with the goal of improving the accuracy of ETs for cotton fleahoppers and reducing pesticide use.

In addition, more research is needed to identify alternatives to insecticides for fleahopper control. Trap cropping, for instance, has been successfully used to reduce pesticide use against other mirid species by attracting mirids out of cotton fields. For example, Godfrey and Leigh (1994) found that alfalfa, *Medicago sativa* (Fabaceae), was an efficient trap crop for *L. herperus* Knight in the United States and Lu et al. (2009) found that mungbean, *Vigna radiates* (Fabaceae), was an efficient trap crop for *Apolygus lucorum* Meyer-Dur in China. The applicability of trap cropping for cotton fleahopper control, however, is unknown. Follow up work to Barman et al. (2012a) is needed. He found that cotton fleahoppers prefer horsemint, *Monarda punctatae* (Lamiaceae), over cotton and predicted that horsemint could be used as an effective trap crop in West Texas (Barman et al. 2012a, 2012b). Sex pheromones could also be developed to trap, kill, or monitor cotton fleahoppers, or disrupt their mating. Sex pheromones have been identified for many mirid species worldwide, but research on their application is just beginning (Innocenzi et al. 2005, Lowor et al. 2009, Zhang et al. 2015)

Finally, research is needed to determine the genetic mechanisms which underlie cotton's compensatory responses. Genetic analysis of tolerant genotypes could advance cotton breeding efforts and perhaps determine why, physiologically, pilose (hairy) cotton is more tolerant to fleahopper herbivory than smooth leaf cotton despite attracting higher fleahopper densities (Knutson et al. 2013). Recently, Siddappaji et al (2013) used QTL and microarray analysis to identify *G6PDH1* as having a significant role in *Arabidopsis* overcompensation. *G6PDH1* encodes a regulatory enzyme in the oxidative pentose-phosphate pathway (OPPP) which is responsible for converting glucose to ribose-5-phosphate and ultimately leads to nucleotide synthesis (Hauschild and von Schaewen 2003). *G6PDH1* up-regulation, therefore, is consistent with increased DNA content due to endoreduplication (i.e., genome replication without mitosis) triggered by apical damage to *Arabidopsis* (Scholes and Paige 2011). Similar genetic analyses of cotton could revolutionize production if analogous genes could be located and constitutively up-regulated in cotton through genetic modification (Siddappaji et al. 2013). Endoreduplication is currently studied in cotton in regards to its role in the elongation of fiber (Breuer et al. 2014), but research on endoreduplication following meristem removal in cotton has yet to be undertaken.

In summary, we found that cotton can compensate for moderate fleahopper herbivory, regardless of timing of herbivory. Fleahoppers, however, modified cotton's canopy structure by increasing branching. Our study supports others which find that cotton can compensate for square loss and apical damage, such as that caused by mirids like the cotton fleahopper (Baugh et al. 2003, Barman and Parajulee 2013). Therefore,

delaying spraying until mirids are above thresholds can be economically advantageous (Whitehouse 2011). Continued work to clarify cotton's compensatory responses under various conditions can help producers avoid unnecessary insecticide use when mirid herbivory will not influence yield (Rosenheim et al. 1997, Baugh et al. 2003, Abrol 2014).

CHAPTER IV  
INVESTIGATION INTO THE POLLINATION EFFICIENCY OF A PLANT BUG  
(HEMIPTERA: MIRIDAE)

**Introduction**

Insect pollinators are frequently studied to determine their economic impact on crop production (Klein et al. 2007, Aizen et al. 2009). For many of the world's crops, they increase yields by cross fertilizing flowers (Klein et al. 2007, Garibaldi et al. 2013). Honey bees, *Aphis mellifera* (Hymenoptera: Apidae), in particular, are introduced to many fields due to their morphological and behavioral adaptations to collect, carry, and transfer pollen between flowers (Kevan and Baker 1999, Larson et al. 2001). With the global decline of honey bee health, however, more attention is being paid to other insect pollinators, such as wild bumble bees *Bombus spp.* (Hymenoptera: Apidae), carpenter bees *Xylcopa spp.* (Hymenoptera: Apidae), and flies (Diptera) (Potts et al. 2010, Garibaldi et al. 2013, Garratt et al. 2014, Orford et al. 2015). Notably, it has been found that for many crops, pollinator diversity contributes more to increasing yields than pollinator abundance (Hoehn et al. 2008, Brittain et al. 2013, Rogers et al. 2014). Pollinators can have different preferences for flower heights, visit flowers at different times of day, and have different behaviors for manipulating the pollen they carry (Hoehn et al. 2008). As a result, pollination services by multiple species can be complementary and increase cross-pollination among flowers (Hoehn et al. 2008). A better understanding of pollination services provided by diverse pollinators will aid the

development of sustainable agricultural practices (Gaffney et al. 2011, Garratt et al. 2014, Gill and O'Neal 2015).

In general, pollination by insects is understudied for fiber crop cotton. It is likely that pollination by insects in cotton fields has been limited in the past due to high pesticide use (Pimentel et al. 1992, Ward and Ward 2001). In addition, pollinators may have been overlooked because cotton is a self-pollinating crop and pollination services by insects are not necessary for cotton to develop fruit (McGregor 1976). Nevertheless, a handful of studies have shown that when pollinators are introduced into cotton fields, seed and lint yield can be increased. For example, introducing honey bees was found to increase cotton yield by 15%-25% (McGregor et al. 1955, Rhodes 2002) and introducing bumble bees was found to increase cotton yield by 15- 32% (Saeed et al. 2012). Overall, these studies suggest that insect pollinators may be important and greatly underappreciated contributors to cotton production, especially now that pesticide use has been significantly reduced in many cotton fields (Free 1993, Ward and Ward 2001, Pires et al. 2014).

For many crops, including cotton, there are numerous, less conspicuous insect visitors to flowers, such as beetles (Coleoptera), thrips (Thysanoptera), and true bugs (Hemiptera) (Ananthakrishnan 1982, Kevan and Baker 1983, Young 1986, Willemstein 1987, Wheeler 2001). There is little information available, however, about the capacity for these insects to be pollinators (Kevan and Baker 1983, 1999, Alarcon 2010). Pierre and Hofs (2010) provide the only exception we are aware of for cotton. They found that flower beetles, *Astylus atromaculatus* (Coleoptera: Melyridae) were unexpected, but

efficient pollinators of cotton in South Africa. These beetles frequently visited flowers and carried a similar pollen load as honeybees. Although these beetles are also considered pests of cotton seeds and seedlings, they could provide some benefit to crop production once the plant reaches the flowering stage by cross-fertilizing flowers (McGregor 1976, Pierre and Hofs 2010). Cotton flowers are only open for one day for fertilization before withering (Stewart et al. 2010), and so, opportunities to cross-pollinate cotton with viable pollen grains are limited. An understanding of what insects are visiting cotton flowers and capable of cross-pollinating, could contribute to increasing cotton yields.

We observed that plant bugs, cotton fleahoppers *Pseudatomoscelis seriatus* (Hemiptera: Miridae), are frequent flower visitors of upland cotton, *Gossypium hirsutum* (Malvaceae) in Texas. Cotton fleahoppers are considered early season pests of cotton because they feed on flower buds and cause them to abscise (Stewart and Sterling 1989). Once the cotton is in its flowering stage, however, fleahoppers can be seen dusted with pollen while foraging within cotton flowers (L Garcia personal observation). These fleahoppers are likely visiting flowers to feed on pollen grains (Burden et al. 1989, Wheeler 2001), but because fleahoppers are very mobile insects (Reinhard 1926), we hypothesized that fleahoppers might contribute to cross-pollination of cotton as they forage among flowers while carrying pollen grains.

Here we present the results of our investigation into the pollination efficiency of the cotton fleahopper. We quantified how frequently fleahoppers visited cotton flowers and how many pollen grains they carried on their bodies (i.e., their pollen load). We



also used fluorescent powder as a pollen analog to estimate fleahopper dispersal among flowers while carrying a pollen load. Finally, we determined the capacity of cotton fleahoppers to cross-fertilize flowers by measuring seed and lint yield of self-sterile flowers visited by fleahoppers carrying pollen grains (i.e., their pollination efficiency).

## **Methods**

### *Study site*

Fleahopper flower visitation, pollen load, and dispersal experiments were conducted in summer 2013 and fleahopper pollination efficiency experiments were conducted in the same field in summer 2014. Seeds of cotton cultivar ‘Deltapine 174 RF’ were planted in a conventionally managed 11 hectare field at the Texas A&M Field Laboratory in Burleson Co., TX. Irrigation was applied to the field approximately biweekly. Glyphosate was used to control weeds but no insecticide was used at this field site.

### *Fleahopper flower visiting frequency*

Observations of fleahoppers at flowers were conducted using an instantaneous scan sampling technique (Altmann 1974). Forty randomly chosen flowers were observed on July 9<sup>th</sup>, July 25<sup>th</sup>, July 30<sup>th</sup>, and August 7<sup>th</sup> 2013 at 1100, 1300, and 1500. The number of adult fleahoppers at each flower observed at each time point was recorded. These dates were mostly sunny with an average high temperature of 38.75°C and low temperature of 25.28°C. We determined how observation date and time affected fleahopper flower visiting frequency using a Chi Square analysis (JMP, Version 11, SAS Institute Inc., Cary, NC 1989-2007).

### *Fleahopper pollen load*

Pollen load was counted from thirty-two fleahoppers collected while foraging freely in cotton flowers on August 2<sup>nd</sup> 2013 between 1500 and 1700. Fleahoppers were frozen until grains could be counted under a microscope at 8X magnification. To prepare the samples for the microscope, we removed pollen grains from fleahoppers, dyed the grains, and mounted them to slides. To make the dye solution, 1g of Safranin O (Sigma-Aldrich Saint Louis, MO) was mixed with 100 ml of 50% ETOH (Jones 2012). Then, we placed the fleahopper into a microcentrifuge tube with 40  $\mu$ l of the dye solution. We vortexed the sample for 1 min to dislodge pollen grains from the fleahopper body and then centrifuged the sample at 10000gs for 15 seconds. We used a pipette to transfer the liquid solution containing pollen grains one drop at a time to a glass microscope slide sitting on a hot plate set at 70°C, waiting for the ETOH to evaporate in-between adding drops. Once all the ETOH evaporated, only dyed pollen remained on the slide. To complete slide preparation, a small amount of Glycerin (Sigma-Aldrich Saint Louis, MO) was added and the sample was covered with a cover slip and sealed by painting the edges of the cover slip with clear nail polish.

### *Fleahopper dispersal*

In order to estimate fleahopper dispersal among flowers while carrying a pollen load we used fluorescent powder as a pollen analog and examined cotton stigmas for evidence of fluorescent powder left by foraging fleahoppers. Florescent powder is an appropriate pollen analog for studying pollination efficiency in many systems (Adler and Irwin 2006). Preliminary testing demonstrated that dusted fleahoppers can survive in the

lab for at least 24 hours and transfer the fluorescent powder to excised cotton stigmas inside a vial. Fleahoppers used in this experiment were collected from nearby feral fields of silverleaf nightshade, *Solanum elaeagnifolium*, and maintained in the lab with organic green beans (*P. vulgaris*) until use. On the morning of August 2<sup>nd</sup>, 2013 we dusted 240 fleahoppers with fluorescent powder (Bioquip Products Luminous Powder, Rancho Dominguez, CA). At 1200 we released 24 dusted fleahoppers onto ten 1.8m<sup>2</sup> lumite field cages that had, on average, eight flowering cotton plants, and 14 flowers in each cage. Fleahoppers were released onto the tops of plants nearest to the cage's four corners (6 fleahoppers per corner). We recorded fleahopper visits to flowers using instantaneous scan sampling of all flowers inside the cages at 1400 and 1600. At 1700, 5 hours after the fleahopper were initially released, we harvested all the flowers in each field cage and stored them in plastic bags. Flowers were kept refrigerated until their organs could be checked for fluorescent powder deposition under a dissecting microscope using a UV light.

