

DYNAMICS OF TRITROPHIC INTERACTIONS BETWEEN *SOLENOPSIS*
INVICTA, *ANTONINA GRAMINIS*, AND *NEODUSMETIA SANGWANI*: DO FIRE
ANTS NEGATIVELY IMPACT THE SUCCESS OF A BIOLOGICAL CONTROL
SYSTEM?

A Thesis

by

JILLIAN MARIE CHANTOS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE

August 2007

Major Subject: Entomology

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ABSTRACT

Dynamics of Tritrophic Interactions Between *Solenopsis invicta*, *Antonina graminis*, and *Neodusmetia sangwani*: Do Fire Ants Negatively Impact the Success of a Biological Control System? (August 2007)

Jillian Marie Chantos, B.S., St. Ambrose University

Chair of Advisory Committee: Dr. S. B. Vinson

Solenopsis invicta, the red imported fire ant, has recently become associated with *Antonina graminis*, an invasive pest, and *Neodusmetia sangwani*, biological control agent, and maybe negatively affecting established biological control. A preliminary survey outlined the range of *A. graminis* and its parasitoids, and found *N. sangwani* was present at a reduced rate in South Texas and in the southeastern United States.

A greenhouse experiment demonstrated that *S. invicta* decreased the rate of parasitism of *A. graminis* by *N. sangwani*, with *S. invicta* directly interfering with oviposition. Interactions between *S. invicta* and *A. gaminis* may be facilitating the spread and establishment of two invasive pests which has a negative impact on established classical biological control of *A. graminis* by *N. sangwani*.

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CHAPTER I

INTRODUCTION

Ants, plants, and Hemiptera have been in existence for over 100 million years. During that time, mutualisms between these organisms have evolved and become important in the ecology of many species. There are a number of reviews of ant-Hemiptera interactions (Way 1963; Buckley 1987; Stadler and Dixon 2005; Styrsky and Eubanks 2007) describing the costs and benefits to plants, insects, and ecological communities. Trophobiosis, a symbiotic relationship between ants and insects trophobionts, where ants obtain honeydew from trophobionts and in turn trophobionts are protected from natural enemies. This behavior is commonly observed in ant-hemipteran interactions, and is believed to have facilitated the radiation of highly evolved and diverse subfamilies, such as *Formicinae* and *Dolichoderinae* (Maschwitz et al. 1986).

Hemipterans provide ants with honeydew, a predictable and renewable source of carbohydrates and amino acids processed from plant phloem (Mittler 1958; Douglas 1993; Way 1963; Buckley 1987), and in return honeydew-producing hemipterans are protected from predators and parasitoids. Numerous studies have documented that

This thesis follows the style of Environmental Entomology.

attending ants provide protection, reducing the abundance of parasitoids by attacking ovipositing females, and killing developing parasitoid larvae inside the hemipteran host (Vinson, 1994); such attacks are not always predatory, but rather are a defense of a resource at stake. (Barlett 1961; Way 1963; Volkl and Mackauer 1993; Stechmann et al. 1996).

Ant-hemipteran interactions dramatically increase the effects of ants as predators, causing ants to become more hostile and attack insects they might otherwise disregard, including other non-honeydew producing herbivores (Way 1963). In a large-scale field manipulation, interactions between the cotton aphid (*Aphis gossypii*) and the red imported fire ant (*Solenopsis invicta*) resulted in a 27-33% reduction in herbivore taxa, and a 40-47% reduction in predator taxa (Kaplan and Eubanks 2005). Tending ants can also change the abundance and distribution of generalist and specialist predators and parasitoids, and multiple species of herbivores in several feeding guilds, resulting in changes to local species diversity.

Increased fitness in honeydew-producing hemipterans is correlated with protection and also with ant tending, such as the continuous removal of honeydew reducing the probability of fungal infection (Fokkema et al. 1983; Haines and Haines 1978). Ants also dispose of dead or parasitized individuals reducing density-dependent mortality due to overcrowding (Washburn et al. 1985), leading to increased population growth (Buckley 1987).

The interactions between ants and honeydew producing-hemipterans facilitates an increase in the growth potential of both insects (Porter 1989). Attending ants have

been linked with honeydew-producing hemipteran outbreaks (Beattie 1985; Carter 1962; Buckley 1987; Delabie 2001; Holway et al., 2002), and increased defense of hemipteran-tending ants foraging territories reduces density and diversity of other ants, resulting in a 'mosaic' distribution of subdominant and dominant ant species (Bluthgen et al. 2000; Dejean and Corbara 2003). Ant-hemipteran mutualisms are thought to be detrimental to biological control due to increased attacks of hemipteran predators by ants. This aggressive ant behavior may have a major effect in shaping food web dynamics and trophic interactions in agroecosystems (Vinson and Scarborough 1991; Jiggins et al. 1993; Reimer et al. 1993; Stechmann et al. 1996; Dutcher 1998).

Most importantly, hemipteran interactions are common with invasive ants, which are noted for their aggressive demeanor, overwhelming abundance, and negative ecological impacts in invaded habitats (Holway et al. 2002; Helms and Vinson 2002). Collection and exploitation of honeydew and plant extrafloral nectar is believed to enhance the ecological dominance of invasive ants (Holway et al. 2002; Helms and Vinson 2002; Lach 2003; Ness and Bronstein 2004).

Solenopsis invicta is an aggressive and dominant invasive ant that was introduced into Mobile, Alabama, from South America. *S. invicta* spread through the Southern United States displacing native ant fauna, and causing agricultural and economic problems. On top of being a direct health treat to humans and a common nuisance pest of homes and landscapes, the predatory habit of *S. invicta*, and its ability to out compete surface-dwelling arthropods has produced negative ecological effects (Porter and Savingnano, 1990). *S. invicta* has been correlated with the decrease of native

invertebrates (Porter and Savingnano, 1990), and vertebrates (Allen et al. 1995), and may affect the dispersal and survival of native plants (Ready and Vinson 1995). These effects have resulted in a decline of biodiversity, and simplification of ecological communities in both natural and managed systems (Vinson 1994; Wojcik et al. 2001).

Worldwide there are 46 known species of mealybugs, in 16 genera known as legless mealybugs. They possess functional legs during the first instar only, the crawler phase, and adult females colonize grasses at the crown, nodes, and under leaf sheaths (Hendricks and Koszta 1999). The Rhodes-grass mealybug, *Antonina graminis* Maskell, was described in 1897 from specimens discovered in Hong Kong, China (Dean et al. 1979), and has since been recorded throughout the world (Ben-Dov et al. 2001). *A. graminis* is a parthenogenetic pseudococcid that reproduces ovoviviparously and produces five generations per year. As adults, *A. graminis* produces felt-like wax secretions that cover the body, and has a wax excretory tube from which honeydew is discharged (Bartlett 1978).

A. graminis was considered a serious rangeland pest shortly after its discovery in 1942 in Texas, and can be found on approximately 70 different grass hosts through the Southern United States (Chada and Wood 1960). Infestations of *A. graminis* on rangeland grasses result in brown discolored foliage, and eventual plant death (Chada and Wood 1960). Economically important hosts include Rhodes-grass, (*Chloris gayana*), St. Augustine, (*Stenotaphrum secundatum*), Johnson grass, (*Sorghum halepense*), and Bermuda grass, (*Cynodon dactylon*) (Bartlett 1978).

Due to negative economic impacts, an extensive biological control effort against *A. graminis* was conducted in Southern Texas during the late 1940s through the 1950s by introducing two parasitoids (Encyrtidae) of the pest: (1) *Anagyrus antoninae* Timberlake, in 1949, a Hawaiian import, and (2) *Neodusmetia sangwani* Rao, from India in 1959 (Riherd, 1950; Schuster and Dean 1976). These parasitoids were considered “ecological homologs,” occupying 3rd instar and adult *A. graminis*. *A. antoninae* was not a successful biological control agent in the arid regions of Texas and Mexico (Schuster and Dean 1976), while, *N. sangwani* was successfully colonized and produced complete biological control of *A. graminis* throughout southern Texas (Dean et al. 1979).