#### *Pollination efficiency*

The capacity of cotton fleahoppers to cross-fertilize flowers was determined by measuring seed number, seed weight, and lint yield of self-sterile flowers visited by fleahoppers carrying pollen grains. Self-sterilization (i.e., emasculation) was conducted in order to prevent confounding fleahopper fertilization with self-fertilization in our results. Flower treatments in this experiment were: (1) no pollination, (2) self-pollination (3) fleahopper pollination, (4) natural pollination (control). On three dates in August (5<sup>th</sup>, 6<sup>th</sup>, and 13<sup>th</sup>) randomly chosen flowers in our field were prepped for each

treatment in this experiment. We chose flowers opened closest to the mainstem (i.e., the first fruiting position on a fruiting branch) because flowers at different positions on branches produce different sized fruits (Bednarz and Roberts 2001). For the no pollination treatment, between 0700 and 0900 ten to fifteen flowers were emasculated by submerging the floral organs in water for 1 minute and then bagging the flowers to prevent pollinator visitation. Water destroys cotton pollen grains and is a proven emasculation tool, but pollen grains placed on the stigma after it has dried can fertilize the flower (Burke 2002). For the self-pollination treatment, between 0700 and 0900 ten to fifteen flowers were placed inside an 8cm<sup>2</sup> organdy drawstring bag to prevent pollinator visitation during the day. For the fleahopper-pollination treatment, between 0700 and 0900 ten to fifteen flowers were emasculated as described above and two adult fleahoppers carrying pollen were added to a mesh cage enclosing the flower after the flowers dried. Fleahoppers were collected from nearby feral fields of silverleaf nightshade, *Solanum elaeagnifolium*, the day before the experiment and fed organic greenbeans, *Phaseolus vulgaris* (Fabaceae), in the lab (Breene et al. 1989). We placed two fleahoppers in a vial with an excised cotton stigma and allowed the fleahoppers to forage on anthers for one hour to pick up pollen before transferring them to the emasculated flower cages. Fleahoppers remained in the cages until 1700 and cages prevented flower visitation by other pollinators throughout the day. Finally, for natural pollination (control) we allowed ten to fifteen flowers to self and/or out-cross as they would naturally. At the end of each day, flowers from all treatments were placed inside 8cm<sup>2</sup> organdy drawstring bags to protect developing fruit from herbivores. When the

fruits matured, they were collected and ginned to separate lint from seeds for counting and weighing. Data were analyzed using an ANOVA model and means comparison tests were performed using Tukeys HSD ( $\alpha= 0.05$ ) (JMP, Version 11, SAS Institute Inc., Cary, NC 1989-2007).

## **Results**

### *Fleahopper flower visiting frequency*

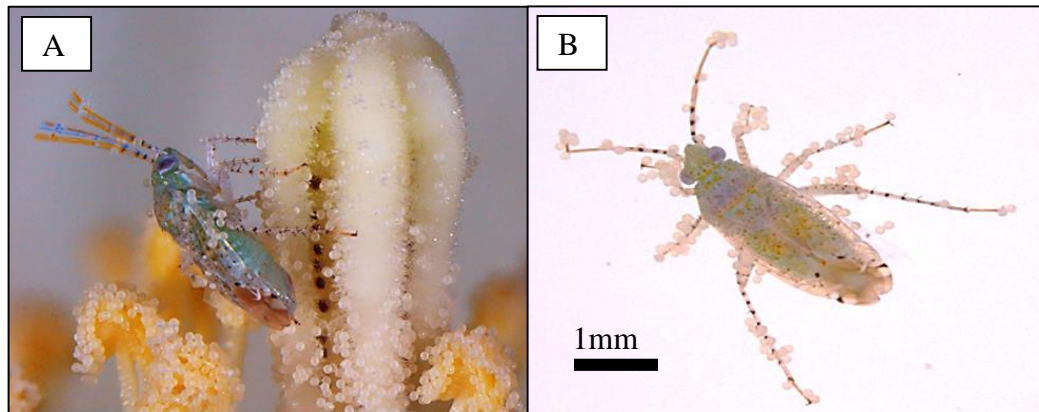
Fleahoppers frequently visited flowers in our study site. Fleahoppers were observed during 19.5% of all scan sampling time points; in total we observed 113 adult fleahoppers visiting flowers. An average of  $1.2 \pm 0.05$  adult fleahoppers (min: 1, max: 3) were observed in 43.1% of all flowers (69/160flowers). Observation date or time did not influence fleahopper flower visiting frequency ( $\chi^2_{(6,86)}=4.996$ ,  $p=0.5433$ ).

### *Fleahopper pollen load*

The majority of fleahoppers (85%) were carrying pollen grains (Figures 13A and 13B) and on average, fleahoppers carried an average of  $25.06 \pm 7.21$  pollen grains per insect (median: 5.5 pollen grains). The maximum number of pollen grains observed per fleahopper was 163 pollen grains.

### *Fleahopper dispersal*

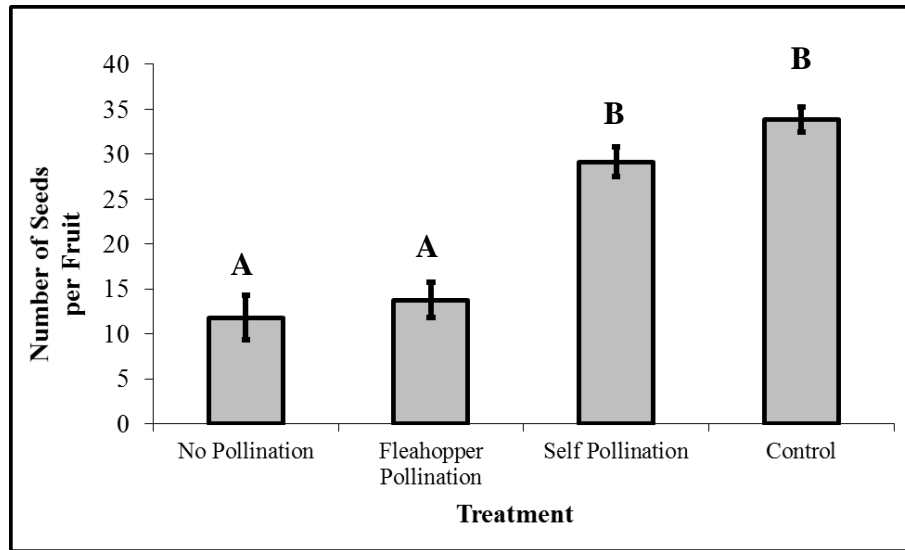
At both observation times, 17% of the powder dusted fleahoppers we released were observed foraging in flowers and they visited 30% of the flowers inside the cages throughout the day. In addition, 12.5% of visited flowers had fluorescent powder on their floral organs at the end of the experiment. Half (50%) of the flowers with powder had powder on stigmas, 12.5% had powder on anthers, and 37.5% had powder on petals.



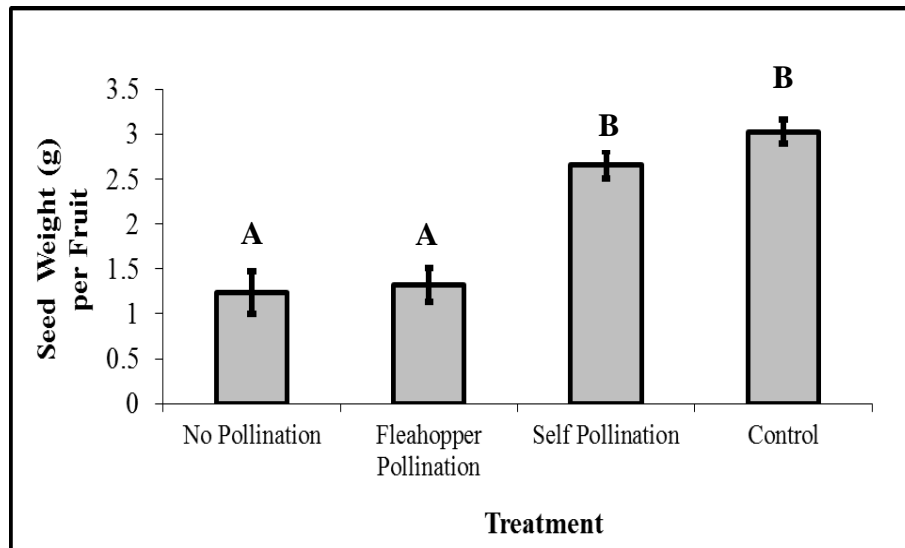
**Figure 13.** Photographs of a cotton fleahopper under a dissecting microscope (A) foraging on a cotton stigma and (B) carrying cotton pollen grains.

#### *Fleahopper pollination efficiency*

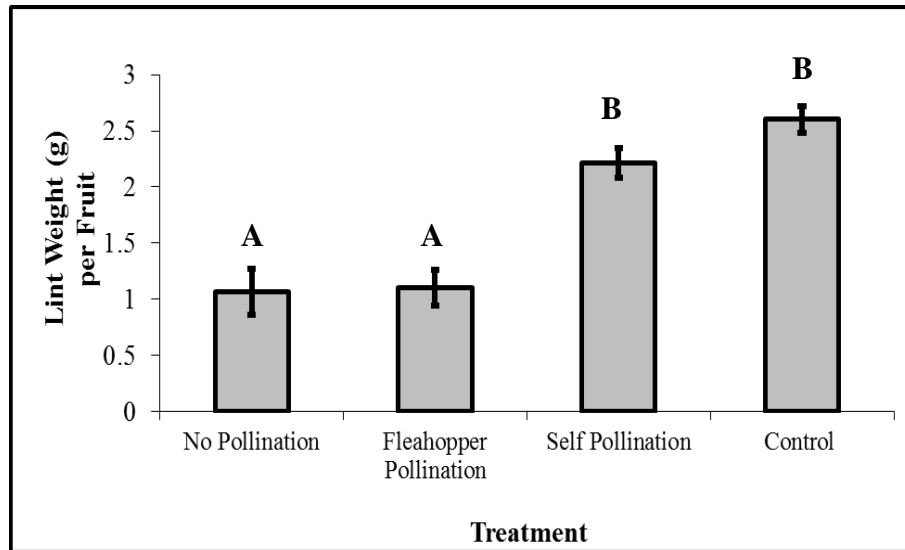
Seed number, seed weight and lint yield varied among treatments. Control and self-pollinated flowers developed into fruits with significantly more seeds ( $F_{3,80} = 34.31$   $p < 0.0001$ ; Figure 14), heavier seeds ( $F_{3,80} = 15.24$   $p < 0.0001$ ; Figure 15), and more lint yield ( $F_{3,80} = 11.31$   $p < 0.0001$ ; Figure 16) than emasculated and fleahopper pollinated plants. Our emasculation treatment was likely successful, as evidenced by significantly lower yields from emasculated flowers compared to self-pollinated flowers. Measurements from emasculated flowers and fleahopper pollinated plants, however, did not differ. In addition, emasculated flowers had the most abscised fruits (56.5%) followed by fleahopper-pollinated flowers (53.0%). Far fewer self-pollinated flowers (18.4%) or control flowers (20.0%) abscised.



**Figure 14. Number of seeds per fruit among pollination treatments.** Bars represent treatment means and error bar represents  $\pm$  standard error of the mean. Treatment means listed with the same letter are not significantly different ( $P=0.05$ ).



**Figure 15. Seed mass per fruit among pollination treatments.** Bars represent treatment means and error bar represents  $\pm$  standard error of the mean. Treatment means listed with the same letter are not significantly different ( $P=0.05$ ).



**Figure 16. Lint weight per fruit among pollination treatments.** Bars represent treatment means and error bar represents  $\pm$  standard error of the mean. Treatment means listed with the same letter are not significantly different ( $P=0.05$ ).

## Discussion

Cotton fleahoppers are clearly anthophilous (flower-loving) insects. We observed adult cotton fleahoppers frequently foraging in cotton flowers and with pollen grains attached to their legs, abdomen, and antennae. In addition, carrying a pollen analog did not hinder their dispersal among flowers inside field cages. Fleahopper size (3.0-4.0mm), however, likely limits their ability to carry enough grains to contribute to development of fully out-crossed cotton flowers. Cotton flowers require fertilization with at least 50 viable pollen grains to develop into a full sized fruit (McGregor 1976), but we found that most fleahoppers could not carry that size of pollen load. Correspondingly, fleahopper-pollinated plants produced a similar number of seeds, seeds of similar mass, and a similar lint yield as emasculated flowers in our study.



Cotton flowers and pollen grains are very large compared to the size of cotton fleahoppers; *G. hirsutum* flowers are around 75mm in width and pollen grains are approximately 100µm (Jones and McCurry 2012). Cotton fleahoppers, therefore, can carry a limited number of cotton pollen grains compared to other insects due to their small size. Honey bees, for instance, are up to four times larger than fleahoppers (12-15mm) can carry around 500 cotton pollen grains (Pierre and Hofs 2010), while bumble bees, can be seven times larger and can carry thousands of grains (Berger et al. 1988). Insect pollinator size is very an important trait in regards to its pollination efficiency because the pollinator needs to carry a suitable number of viable grains and they need to contact the flower's stigma while foraging (Maiti et al. 2012). Despite their small size, however, cotton fleahopper mobility was not hindered by carrying a pollen analog and they readily deposited fluorescent powder on cotton stigmas. It is possible, therefore, that while individual cotton fleahoppers are not important cotton pollinators, cotton fleahoppers could contribute to cotton cross-fertilization as part of a community of flower visitors (Wheeler 2001). In addition, there are larger plant bugs in other cotton growing regions that may be able to carry more pollen than the cotton fleahoppers and contribute more to cotton pollination than the mirid we investigated.

Notably, our study supports others which suggest that insect pollinators could be important contributors to cotton production (McGregor et al. 1955, Free 1993, Ward and Ward 2001, Rhodes 2002, Pierre and Hofs 2010). Like Saeed et al. (2012), we found that flowers exposed to pollinators produced fruits with about 15% more seed and lint yield than self-pollinated flowers. A 15% increase in yield could translate into

considerable financial gain for growers. In order to capitalize on these benefits, much more study is needed on the pollination ecology of cotton. Avenues of future research include documenting flower visitor diversity in different cotton growing regions, measuring the effects of landscape management on pollinator populations, and measuring the effects of *Bt* cotton varieties on pollinator communities (Klein et al. 2007, Ricketts et al. 2008). Managing pollination services in cotton agriculture to is expected to be an sustainable approach to increase yield without increasing the area of cultivated land (Klein et al. 2007, Kevan et al. 2009).

In addition, we predict that the small size of cotton fleahoppers would not prevent them from being pollinators of other host plants with smaller or composite (i.e. clustered flowers) flowers, like those in the plant family Asteraceae or Apiaceae (Willemstein 1987, Wheeler 2001). Levin et al (1967), for example, found that *Lygus hesperus* Knight was an efficient pollinator of safflower, *Carthamus tinctorius* (Asteraceae) which has a composite flower head that is only 15mm in width and pollen grains that are half the size of cotton pollen gains, measuring 52-67  $\mu\text{m}$  (Smith 1996). These small flowers were easily cross-pollinated by *L. hesperus*, which was able to transfer pollen to 28% of self-sterile safflower inside field cages (Levin et al. 1967). For comparison, honey bees cross-pollinated 56% of the plants and paper wasps, *Polistes exclamans exclamans*, cross-pollinated 53% of the plants (Levin et al. 1967). Like *L. hesperus*, cotton fleahoppers frequent many other host plants with much smaller flowers than cotton, such as wholly croton, *Croton capitatus* (Euphorbiaceae), silverleaf nightshade, *Solanum elaeagnifolium* (Solanaceae), and horsemint, *Monarda punctata*

(Lamiaceae) (Esquivel and Esquivel 2009). Our study, however, is the only study of cotton fleahopper pollination efficiency and how they affect the reproduction of their wild hosts is unknown.

Overall, few authors have investigated the pollination abilities of plant bugs (Wheeler 2001). Several authors have reported that plant bugs are inefficient pollinators for some plants (Bohart and Nye 1960, Lindsey 1984), but the notion they could be minor pollinators for others should not be disregarded without experimentation (Scott 1983, Wheeler 2001). We found that cotton fleahoppers can readily transfer a pollen analog to cotton stigmas and we suggest that they could contribute to cotton pollination as part of a community of pollinators, or pollinate some of their wild hosts. When studying pollinator communities, plant bugs should not be overlooked. Frequent flower visitors like plant bugs could contribute to the pollinator diversity that we will rely on to increase crop yields by transferring pollen grains among flowers as they forage.

CHAPTER V  
PLANT-MEDIATED INTERACTIONS BETWEEN COTTON FLEAHOPPERS AND  
LEPIDOPTERAN PESTS

**Introduction**

Plants are not defenseless against herbivores. They have many morphological and physiological defenses which can reduce or deter herbivory (Karban and Baldwin 1997, Taiz and Zeiger 2010). Some defenses are constitutive, meaning that they are always present, but others are induced and are produced only following damage. Induced responses have been intensely studied in order to determine their effects on the attacking herbivore (Karban and Baldwin 1997, Agrawal 2005). They can, however, initiate plant-mediated interactions among herbivores by affecting subsequent herbivores which may be temporally or spatially separated (Denno and Kaplan 2007, Kessler and Halitschke 2007, Kaplan et al. 2009).

In some cases, defenses induced by one herbivore can increase a plant's resistance to subsequent herbivory by other species (Agrawal 1998, 1999). In this way, induced resistance can have positive effects on plant fitness, when damage by more a harmful herbivore is reduced or prevented following induction of defenses by a less harmful herbivore. Kessler and Baldwin (2004) called this effect an herbivore-induced plant vaccination. They found, for instance, that plant bugs, *T. notatus* (Hemiptera: Miridae), vaccinated wild tobacco, *Nicotinana rustica* (Solanaceae), against hornworms, *Manduca quinquemaculata* and *M. sexta* (Lepidoptera: Sphingidae) (Kessler and

Baldwin 2004). Hornworms developed slower and gained less weight while feeding on plants previously damaged by the plant bugs. As a result, plant bug herbivory increased wild tobacco fitness when both plant bugs and caterpillars were present. *T. notus* herbivory alone did not affect wild tobacco fitness, but caterpillar herbivory would have been harmful.

Alternatively, induced changes can increase plant susceptibility to herbivores (Agrawal 2005, Denno and Kaplan 2007). Agrawal and Sherriffs (2001) found, for example, that damage by *Pieris rapae* larvae (Lepidoptera: Pieridae), made wild radish, *Raphanus raphanistrum* (Brassicaceae), more susceptible to subsequent oviposition by adult *P. rapae* and to feeding by flea beetles, *Phyllotreta* spp. (Coleoptera: Chrysomelidae). Induced glucosinolates and other volatiles in wild radish were thought to have assisted the flea beetle, which is a specialist, to find its host. Induced susceptibility can also be due to increased nutritional quality of damaged plants. Root feeding beetles *Phyllopertha horticola* (Coleoptera:Scarabidae), for instance, induced increased foliar nitrogen in *Capsella bursa-pastoris* (Brassicaceae) (Gange and Brown 1989). Foliar feeding aphids, *Aphis fabae* (Hemiptera: Aphididae), benefited from this nutritional change and grew faster, had higher fecundity, and developed higher densities on damaged plants. Finally, in other cases, herbivores can interfere with the production of defenses that would have protected the plant against other herbivores. Nematode root herbivory, for example, interfered with nicotine production in tobacco, *Nicotiana tabacum* (Solanaceae). As a consequence, tobacco became more susceptible to

caterpillar, *Trichoplusia ni* (Lepidoptera: Noctuidae) and *Epitrix spp.* flea beetles (Coleoptera: Chrysomelidae) (Kaplan et al. 2008, 2009).

How plants benefit from induced resistance, or are harmed by induced susceptibility has immense applied significance. Typically, pest management strategies are geared to target a single pest species and do not consider how plant mediated interactions of the target pest with other herbivores can affect yield. Although only a few researchers have investigated this matter, their findings suggest that this traditional approach disserves growers. Wielgoss et al. (2012), for instance, found that plant bug, *Helopeltis sulawesi* (Hemiptera: Miridae), deters oviposition by cocoa pod borer, *Conopomorpha cramerella* (Lepidoptera: Gracillariidae) on cacao trees *Theobroma cacao* (Malvaceae). The cocoa pod borer is a major cacao pest, and so, when both the plant bug and pod borer are present the plant bug facilitates increased yields by inducing resistance against the pod borer. Remarkably, models predicted that optimal yield could be achieved when 50% of *cacao* pods are damaged by *H. sulawesi*.

We investigated ability of another plant bug, the cotton fleahopper, *Pseudatomoscelis seriatus* (Hemiptera: Miridae), to induced resistance or susceptibility in upland cotton, *Gossypium hirsutum* (Malvaceae), to Lepidopteran pests. Cotton fleahoppers are piercing sucking herbivores that feed on cotton flower buds (i.e., squares) and terminal meristems (Stewart and Sterling 1989). Whether the cotton fleahopper can induce plant defenses is unknown, but they have been shown to induce ethylene production in cotton tissues (Duffey and Powell 1979, Grisham et al. 1987). Ethylene is a plant hormone that mediates production of defense proteins,

polyphenoloxidase (PPO) peroxidase (POD), and proteinase inhibitors (PIs) in some plants (Kruzmane et al. 2002, Steinite et al. 2004). These proteins are effective defenses against lepidopteron larvae (Cipollini et al. 2004, Kessler et al. 2004). We hypothesized that cotton fleahoppers could positively influence cotton yield by vaccinating it against lepidopteran pests by inducing defenses, such as PPO, POD and PIs. Alternatively, cotton fleahoppers could induce nutritional changes that increase cotton susceptibility to caterpillars. Holman and Oosterhuis (1999), for instance, found that damage to cotton squares created a carbon sink in the terminal tissues, while Sadras (1996b) found that injury increased leaf nitrogen content. If fleahopper herbivory caused similar effects they could improve the performance of subsequent herbivores and exacerbate pest problems in cotton (Showler 2001, Diamond et al. 2008).