N. sangwani is an internal gregarious parasitoid of *A. graminis* whose females are wingless and is capable of dispersing 0.8 kilometers per year in grasslands with normal mealybug populations (Dean et al. 1979). Under controlled laboratory conditions, *N. sangwani* can complete a generation in 17-20 days at 30°C and 53-56 days at 20°C (Gerson et al. 1975). Adults emerge from *A. graminis* with a 7:1 ratio of females to males, and are commonly short lived, surviving approximately 48 hours (Bartlett 1978). *N. sangwani* is reported to reduce *A. graminis* populations by 69% in Texas, and specifically in the Rio Grande Valley of Texas, scale numbers were reduced by 50 to 83% from October to December (Schuster and Dean 1976).

Understanding the interactions between *A. graminis*, *S. invicta*, and *N. sangwani* could contribute to developing strategies for reducing *S. invicta* populations by limiting the amounts of renewable carbohydrates available to colonies through the reduction of a

known carbohydrate resource. It is also important to investigate if *S. invicta* interferes with *N. sangwani*, which may be responsible for the current abundance of *A. graminis* in rangeland and turf grasses. A better understanding of the costs and benefits distribution within this system may provide a crucial link in the success of two invasive species, *A. graminis* and *S. invicta*.

The research reported herein investigated whether *S. invicta* workers affect the rate of parasitism of *A. graminis* by *N. sangwani*, and whether *S. invicta* directly interacts with *N. sangwani* to prevent parasitism. A greenhouse experiment addresses interactions between *A. graminis*, *N. sangwani* and *S. invicta*, and potential impacts on biological control. In addition, an exploratory survey documented parasitoid species utilizing *A. graminis* as a host in parts of Texas and the southern United States.

CHAPTER II

EFFECT OF *SOLENOPSIS INVICTA* ON THE RATE OF PARASITISM OF

ANTONINA GRAMINIS BY *NEODUSMETIA SANGWANI*

Introduction

The Rhodesgrass mealybug, *Antonina graminis*, was discovered in Texas and Mexico in 1942, was quickly considered a serious rangeland pest (Chada and Wood 1960; Dean et al. 1979). A massive biological control effort was launched against *A. graminis* through the introduction of 3 encyrtid parasitoids. In 1959, *N. sangwani* was introduced into the United States from India and provided complete biological control of *A. graminis*, reducing populations by up to 68.8% in Texas, and 50-83% in the Rio Grande Valley (Schuster and Dean 1976). Currently *A. graminis* can be found on over 100 grasses throughout Texas and the southeastern United States (Helms and Vinson 2000).

The red imported fire ant, *Solenopsis invicta*, was introduced into Mobile, Alabama from South America ca. 1930, and has spread through the southern United States. *Solenopsis invicta* has had important ecological impacts that include displacement of native ant fauna (Porter and Savignano 1990), and decline in local biodiversity (Kaplan and Eubanks 2005). *S. invicta* entered Texas in the 1940's and specifically the Rio Grande Valley in the mid 1970's, at which time interactions between *A. graminis* and *S. invicta* may have first occurred in Texas.

S. invicta has been recorded tending Hemipterans, harvesting honeydew, and constructing shelters around the base of grasses that are common hosts to honeydew producing Hemiptera. Shelters are commonly in close approximation to fire ant mounds, and mealybug numbers reportedly increase as the distance from *S. invicta* mounds decreases (Helms and Vinson 2002). In Texas and the southeastern United States, *A. graminis* is often tended by *S. invicta* (Helms and Vinson 2002). The success of *S. invicta* maybe attributed to the collection of honeydew, which has been reported to supply 16-48% of the energy requirements of an average *S. invicta* mound (Helms and Vinson 2003), with *A. graminis* responsible for approximately 70% of honeydew collected by *S. invicta* (Helms and Vinson 2002).