We suggest that a better understanding of how cotton fleahoppers interact with other herbivores through induced plant resistance or susceptibility can improve pest management strategies. Here we describe our preliminary work to determine whether cotton fleahopper herbivory induces resistance or susceptibility of cotton to beet armyworm larvae, *Spodoptera exguia* (Lepidoptera: Noctuidae). Beet armyworms are chewing herbivores that feed on fruits and skeletonize cotton leaves. We conducted a field study to determine the effects of fleahopper induction on beet armyworm herbivory and cotton yield. We conducted a greenhouse study to determine the effects of fleahopper induction on beet armyworm larvae growth and damage to cotton leaves. We also sought to use RT- QPCR to determine what cotton plant defense genes are affected by cotton fleahopper herbivory and if defenses are mediated by ethylene.

## Methods

### *Field study*

On April 24, 2012 cotton cultivar “Deltapine 174RF” was planted in a grow room (14/10 light:dark, average: 33.5°C, 30% relative humidity) in 1.5L pots with soil (SunGro Sunshine Mix #1) and Osmocote time-release fertilizer (14:14:14, N-P-K). Plants were rotated twice weekly to promote even growth. When the plants reached 4-6 leaves in June 2012, eight plants were transplanted into twelve 1.8m<sup>2</sup> field cages (Lumite Inc. Alto, Georgia) erected in a conventionally managed field plot at the Texas A&M Field Laboratory in Burleson County, TX. Plants were watered heavily for 2 weeks following transplantation (every 4-5 days), and then watered approximately weekly. When the plants reached the squaring stage, four plants of similar size in each cage were selected. This experiment had a 2x2 factorial design; factors were fleahopper induced (present or absent) and caterpillar herbivory (present or absent). Each cage was considered a block and contained one replicate of each treatment (n=12).

The top two terminal nodes of the plants were enclosed using cages constructed with 8oz Styrofoam cups cut to fit around the mainstem. The Styrofoam cup supported No-see-um Nylon Netting (BioQuip Products, Rancho Dominguez, CA); openings of the cage were closed off with Velcro. We collected adult fleahoppers from nearby fields of silverleaf nightshade, *Solanum elaeagnifolium* (Solanaceae) and fed them organic green beans, *Phaseolus vulgaris* (Fabaceae), for 1-3 days in the lab until use. On the fleahopper induced plants, two adult fleahoppers were placed in each cage for 48 hours, while on control and caterpillar only plants cages were left empty. After 24 hours, cages



were checked and dead or missing fleahopper were replaced. After 48 hours, the fleahoppers and terminal cages were removed from plants and ten second instar beet armyworm caterpillars were added to the plants and the whole plant was enclosed in No-see-um Nylon Netting cage.

Beet armyworms eggs were obtained from Benzon Research, Inc. (Carlisle, PA, USA) and reared on an artificial diet provided from the company in an incubator on a 16:8 light:dark cycle at 29°C and 60% relative humidity. Rearing was timed so that larvae would be 72-96 hours old on the same day fleahoppers had been feeding on the greenhouse plants for 48 hours. One day, three days, and seven days after placing the caterpillars on plants, we checked for caterpillar retention on the plants. After the seven-day period, all caterpillars were removed. At the end of the growing season, on October 18<sup>th</sup>, 2012, we counted the total number of fruits (squares, flowers, green bolls and open bolls), the proportion of fist position fruits retained, and the number of fruiting and vegetative branches. We could not wait for the plants to reach full maturity (70-80% open bolls) because of government imposed limitations to the length of the cotton growing season.

We used multivariate repeated-measures ANOVA (SAS Institute, version 9.3) to compare the number caterpillars retained on fleahopper induced and control plants. Means for the repeated measures analysis were also separated by Fisher's least significant difference at  $\alpha = 0.05$  level. Total number of fruits (squares, flowers, green bolls and open bolls), the proportion of fist position fruits retained, and the number of fruiting and vegetative branches were analyzed using a two-way ANOVA using PROC

GLM (SAS Institute, version 9.3). Fleahopper induction and caterpillar infestation were treated as fixed effects while cage was used as a random effect. Means were separated by Fisher's least significant difference at  $\alpha = 0.05$  level.

#### *Greenhouse study*

On May 28<sup>th</sup> cotton cultivar "Deltapine 174RF" was planted in a grow room (14/10 light:dark, average: 33.5°C, 30% relative humidity) in 6.5L pots with soil (SunGro Sunshine Mix #1) and Osmocote time-release fertilizer (14:14:14, N-P-K). Plants were rotated twice weekly to promote even growth. When the plants reached 4-6 leaves, they were transferred to the greenhouse (14/10 light: dark, 21-38°C, 60-80% relative humidity). Plants were arranged in pairs of similar sized plants. One plant in each pair was randomly assigned to be a control (no induction) or fleahopper induced plants.

In the greenhouse we monitored all plants twice a week for the development of squares. At the first or second week of squaring, plants were enclosed at their terminal using cages constructed with 8oz Styrofoam cups cut to fit around the mainstem. The Styrofoam cup supported No-see-um Nylon Netting (BioQuip Products, Rancho Dominguez, CA) which enclosed the two uppermost nodes of the plant. Openings of the cage were closed off with Velcro. We collected adult fleahoppers from nearby fields of silverleaf nightshade, *S. elaeagnifolium*, and fed them organic green beans (*P. vulgaris*) for 1-3 days in the lab until use. On the fleahopper induction plants, two adult fleahoppers were placed in each cage for 48 hours, while control cages were left empty. After 24 hours, cages were checked and dead or missing fleahopper were replaced.

After 48 hours, the fleahoppers were removed from plants and ten second instar beet armyworm caterpillars were added to the plants.

Beet armyworms eggs were obtained from Benzon Research, Inc. (Carlisle, PA, USA) and reared on an artificial diet provided from the company in an incubator on a 16:8 light:dark cycle at 29°C and 60% relative humidity. Rearing was timed so that larvae would be 72-96 hours old on the same day fleahoppers had been feeding on the greenhouse plants for 48hours. Prior to placing the larvae on the cotton plants, larvae were weighed in sets of ten, and we took photographs of the leaves inside the terminal cages. Larvae were placed on the plants using damp paintbrushes. Every 24 hours for 72 hours, we recorded the number caterpillars remaining, larval weight, and took photographs of the leaves they damaged. After 72 hours, any remaining caterpillars were removed. Daily leaf area damaged was determined from the photographs using ImageJ software (Glover et al. 2010).

We found it difficult to maintain large sample sizes of healthy mature cotton plants in our greenhouse. In a first trial we only were able to maintain a sample size of four plants, and so here, we present the data of our second trial (n=9). In both trails, plants would become abnormally tall and seem to decrease in health as they aged, although we used fertilizer, maintained reasonable temperatures in the greenhouse, and kept the plants well watered. We observed that at the squaring stage many plants began to abscise their leaves, which made the plants unsuitable for the experiment. We suspect that plants may have been photo-damaged, because the plants became so tall that they would reach the height of the greenhouse lights. We moved the plants so they would not

be directly under the lights, but their health still decreased. We also were unable to keep the plants free of greenhouse pests, especially spider mites, so we were unable to collect ideal samples for molecular analysis (see below). Caging the plants with screening only exacerbated problems with the plants growing too tall.

Data were analyzed using repeated-measures PROC MIXED ANOVA to compare the percent of leaf area damaged and the amount of leaf area damaged over 3 days (SAS Institute, version 9.3). Caterpillar weight gain after 72hours of feeding on fleahopper induced plants and control plants was analyzed using 1-way PROC GLMM ANOVA (SAS Institute, version 9.3). Means were separated by Fisher's least significant difference at  $\alpha = 0.05$  level.

#### *Expression of induced defense and ethylene pathway genes*

We intended to examine the expression of defense and ethylene pathway genes using RT-qPCR. The uppermost true leaf from five pairs of plants in the greenhouse study were collected after the 48hour fleahopper induction period. For preliminary work, we used samples collected from a field experiment conducted in 2011. In 2011, cotton cultivar "Deltapine 174RF" was planted in a conventionally managed plot at the Texas A&M Field laboratory in Burleson Co. TX (Chapter 2). Two adult fleahoppers were caged to the terminals of cotton plants during the first week of squaring, as previously described. The uppermost squares (1-2 squares) were flash frozen in liquid nitrogen after 48hours of fleahopper infestation and stored at  $-80^{\circ}\text{C}$ . RNA extractions were performed using RNeasy Plant Kit (Qiagen, Valencia, CA USA) (Szczepaniec et al. 2013). RNA quantity and quality were measured using NanoDrop (FisherScientific,

Pittsburg, PA, USA) and integrity was confirmed using 1% (v/w) agarose gel electrophoresis. cDNA synthesis was completed used SuperScript III First-Strand Systems (Invitrogen, Carlsbad, CA USA).

Genes selected for expression analysis were protein defenses: trypsin proteinase inhibitor (*PI*) and Chitinase (*Chi*) (Szczepaniec et al. 2013), and genes in the ethylene biosynthesis pathway: ethylene insensitive-4 (*EIN4*), 1-aminocyclopropane-1-carboxylic acid oxidase-5 (*ACO5*) and Li-tolerant lipase 1 (*LTL1*) (Su and Finlayson 2012) (Table 7). PCR was conducted using Herculanase II Kit (Agilent Technologies Santa Clara, CA), but were unable to successfully verify specificity of the primers on our cDNA samples and so we did not continue with RT-qPCR analysis.