Interactions between *S. invicta* and *A. graminis* may not only facilitate the spread and establishment of *S. invicta*, but also interfering with the established biological control of *A. graminis* by *N. sangwani*. *A. graminis* is currently abundant, on a variety of grass hosts, throughout the southeastern United States including Texas, and has become widely associated with *S. invicta* (Helms and Vinson 2002). While *S. invicta* is known to benefit form *A. graminis* honeydew, it is unknown whether *A. graminis* benefits from *S. invicta*, and specifically, whether *S. invicta* protects *A. graminis* from *N. sangwani*. In general, honeydew-producing Hemiptera are often afforded some degree of protection from their natural enemies by ants (Way 1963; Holldobler and Wilson 1990). However, there has been no direct test of whether *S. invicta* protects *A. graminis* from natural enemies. In order to do so, we conducted a greenhouse experiment to test

whether *S. invicta* decreases the rate at which *N. sangwani* parasitize *A. graminis*, and if so, how such protection may occur.

Materials and Methods

Greenhouse Experiment

It was tested whether *S. invicta* protects *A. graminis*, from *N. sangwani* in a greenhouse experiment. The experiment was composed of four treatments: mealybugs alone (MB), mealybugs with parasitoids (MB+P), mealybugs with ants (MB+A), and mealybugs with parasitoids and ants (MB+P+A). Each replicate of each treatment was housed in a 38cm x 55cm plastic box with fluon applied to the sides, and covered with a fabric screen held in place with modeling clay to prevent the escape of insects. Each box contained two Bermudagrass pots (2.5 liter), which served as a host for *A. graminis*. All boxes were housed in a greenhouse divided into two sections by a glass wall. Each greenhouse section held 14 replicates of each of the four treatments, which were randomly distributed. Preliminary analysis showed that there were no significant differences in parasitism rates ($P = 0.829$, $F = 0.047$, $DF = 54$), so replicates from both greenhouse sections were combined for all subsequent statistical analyses.

Establishment of Bermudagrass

Bermudagrass stolons were collected near College Station, TX, and soaked in insecticidal soap to remove any non-target insects, rinsed thoroughly, and cut into approximately 15 cm segments. Bermudagrass stolons were planted into a commercial

potting soil mix in 2.5 liter plant nursery containers, and placed in a greenhouse in early March, providing 12:12 (hr) daylight to darkness. Plants were watered as needed, and were trimmed daily to maintain a grass height of approximately 20 cm.

Collection and Introduction of *Antonina graminis*

A. graminis were collected locally and returned to the laboratory where 50 individuals were placed into glass rearing chambers (112 rearing chambers total) and kept in an incubator at 28°C for 7 days to allow crawlers to emerge. Rearing chambers were ranked according to crawler numbers as low (0-50), medium (51-100), or high (100+) density. One rearing chamber per pot (two per replicate) was randomly distributed into the four treatments. Rearing chambers were removed from the boxes after 7 days, and crawlers were left for approximately 7 weeks to establish and mature prior to beginning the experiment.

Rearing *Neodusmetia sangwani*

Neodusmetia sangwani was collected near Port Lavaca, TX, from *A. graminis* on Bermudagrass. Excess Bermudagrass was cut and discarded in the laboratory; leaving only grass clippings with *A. graminis*. The clippings were placed into rearing chambers with 10 ml deionized water, and plugged with cotton. The tubes were held in an incubator at 30°C for 22-28 days, set, and inspected daily for emerging *N. sangwani* adults. Upon emergence of *N. sangwani*, new *A. graminis* collected from Bermudagrass in College Station and Bryan, TX, and prepared in the manner as described previously.

Adult *N. sangwani* were transferred into new tube holdings. This process was repeated until 10 adult female *N. sangwani* per replicate (600 total) were available. Parasitoid treatments for the experiment were obtained by introducing 2 tubes each holding 10 *N. sangwani* adult females into the corresponding boxes. One *Solenopsis invicta* colony was introduced into corresponding boxes 48 hours after introducing *N. sangwani*.

Collection and Introduction of *Solenopsis invicta*

Solenopsis invicta was collected from field sites in the College Station, TX area. Mounds were excavated, placed into 19 liter buckets with a talcum powder ring around the inside upper edge to prevent escape. Colonies were then brought into the lab and water was slowly dripped into the bucket to raise the water table, and rafting ants were scooped out and placed into 30 x 46 cm containers. Colony composition varied in queen number (some were monogyne, others were polygyne), and numbers of broods and workers. Colonies were fed a standardized amount of honey water, mealworms, and crickets. Two weeks before using in the greenhouse experiment each colony was adjusted to 11 g +/- 0.8g, including brood (eggs, larvae, reproductives and pupae) workers, and queens to ensure colony success during the greenhouse experiment. During the experiment, *S. invicta* colonies were fed (mealworms and crickets), and water ad libitum.

Determination of Predation on Mealybugs

A. graminis parasitized by *N. sangwani* were divided into two categories, “parasitized/emerged” and “parasitized/eaten”. Parasitized/emerged *A. graminis* were those that yielded adult *N. sangwani* and were identified by having a single, symmetrical, pinhole size opening, 1mm in diameter, in the exoskeleton. Parasitized/eaten *A. graminis* were those that were consumed by *S. invicta*, and were identified by having a large irregular opening in the exoskeleton, and contained *N. sangwani* meconia. Parasitized *A. graminis* appear discolored amber, while a healthy *A. graminis* is dark red/brown.

Data Collection and Statistical Analysis

The experiment was conducted for 27 days, the amount of time required for two generations of *N. sangwani*. Generation time was monitored by placing rearing chambers containing parasitized *A. graminis* into corresponding greenhouses. Experimental arenas were brought into the lab where all *A. graminis* were removed from the plants. *Antonina graminis* individuals were counted and inspected for evidence of parasitism, and were separated into second categorization: those that occurred above ground level and those that occurred below ground level. For treatments that included *S. invicta*, *A. graminis* that occurred within *S. invicta* constructed shelters were included in the below ground category. All *A. graminis* were placed into glass rearing chambers, approximately 50 individuals per chamber, and were placed into an incubator at 30°C. Tubes were checked daily for emergence of *N. sangwani* after approximately 15 days

following emergence of *N. sangwani* the rearing chambers were placed into a freezer precluding *N. sangwani* third generation development and emergence.

In order to assess second generation parasitism, each *A. graminis* individual was inspected for evidence of an emergence hole. *A. graminis* were recorded as “parasitized/emerged” and “parasitized/eaten” using criteria described above.

To determine if the rate of parasitism in greenhouse 1 (G1) was equal to the rate of parasitism in greenhouse 2 (G2) an analysis of variance (ANOVA) was conducted on the environmental conditions of each greenhouse. ANOVA analysis revealed no significant difference between G1 and G2, ($F = 0.047$, $P\text{-value} = 0.829$, $DF = 1-110$, i.e. Temperature, humidity, relative humidity, and photoperiod), allowing experiments to be conducted in each greenhouse equivalently. All proportions were normalized using an arcsine transformation. ANOVA was performed to test for significant differences in the proportions of *A. graminis* parasitized by *N. sangwani* between M+P+A and M+P treatments for first and second generation *N. sangwani*, and the proportion of *N. sangwani* emergence of generation 1. Scheffe’s multiple comparison model was used to compare normalized data among all four treatments. Mean proportions, and the standard error of the means were generated using SPSS.

Results

Solenopsis invicta did not significantly affect the initial rate parasitism of *A. graminis* by *N. sangwani* during the first generation ($F = 0.060$, $P = 0.808$, $DF = 54$) (Figure 2.1). The presence of *S. invicta* was observed to significantly increase the

proportion of first generation parasitized/eaten *A. graminis* compared to the absence of *S. invicta* ($F = 67.34$, $P < 0.001$, $DF = 54$). There was no evidence of worker predation of *A. graminis* in the remaining 3 treatments. This behavior correlated with a significant difference in the number of fertile females that emerged from parasitized *A. graminis* individuals (Figure 2.2) ($F=120.200$, $P < 0.001$, $DF= 54$). *Solenopsis invicta* significantly reduce the proportion of *A. graminis* parasitized by second generation *N. sangwani* ($F= 547.341$, $P < .001$, $DF = 54$) (Figure 2.3).