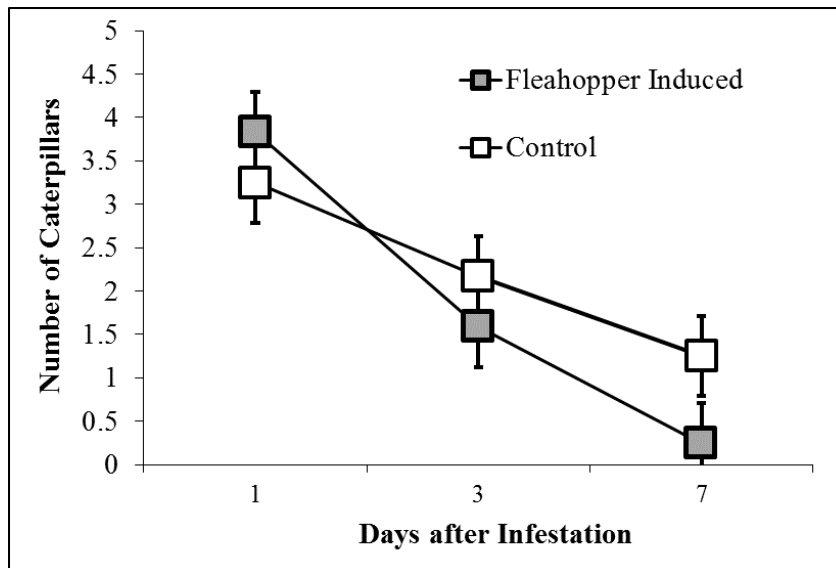
**Table 7. Primer sequences for qPCR analysis.**

Gene	Forward Primer	Reverse Primer	Accession Number
<i>PI</i>	ACCTACCCCGTGCATGCCAAC	ACGGCGGGCCCAGGTGAATTTA	CD486015
<i>Chi</i>	TCTGGACAAGGATTTGGCCCAACA	AGCAACAGTTTGTGGATTACCACCA	CD485829
<i>EIN4</i>	TTCAGAAGGTAATGAGTGATGGAA	TCATCATCGAATCAACAATAATCC	DW482730
<i>ACO5</i>	CAAGAAATGCATGGAGCAGA	GATTCAGGGAGATGGCGTAA	DW519982
<i>LTL1</i>	TGGTATTGGGTTATGCACGA	TAGCTCTCCGAAGGATGGA	DT554240

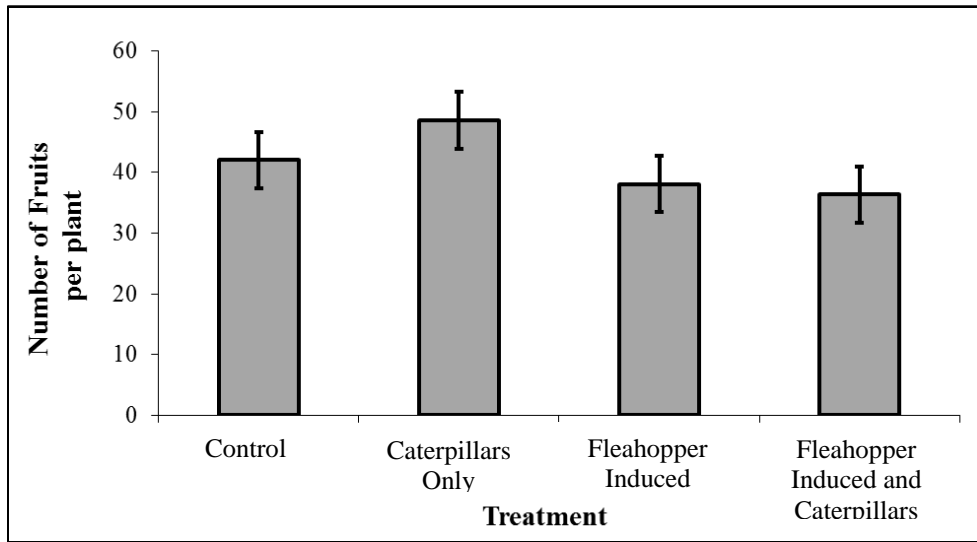
## Results

### *Field study*

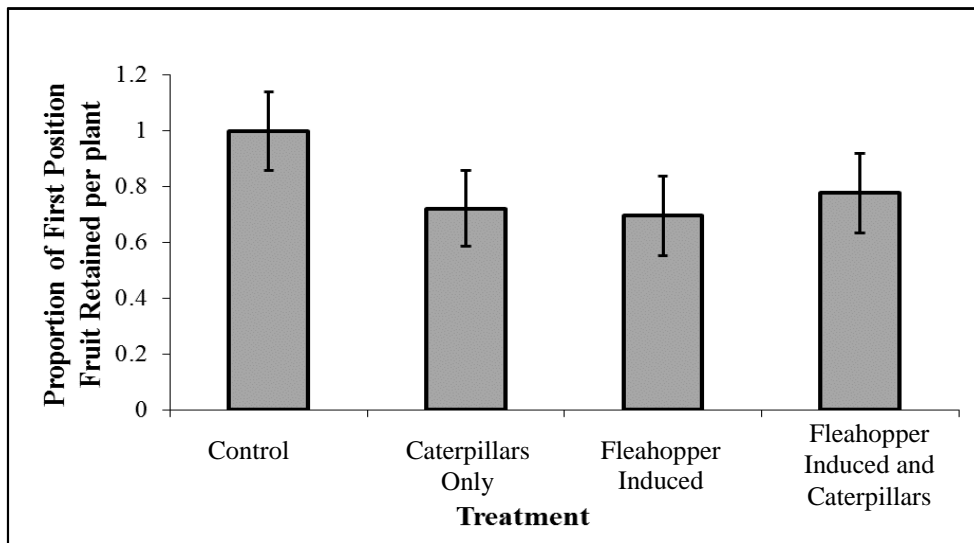
The number of caterpillars remaining did not differ between fleahopper induced plants and uninduced plants ( $F_{2,44} = 2.47$   $p = 0.09$ ; Figure 17). After seven days, control plants had an average of 1.24 caterpillars per plant, while fleahopper induced plants had an average of 0.25 caterpillars per plant. Fleahopper induction or caterpillar herbivory also had no effect on the total number fruits ( $F_{14,33} = 1.36$   $p = 0.273$ ; Figure 18), the retention of first position fruit ( $F_{14,28} = 0.21$   $p = 0.892$ ; Figure 19), the number of vegetative branches ( $F_{15,32} = 1.36$   $p = 0.27$ ; Figure 20) and the number of fruiting branches ( $F_{15,32} = .6948$   $p = 0.56$ ; Figure 20) at the end of the growing season. Field cages effects were only significant for branching.



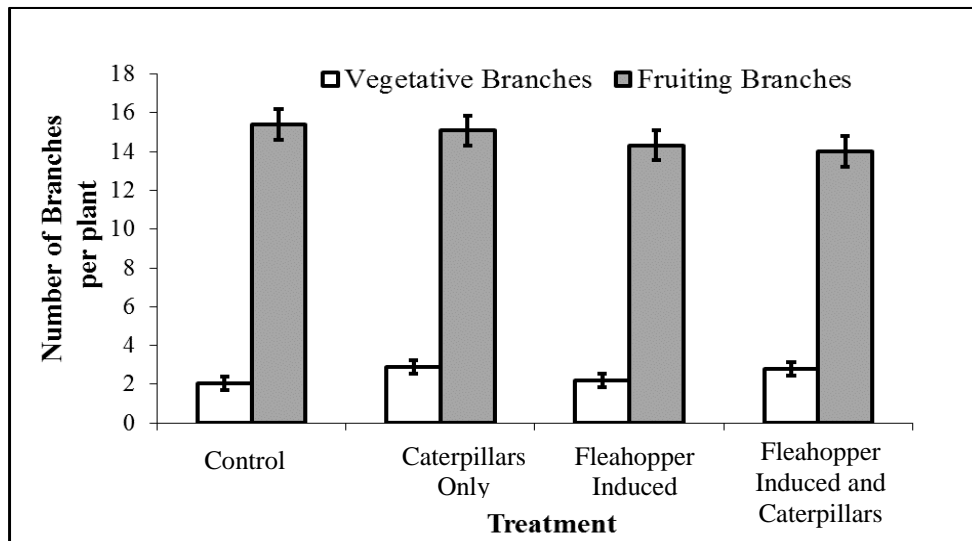
**Figure 17. Retention of caterpillars on fleahopper induced plants in a field experiment.** Bars represent  $\pm$  standard error of the mean.



**Figure 18. Number of fruits (squares, flowers, green bolls and open bolls) per plant on fleahopper induced plants at the end of the growing season. Bars represent  $\pm$  standard error of the mean.**



**Figure 19. Proportion of first position fruits retained on fleahopper induced plants in a field experiment. Bars represent  $\pm$  standard error of the mean.**



**Figure 20. Branches on fleahopper induced plants in a field experiment.** Bars represent  $\pm$  standard error of the mean.

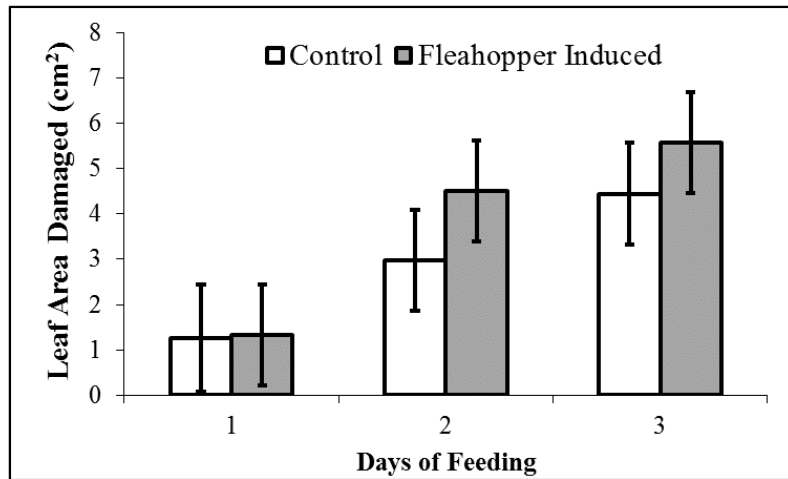
#### *Greenhouse study*

Fleahopper induction had no effect on the total amount of leaf area eaten by caterpillars over three days ( $F_{2,47}=0.22$ ,  $P=0.8053$ ; Figure 21) or the percent of leaf area eaten ( $F_{2,47}=0.42$ ,  $P=0.6602$ ; Figure 22). Fleahopper induction also had no effect on caterpillar weight gain ( $F_{1,8}=0.07$ ,  $P=0.8086$ ; Figure 23) after 72 hours of feeding.

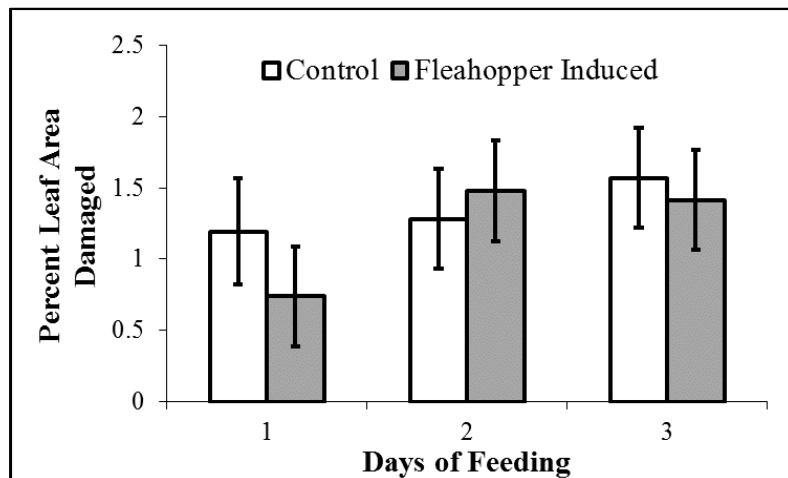
#### **Discussion**

Our preliminary work is inconclusive due to small sample sizes in our field and greenhouse studies and protocol difficulties encountered during our molecular analysis. Despite these problems, we suggest that this research deserves further investigation because very little is known about how fleahoppers interact with other arthropods in

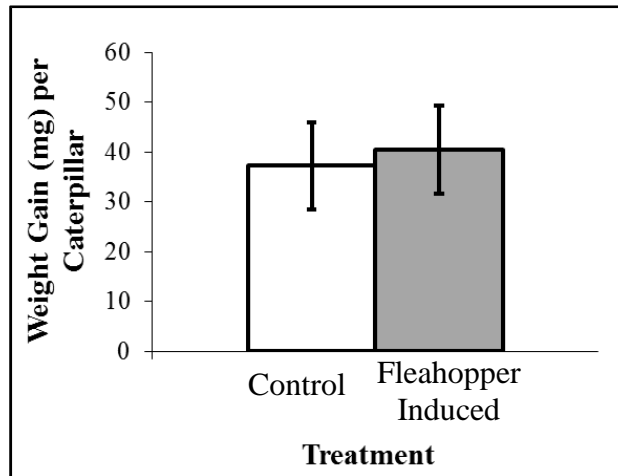




**Figure 21. Leaf area damaged by caterpillars on fleahopper induced plants in a greenhouse experiment over three days of feeding.** Bars represent  $\pm$  standard error of the mean.



**Figure 22. Percent leaf area damaged by caterpillars on fleahopper induced plants in a greenhouse experiment over three days of feeding.** Bars represent  $\pm$  standard error of the mean.



**Figure 23. Weight gain by caterpillars on fleahopper induced plants in a greenhouse experiment over three days of feeding.** Bars represent  $\pm$  standard error of the mean.

cotton fields. Previous work indicated that cotton aphid, *Aphis gossypii* (Hemiptera: Aphididae), herbivory induces resistance against *S. exigua* by triggering chitinase, peroxidase, and trypsin inhibitor production in cotton leaves (Frank et al. in review). When *S. exigua* caterpillars fed on plants induced by cotton aphids, they had less mass and longer development times, suggesting that aphids vaccinated cotton against the caterpillars. Moreover, *S. exigua* egg production decreased on induced plants (Frank et al. in review). Economic thresholds for aphids, therefore, may need an adjustment to account for the yield benefits incurred by the induction of defenses, which resist Lepidopteran pests. Whether or not this is also the case for cotton fleahoppers remains to be seen.

We thought it would insightful to determine if fleahopper induced ethylene production was correlated with cotton defense proteins synthesis because ethylene's

participation in plant defense against insect herbivores is not well understood (Adie et al. 2007, von Dahl and Baldwin 2007, Wu and Baldwin 2010). In other crops, such as beans, *P. vulgaris* (Fabaceae), and potatoes, *Solanum tuberosum* (Solanaceae), Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae), regurgitate induced both ethylene synthesis and POD and PPO activities (Kruzmane et al. 2002, Steinite et al. 2004). In addition, 1-methylcyclopropene(1-MCP),an inhibitor of ethylene perception, suppressed POD and PPO activities in bean plants, suggesting that ethylene was needed to mediate the production of these defensive proteins (Kruzmane et al. 2002). These types of responses, however, may be specific to plant or herbivore species. Tian et al. (2014), for instance, reported that ethylene suppressed synthesis of proteinase inhibitors in tomato, *Solanum lycopersicum* (Solanaceae). They found that ethephon application, which decomposes to ethylene inside plant tissues, led to increased susceptibility of tomato plants to corn earworm, *Helicoverpa zea* (Lepidoptera: Noctuidae). Similarly, Stotz et al (2000) found that ethylene induced the susceptibility of *Arabidopsis thaliana* (Brassicaceae) to Egyptian cotton worm, *Spodoptera littoralis* (Lepidoptera: Noctuidae). To my knowledge, ethylene mediated defenses have not been studied in cotton and again it is unknown whether fleahopper herbivory induces resistance, susceptibility, or no effects on subsequent herbivory.

Lastly, there has been little work on the nutritional changes in cotton following herbivory. If fleahoppers induced increased foliar nitrogen, as suggested by Sadras (1996), then Lepidopteran pests could perform better on fleahopper-damaged plants. Pest management may be improved by understanding how early-season pests affect the

nutritional ecology of crops and how these changes affect later season pest dynamics (Lynch et al. 2006). Recent research suggests that nutritional changes may be more important than previously appreciated. Sconiers (2014), for instance, found that nutritional changes in water stressed plants had stronger effects on herbivore performance than changes in defenses.

In conclusion, insect communities form intricate interactions that are affected by herbivore induced changes in plant morphology and physiology (Craig 2010, Ohgushi 2012). Integrated pest management strategies can be improved by considering plant mediated induced resistance and susceptibility triggered by crop pests. Research should document (1) herbivore induced changes in plant defenses and resource (e.g., nitrogen) allocation (2) effects of induced changes on subsequent herbivory and (3) the impact of plant-mediated herbivore-herbivore interactions on yield.

## CHAPTER VI

### CONCLUSIONS

Thousands of plant-herbivore interactions have been studied in order to gain a better understanding of how herbivores affect plant growth and fitness. Although it is known that herbivory is most often detrimental to plants, I assert that to fully understand their co-evolutionary relationships we need to continue to investigate direct and indirect positive interactions between plants and herbivores, such as plant overcompensation and plant vaccination. Knowing that overcompensation had been documented following herbivory by vertebrates in numerous plant species, I speculated in Chapter II that overcompensation for insect herbivory was also more common than previously thought. Insect herbivory is so ubiquitous and pervasive, it was hard for me to image that plants did not respond positively to invertebrate damage in similar ways as they did for vertebrates. In addition, although overcompensation had been a highly debated outcome for plant-herbivore interactions a few decades ago, discussion has waned in recent years.

In order to stimulate future discussions on overcompensation, I conducted the only review to date on overcompensation for insect herbivory. In my literature review, I confirmed that overcompensation for insect herbivory is more prevalent than previously thought and that a diverse species of both plant and insect herbivores participate in this mutually beneficial interaction. My intention for using a meta-analysis was to reveal patterns, if there are any, that could help clarify when and where plants overcompensate for insect herbivory. What stood out from the data, however, were cases where there

were no patterns at all. For example, I would have expected annual plants to overcompensate to a greater degree than perennial plants because annual plants only have one opportunity to maximize their fitness, while perennial plants could have multiple opportunities. In addition, it was surprising that damage intensity caused no significant variation in overcompensatory responses. This data suggests that biologists should not underestimate the ability of plants to withstand large amounts of damage. Future work should focus on the physiological and genetic mechanisms that underlie overcompensation. Although many plant species were able to overcompensate, and many insect herbivores were able to stimulate it, I hypothesize that different plant types (e.g., wood or herbaceous and annuals or perennials) likely have different means of doing so. If we had a better understanding of how, when, and where plants overcompensate, we would be better prepared to facilitate overcompensation in crop plants and to control weedy species.

In chapters III and V, I investigated potential direct and indirect benefits of cotton fleahopper herbivory for cotton. It is important to consider how herbivores may benefit crops so that we can develop strategies to limit pesticide use. Pesticide use particularly intense in cotton agriculture and causes a great deal of environmental and human health risks worldwide. Chapter III supports many other studies which find that cotton can compensate for moderate early season damage to squares and terminal meristems, such as the damage caused by cotton fleahoppers. Although timing of herbivory did not affect compensation in my study, it revealed that timing of herbivory

influences morphological changes in the plants following damage by cotton fleahoppers. Future work should concurrently consider timing and intensity of herbivory.

Chapter V outlines preliminary work to determine whether cotton fleahoppers induced defenses in cotton that could vaccinate it against Lepidopteran pests. I also set out to determine whether ethylene, a plant hormone, mediated plant defenses in cotton. Since ethylene is a gas, we decided it would best to study the up-regulation of genes in the ethylene biosynthesis pathway, rather than measure actual ethylene emissions from plant tissues. Previous work to measure ethylene emission in squares following fleahopper herbivory was inconclusive; there was too much pollution in our greenhouse to get accurate measurements of ethylene emissions in air samples. We also ran into problems, however, troubleshooting primers designed to target ethylene-related and protein defense genes in RT-qPCR analysis. Therefore, we were unable to determine whether cotton fleahoppers induced cotton defense genes, or whether the defenses were regulated by ethylene production in cotton. In addition, trends in our field and greenhouse study were contradictory. In the field, we observed fewer numbers of caterpillars remaining on fleahopper induced cotton plants than on control plants, but in the greenhouse, we observed a trend for caterpillars to feed more fleahopper induced cotton plant than control plants. Despite these problems and contradictory results, we suggest that this research deserves further investigation because very little is known about how cotton fleahoppers interact with other arthropods in cotton fields through herbivory induced changes in plant physiology. Future work should document (1) herbivore induced changes in plant defenses and resource (e.g., nitrogen) allocation (2)

effects of induced changes on subsequent herbivory and (3) the impact of plant-mediated herbivore-herbivore interactions on yield.

Chapter IV was conceived following observations in the field while completing experiments for Chapter II. We observed that cotton fleahoppers were frequent flower visitors of cotton in our field site and that they were often dusted with cotton pollen grains while foraging within cotton flowers. Although these fleahoppers were likely visiting flowers to feed on pollen grains, we hypothesized that fleahoppers might contribute to cross-pollination of cotton as they forage among flowers while carrying pollen grains. We found that cotton fleahoppers can readily transfer a pollen analog to cotton stigmas, but were likely too small to play a major role in cotton pollination. We suggest, however, that they could contribute to cotton pollination as part of a community of pollinators, or pollinate some of their wild hosts with smaller or composite flowers. Importantly, our study supports others which have suggested that insect pollinators could be significant contributors to cotton production. Flowers exposed to pollinators produced 15% more yield than self-crossed flowers. Therefore, managing pollination services in cotton agriculture is expected to be a sustainable approach to increase cotton yield without increasing the area of cultivated land. This chapter highlights the notion that herbivores in crop plants could fluctuate between being antagonistic to plants to being beneficial throughout the growing season.

In conclusion, my main goal for beginning this dissertation was to increase ecologists' awareness and appreciation of positive interactions between organisms. By focusing on unapparent and paradoxical positive interactions between plants and



herbivores, I hope to encourage researchers to continue to “think outside the box” as they seek to understand how organisms interact, and the consequences of the interaction for the organism, the species, and the ecosystem.

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## APPENDIX 1

Information from studies included in the meta-analysis. These papers document a significant increase in at least one plant fitness or growth parameter following herbivory. When an author reported results on multiple plant species in one study, the study is represented in multiple rows, one per plant species.

Plant characteristics: **plant species**, **family**, **longevity** (L: A, annual; P, perennial; B, Biennial), **functional group** (FG: M, monocot; D, dicot; G, gymnosperm), and **life form** (LF: G, graminoid; H, forb/herbaceous; W, woody; V, vine)

Herbivore Characteristics: **Insect species**, **order** (Mx: more than one herbivore was used in the experiment), **family** (M, mixed herbivore families-more than one herbivore was used in the experiment), **feeding guild** (G: GF, gall forming; C, chewing; LM, leaf mining; PF, phloem-feeding; PS, piercing-sucking; SB, stem boring; X, xylem feeding; M, mixed feeding guilds-more than one feeding guild in experiment), **damage site** (DS: A, apical stem; F, flower; FB, flower bud; L, leaf; R, root; S, stem; T, tubers; M, mixed feeding site- more than one damage site in experiment), and **herbivory intensity** (HI: L, low, M, medium, H, high)

Experiment Characteristics: **Latitude** (E: Tp, temperate; Tr, tropical); **cultivation** (C: U, uncultivated; A, agricultural system), **damage type** (DT: I, insect; S, simulated herbivory), and **experiment environment** (EE: Gh, Greenhouse; F, field; G, garden; N, nursery; C, growth chamber)

Overcompensatory (OC) Response: fitness or vegetative parameter and types of response (A, area; B, biomass; D, diameter; L, linear size; N, number of organs)



**Table 8. Information from studies included in the meta-analysis.**

Study	Plant Characteristics					Herbivore Characteristics						Experiment Characteristics				Over-compensatory Response	
	Species	Family	L	FG	LF	Species	Order	Family	G	DS	HI	L	C	DT	EE	Vegetative	Fitness
1	<i>Ipomoea purpurea</i>	Convolvulaceae	A	D	H	-	Coleoptera	Chrysomelidae	C	L	M	Tp	U	S	Gh	stem (B)	none
2	<i>Raphanus raphanistrum</i>	Brassicaceae	A	D	H	-	Lepidoptera	Pieridae	C	L,A	M	Tp	U	S	Gh	plant (L) leaves (A)	inflorescences (N)
3	<i>Alliaria petiolata</i>	Brassicaceae	B	D	H	<i>Ceutorhynchus scrobicollis</i>	Coleoptera	Curculionidae	C	A	M	T	U	S	Gh	stem (N)	none
4	<i>Vicia sativa</i>	Fabaceae	A	D	H	-	-	-	M	L	M	Tp	U	I	F	leaves (N)	none
5	<i>Poa pratensis</i>	Poaceae	P	M	G	<i>Popillia japonica</i>	Coleoptera	Scarabidae	C	R	M	Tp	A	I	Gh	foliage (B)	not tested
5	<i>Festuca ovina</i>	Poaceae	P	M	G	<i>Popillia japonica</i>	Coleoptera	Scarabidae	C	R	M	Tp	A	I	Gh	foliage (B)	not tested
5	<i>Lolium perenne</i>	Poaceae	P	M	G	<i>Popillia japonica</i>	Coleoptera	Scarabidae	C	R	M	Tp	A	I	Gh	foliage (B)	not tested
5	<i>Festuca arundinacea</i>	Poaceae	P	M	G	<i>Popillia japonica</i>	Coleoptera	Scarabidae	C	R	M	Tp	A	I	Gh	foliage (B)	not tested
6	<i>Erythroxyllum havanense</i>	Erythroxylaceae	P	D	W	-	Lepidoptera	Saturniidae, Geometridae, Lycaenidae	C	L	H	Tr	U	S	F	none	seed (B)
7	<i>Silphium integrifolium</i>	Asteraceae	P	D	H	<i>Antistrophus silphii</i>	Hymenoptera	Cynipidae	G	A	M	T	U	I	F,G	leaf (A) stem (B)	none
8	<i>Rhizophora mangle</i>	Rhizophoraceae	P	D	W	<i>Elaphidion mimeticum</i> , <i>Elaphidion epp.</i>	Coleoptera	Cerambycidae	SB	S	M	Tp	U	S	F	stem (L)	none
9	<i>Trifolium repens</i>	Fabaceae	P	D	H	<i>Sitona lepidus</i>	Coleoptera	Curculionidae	C	R	M,H	Tp	U	I	G	buds (N)	not tested
10	<i>Alliaria petiolata</i>	Brassicaceae	B	D	H	<i>Ceutorhynchus roberti</i> , <i>Ceutorhynchus alliariae</i>	Coleoptera	Curculionidae	SB	S	L, M,H	T	U	I	G	none	inflorescences (N)
11	<i>Glycine max</i>	Fabaceae	A	D	H	<i>Plathypena scabra</i> , <i>Pseudoplusia includens</i>	Lepidoptera	Erebidae, Noctuidae	C	L	L,H	T	A	S	F	not tested	seed (B)

**Table 8. Continued.**

Study	Plant Characteristics					Herbivore Characteristics						Experiment Characteristics				Over-compensatory Response	
	Species	Family	L	FG	LF	Species	Order	Family	G	DS	HI	L	M	DT	EE	Vegetative	Fitness
13	<i>Persicaria perfoliata</i>	Polygonaceae	A	D	V	<i>Rhinoncomimus latipes</i>	Coleoptera	Curculionidae	C	A	H	Tp	U	I	F	nodes (N) terminals (N) plant (B)	none
14	<i>Erysimum strictum</i>	Brassicaceae	B	D	H	-	-	-	-	A	L,M	T	U	S	G	root (B) stem (B)	seed (N, B) fruit (N)
15	<i>Erysimum strictum</i>	Brassicaceae	B	D	H	-	-	-	-	A	M	T	U	S	F	plant (L) stem (N) nodes (N)	none
16	<i>Oryza sativa</i>	Poaceae	A	M	G	<i>Chilo suppressalis</i>	Lepidoptera	Pyalidae	SB	S	M	Tr	A	I	Gh	stem (N)	not tested
17	<i>Erigeron glaucus</i>	Asteraceae	P	D	H	<i>Platyptilia williamsii</i> , <i>Philaenus spumarium</i>	Lepidoptera, Hemiptera	Pterophoridae, Cercopidae	C,M	A,L	M	T	U	I	G	rosettes (N)	none
18	<i>Abies balsamea</i>	Pinaceae	P	D	W	<i>Choristoneura fumiferana</i>	Lepidoptera	Tortricidae	C	A	M	Tp	U	S	N	root (B)	not tested
19	<i>Gossypium hirsutum</i>	Malvaceae	P	D	W	<i>Creontiades dilutes</i> , <i>Helicoverpa armigera</i> , <i>Helicoverpa punctigera</i>	Hemiptera, Lepidoptera	Miridae, Noctuidae	M	A, Fb	M	Tp	A	S	F	stem (N,L)	fruit (N)
20	<i>Aternanthera philozeroides</i>	Amaranthaceae	P	D	H	<i>Agasicles hygrophila</i>	Coleoptera	Chrysomelidae	C	S,L	M,H	Tr	U	I	Gh	stem (N) plant (B) leaf (N)	buds (N)
21	<i>Oryza sativa</i>	Poaceae	A	M	G	<i>Diatraea saccharalis</i>	Lepidoptera	Crambidae	SB	S	M	T	A	I	F	stem (N)	none
22	<i>Oryza sativa</i>	Poaceae	A	M	G	<i>Diatraea saccharalis</i>	Lepidoptera	Crambidae	SB	S	M	T	A	S	F	stem (N)	seed (B)
23	<i>Trifolium aestivum</i>	Poaceae	A	M	G	-	Lepidoptera, Orthoptera	Noctuidae, Acrididae	C	L	L,H	T	A	S	Gh	stem (L)	not tested
24	<i>Quercus crispula</i>	Fagaceae	P	D	W	<i>Orthosia paromoea</i> , <i>Cosmia exigua</i> , <i>Telorta edentata</i>	Lepidoptera	Noctuidae	C	L	L	T	U	I	N	leaf (B)	not tested
25	<i>Sedum maximum</i>	Crassulaceae	P	D	H	<i>Parnassius apollo</i>	Lepidoptera	Papilionidae	C	A	M	T	U	S	F	root (B)	infructescence (B) seed (B)

**Table 8. Continued.**

Study	Plant Characteristics			Herbivore Characteristics							Experiment Characteristics				Over-compensatory Response	
	Species	Family	L FG LF	Species	Order	Family	G DS HI	L M DT EE	Vegetative	Fitness						
26	<i>Oryza sativa</i>	Poaceae	A M G	<i>Orseolia oryzivora</i>	Diptera	Cecidomyiidae	GF S L	Tr A I F	not tested	seed (B)						
27	<i>Helianthus annuus</i>	Asteraceae	A D H	<i>Haploryhynchites aeneus</i>	Coleoptera	Curculionidae	C S M,H	T U S F	stem (N)	inflourescneces (N)						
28	<i>Solanum tuberosum</i>	Solanaceae	P D H	<i>Tecia solanivora,</i> <i>Premnotrypes vorax,</i> <i>Naupactus sp.</i>	Lepidoptera, Coleoptera	Gelchiidae, Curculionidae	C T L,M	Tp A I F,GH	root (B)	not tested						
29	<i>Melaleuca quinquenervia</i>	Myrtaceae	P D W	<i>Oxyops vitiosa</i>	Coleoptera	Curculionidae	C L H	T U I F	nodes (N) stems (N)	none						
30	<i>Convolvulus demissus</i>	Convolvulaceae	P D H	-	Coleoptera	Chrysomelidae	C L M	T U S Gh	stem (N)	not tested						
31	<i>Medicago Sativa</i>	Fabaceae	P D H	<i>Sitona hespidulus</i>	Coleoptera	Curculionidae	C R L	T A I C	nodules (N)	not tested						
32	<i>Sapium sebiferum</i>	Euphorbiaceae	P D W	<i>Malanoplus angustipennis</i>	Orthoptera	Acridiae	C L M	T U S F	stem (D)	not tested						
33	<i>Solanum esculentum</i>	Solanaceae	P D H	<i>Nesidiocoris tenuis</i>	Hemiptera	Miridae	P F H	T A I Gh	not tested	fruit (B, D)						
34	<i>Lythrum Salicaria</i>	Lythraceae	P D H	<i>Galerucella californiensis</i>	Coleoptera	Chrysomelidae	C L L,M,H	T U I G	stem (N)	inflourescneces (N)						
35	<i>Solanum nigrum</i>	Solanaceae	P D H	<i>Manduca sexta</i>	Lepidoptera	Sphingidae	C L M	T U S F	root (B)	none						
36	<i>Melaleuca quinquenervia</i>	Myrtaceae	P D W	<i>Boreioglycaspis melaleucaae</i>	Hemiptera	Psyllidae	P L,S L,H	- U I G	leaf (N)	not tested						
37	<i>Cannabis sativa</i>	Cannabaceae	A D F	<i>Ostrinia nubilalis</i>	Lepidoptera	Pyralidae	SB S M	T A I F	plant (B)	not tested						
38	<i>Cajanus cajan</i>	Fabaceae	P D W	-	-	-	A M	Tp A S F,G	plant (B) stem (N,B) leaf (A)	fruit (B,N) seeds (N)						

**Table 8. Continued.**

Plant Characteristics			Herbivore Characteristics						Experiment Characteristics				Over-compensatory Response				
Study	Species	Family	L	FG	LF	Species	Order	Family	G	DS	HI	L	M	DT	EE	Vegetative	Fitness
39	<i>Glycine max</i>	Fabaceae	A	D	H	-	-	-	-	Fb	L,M,H	T	A	S	F	not tested	seed (B)
40	<i>Salix gilgiana</i>	Salicaceae	P	D	W	<i>Endoclitia excrescens</i>	Lepidoptera	Hepialidae	SB	S	M	T	U	S	F	stem (L,N)	not tested
40	<i>Salix eriocarpa</i>	Salicaceae	P	D	W	<i>Endoclitia excrescens</i>	Lepidoptera	Hepialidae	SB	S	M	T	U	S	F	stem (L,N)	not tested
40	<i>Salix serissaefolia</i>	Salicaceae	P	D	W	<i>Endoclitia excrescens</i>	Lepidoptera	Hepialidae	SB	S	M	T	U	S	F	stem (L,N)	not tested
41	<i>Gossypium hirsutum</i>	Malvaceae	P	D	W	<i>Helicoverpa armigera</i>	Lepidoptera	Miridae, Noctuidae	C	Fb	M,H	Tp	A	S	C	leaf (A) plant (B) stem (B) root (B) leaves (A, N)	fruit (B)
42	<i>Gossypium hirsutum</i>	Malvaceae	P	D	W	<i>Helicoverpa armigera</i>	Lepidoptera	Noctuidae	C	Fb	M,H	Tp	A	S	Ch	stem (B) root (B) seedling (A,D,B,L)	none
43	<i>Pharbitis purpurea</i>	Convolvulaceae	A	D	H	-	-	-	-	L	M	T	U	S	N	root (L)	not tested
44	<i>Pharbitis purpurea</i>	Convolvulaceae	A	D	H	-	-	-	-	C	M,H	T	U	S	N	cotyledon (A,B,D)	not tested

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## APPENDIX 2

Basic information from studies from the literature survey. These papers document a significant increase in at least one plant fitness or growth parameter following herbivory, but lacked information required for inclusion into the meta-analysis.

Plant characteristics: **plant species, family, longevity** (L: A, annual; P, perennial; B, biennial), **functional group** (FG: M, monocot; D, dicot; G, gymnosperm), and **life form** (LF: G, graminoid; H, herbaceous; W, woody; V, vine).

Herbivore Characteristics: **Insect species, order, family, feeding guild** (G: GF, gall forming; C, chewing; M, leaf mining; PF, phloem-feeding; PS, piercing-sucking; SB, stem boring), **feeding site** (FS: A, apical stem; F, flower; FB, flower bud; L, leaf; R, root; S, stem; T, tubers;), and **herbivory intensity** (HI: L, low, M, medium, H, high).

Experiment Characteristics: **Latitude** (L: Tp, temperate; Tr, tropical); **cultivation** (C: U, uncultivated; A, agricultural system), **damage type** (DT: I, insect; S, simulated herbivory), and **experiment environment** (EE: Gh, Greenhouse; F, field; G, garden; N, nursery; C, growth chamber).

Overcompensatory Response: fitness or vegetative parameter, and types of response (A, area; B, biomass; D, diameter; L, linear size; N, number of organs)

**Table 9. Studies with evidence of overcompensation but not included in the meta-analysis.**

Study	Plant Characteristics					Herbivore Characteristics						Experiment Characteristics				Over-compensatory Response	
	Species	Family	L	FG	LF	Species	Order	Family	G	DS	HI	L	C	DT	EE	Vegetative	Fitness
1	<i>Bouteloua gracilis</i>	Pocaeae	P	M	G	<i>Ageneotettix deorum</i>	Orthoptera	Acridiae	C	L	M	T	U	I	F	plant (B)	none
2	<i>Solidago altissima</i>	Compositae	P	D	H	<i>Uroleucon nigrotuberculatum</i>	Hemiptera	Aphididae	P	S	M	Tp	U	I	G	leaves (N)	not tested
3	<i>Populus euramericana</i>	Salicaceae	P	D	W	<i>Chrysomela scripta</i>	Coleoptera	Chrysomelidae	C	L	M	Tp	U	S	C	stem (L, D, B) leaves (B, A)	not tested
4	<i>Populus trichocarpa</i>	Salicaceae	P	D	W	<i>Chrysomela scripta</i>	Coleoptera	Chrysomelidae	C	L	M	Tp	U	S	Gh	leaves (A) plant (B)	not tested
5	<i>Alliaria petiolata</i>	Brassicaceae	B	D	H	<i>Ceutorhynchus scrobicollis</i>	Coleoptera	Curculionidae	C	A	M	Tp	U	S	Gh	stems (N)	none
5	<i>Alliaria petiolata</i>	Brassicaceae	B	D	H	<i>Ceutorhynchus scrobicollis</i>	Coleoptera	Curculionidae	C	L	M	Tp	U	S	Gh	none	reproductive allocation (B) flowers (N) fruit (N, B)
6	<i>Gossypium hirsutum</i>	Malvaceae	P	D	W	<i>Heliothis armigera</i>	Lepidoptera	Noctuidae	C	L	M	Tr	A	S	F	none	reproductive allocation (B) flowers (N) fruit (N, B)
7	<i>Carduus nutans</i> <i>Pinus brutia</i>	Asteraceae <i>Pinus radiata</i>	P	arval survival	H	<i>Trichosiocalus horridus</i>	Coleoptera	G-Curculionidae	C+	L, S0.5	M	Tp	U	I	F	stem (B, N) root (B) leaves (D)	seeds/head (N)
7	<i>Carduus acanthoides</i> <i>Pinus brutia</i>	Asteraceae <i>Pinus radiata</i>	P	Larval survival	H	<i>Trichosiocalus horridus</i>	Coleoptera	G-Curculionidae	C+	L, S0.5	M	Tp	U	I	F	stem (N) leaves (D)	heads (N)
8	<i>Pinus strobus</i>	Pinaceae	P	G	W	<i>Pissodes strob</i>	Coleoptera	Curculionidae	C	A	M	Tp	U	I	F	stem (D)	not tested
9	<i>Cirsium arvense</i>	Asteraceae	P	D	H	<i>Cassida rubiginosa</i>	Coleoptera	Chrysomelidae	C	L	L, H	Tp	U	I	G	root buds (N)	not tested
10	<i>Parthenium hysterophorus</i>	Asteraceae	A		H	<i>Epiblema strenuana</i>	Lepidoptera	Tortricidae	GF	S	M	T	U	I	F	branches (N) plant (L, B)	flowers (N)

11	<i>Linaria vulgaris</i>	Scrophulariaceae	P	D	H	<i>Brachypterus pulicarius</i>	Coleoptera	Kateretidae	SB	S	M	Tp	U	I	F	branches (N) plant (B) clonal shoots (N)	flowers (N)
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**Table 9. Continued.**

Study	Plant Characteristics						Herbivore Characteristics						Experiment Characteristics				Over-compensatory Response	
	Species	Family	L	FG	LF	Species	Order	Family	G	DS	HI	L	M	DT	EE	Vegetative	Fitness	
12	<i>Beta spp.</i>	Chenopodiaceae	A, P	D	H	-	-	-	-	Fb	M	Tp	U	S	Gh	not tested	reproductive meristems (N)	
13	<i>Gossypium hirsutum</i>	Malvaceae	P	D	W	<i>Helicoverpa zea</i> and <i>Lygus Lineolaris</i>	Lepidoptera And Hemiptera	Noctuidae And Miridae	C, P	Fb	M	Tp	A	I	F	plant (L)	fruit (B)	
14	<i>Pinus sylvestris</i>	Pinaceae	P	G	W	-	-	-	C	A	H	Tp	U	S	F	leaves (L, B)	not tested	
15	<i>Betula pendula</i>	Betulaceae	P	D	W	-	-	-	C	L	M,H	Tp	U	S	GC	leaves (A) plant (L)	not tested	
16	<i>Betula pubescens</i>	Betulaceae	P	D	W	<i>Epirrita autumnata</i>	Lepidoptera	Geometridae	C	L	H	Tp	U	I	F	branch (N)	not tested	
17	<i>Alternanthera philoxeroides</i>	Amaranthaceae	P	D	H	<i>Agasicles hygrophila</i>	Coleoptera	Chrysomelidae	C	L	M	Tr	U	I	Gh	stems (N) plant (B)	reproductive buds (N)	
18	<i>Gossypium hirsutum</i>	Malvaceae	P	D	W	-	-	-	-	Fb	L, M, H	Tp	U	S	Gh	plant (L) stem nodes (N) leaves (B) stems (B)	flower buds (N)	
19	<i>Epilobium angustisolium</i>	Onagraceae	P	D	H	-	-	-	-	A	M	Tp	U	I	Gh	plant (B) stem (B) root (B)	none	
20	<i>Centaurea maculosa</i>	Compositae	P/B	D	H	<i>Agapeta zoegana</i>	Lepidoptera	Cochylidae	M	R	M	Tp	U	I	-	root (L)	not tested	
21	<i>Carthamus tinctorius</i>	Asteraceae	A	D	H	<i>Melanoplus sanguinipes</i> , <i>M. packardii</i> , or <i>Cammula pellucida</i>	Orthoptera	Acrididae	C	Mix	M	Tp	U	I	F	none	seed (B) capitula (N)	
22	<i>Verbascum thapsus</i>	Scrophulariaceae	B	D	H	<i>Gymnaetron tetrum</i>	Coleoptera	Curculionidae	C	A	M,H	Tp	U	S	F	branches (N)	seed (B)	
23	<i>Abelmoschus esculentus</i>	Malvaceae	P	D	W	<i>Podagrica spp</i> and <i>Sylepta derogate</i>	Coleoptera Lepidoptera	Curculionidae Pyralidae	C	A, Fb	M	Ap	A	D	F	branches (N)	none	
24	<i>Chamaedorea tepejilo</i>	Arecaceae	P	M	W	<i>Calyptocephala marginipen</i>	Coleoptera	Chrysomelidae	C	L	L, M, H	Tr	U	S	F	leaves (N)	inflorescences (N) fruit (N)	

**Table 9. Continued.**

Plant Characteristics						Herbivore Characteristics						Experiment Characteristics				Over-compensatory Response	
Study	Species	Family	L	FG	LF	Species	Order	Family	G	DS	HI	L	M	DT	EE	Vegetative	Fitness
25	<i>Erysimum strictum</i>	Brassicaceae	B	D	H	-	-	-	-	A	M	Tp	U	S	G	plant (L,B)	fruit (N) seeds (N) germination (N)
26 Avizis (1986)	<i>Pinus resinosa</i> <i>Pinus sylvestris</i>	Pinaceae	PF omi GLar eus val pimi weig per ht	GLar eus val pimi weig per ht	W	<i>Neodiprion lecontei</i>	Hymenoptera	Diprionidae G-SF	C- 0.02	L0.0 ±	M	Tp	U	S	Gh	leaves (N) plant (B)	not tested
27	<i>Zea mays parviglumis</i>	Poaceae	P	M	G	<i>Diatraea grandiosella</i>	Lepidoptera	Pyralidae	C	S	M	Tp	U	I	G	tillers (N)	none
28	<i>Gossypium hirsutum</i>	Malvaceae	P	D	W	<i>Helicoverpa spp.</i>	Lepidoptera	Noctuidae	C	Fb	M	Tp	A	S	F	root (B) shoots (B) leaves (A)	none
29	<i>Glycine max</i>	Fabaceae	A	D	H	<i>Heliothis zea</i>	Lepidoptera	Noctuidae	C	L	L, M, H	Tp	A	S	F	not tested	fruit (B)
30	<i>Gossypium hirsutum</i>	Malvaceae	P	D	W	-	-	-	-	Fb	H	Tp	A	S	F	plant (L)	fruit (N,B)
31	<i>Glycine max</i>	Fabaceae	A	D	H	-	-	-	-	A	M	Tr	A	S	G, F	branches (N,B) plant (B) leaves (N, A, B) root (B)	pods (N, B) seeds (N,B)
32	<i>Rorippa indica</i>	Brassicaceae	P	D	H	<i>Pieris rapae</i> and <i>P. melete</i>	Lepidoptera	Pieridae	C	L	M.H	Tp	U	S	G	not tested	flowers (N) siliques (L)
33	<i>Pinus taeda</i>	Pinaceae	P	G	W	<i>Neodiprion taedae linearis</i>	Hymenoptera	Diprionidae	C	L	L.M.H	Tp	U	I	F	plant (D)	not tested

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