In the MB+P treatment the proportion of mealybugs parasitized by F1 *N. sangwani* below ground was approximately 4 fold higher than the proportion of *A. graminis* parasitized above ground (Figure 2.4) ($F=12.493$, $P<.001$, $DF=54$). In MB+P+A treatment the proportion of *A. graminis* parasitized by F1 *N. sangwani* below ground was also approximately 4 fold higher than the proportion of *A. graminis* parasitized above ground ($F=13.124$, $P<.001$, $DF=54$) (Figure 2.4). Second generation analysis were consistent with first generation oviposition location, resulting in a significantly high proportion of mealybugs parasitized below ground in the absence of *S. invicta* ($F=22.198$, $P<.001$, $DF= 54$) (Figure 2.5). No significant difference was found in oviposition location with the presence of *S. invicta* ($F=1.612$, $P=.210$, $DF=54$) (Figure 2.5).

First Generation
Proportion of *Antonina graminis* parasitized by *Neodusmetia sangwani*

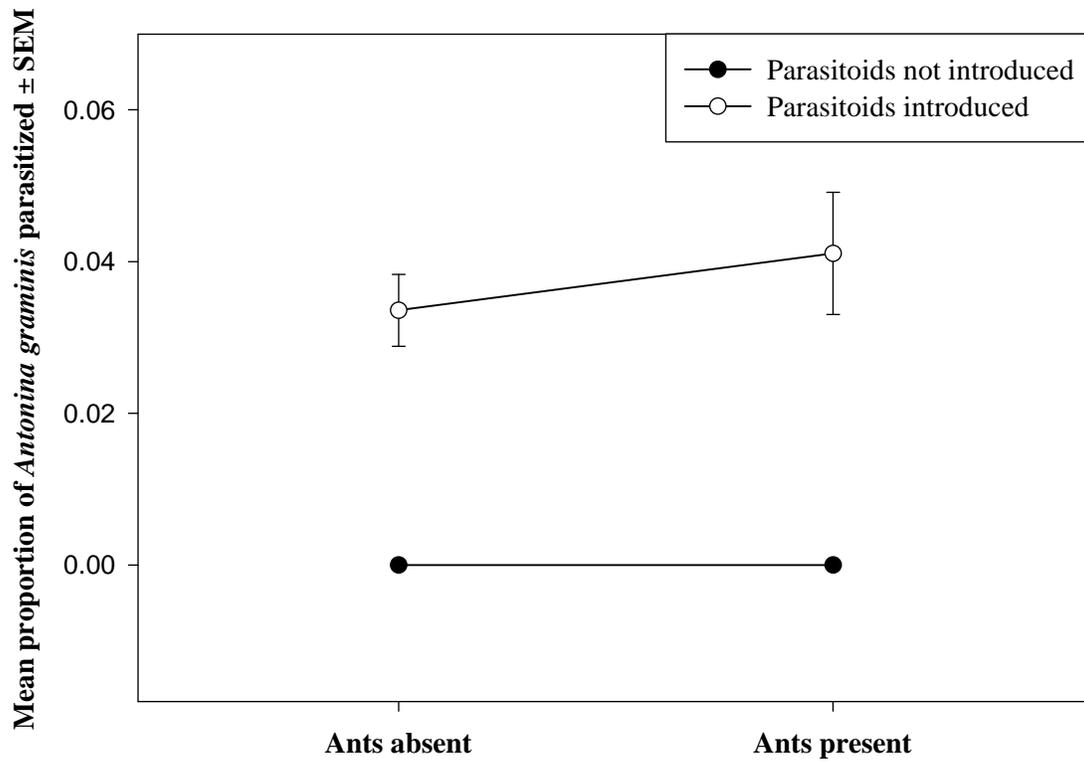


Fig. 2.1. First generation mean proportion of *Antonina graminis* parasitized by *Neodusmetia sangwani* in the presence and absence of *Solenopsis invicta*. *Solenopsis invicta* did not significantly affect first generation proportion of parasitized *Antonina graminis*.

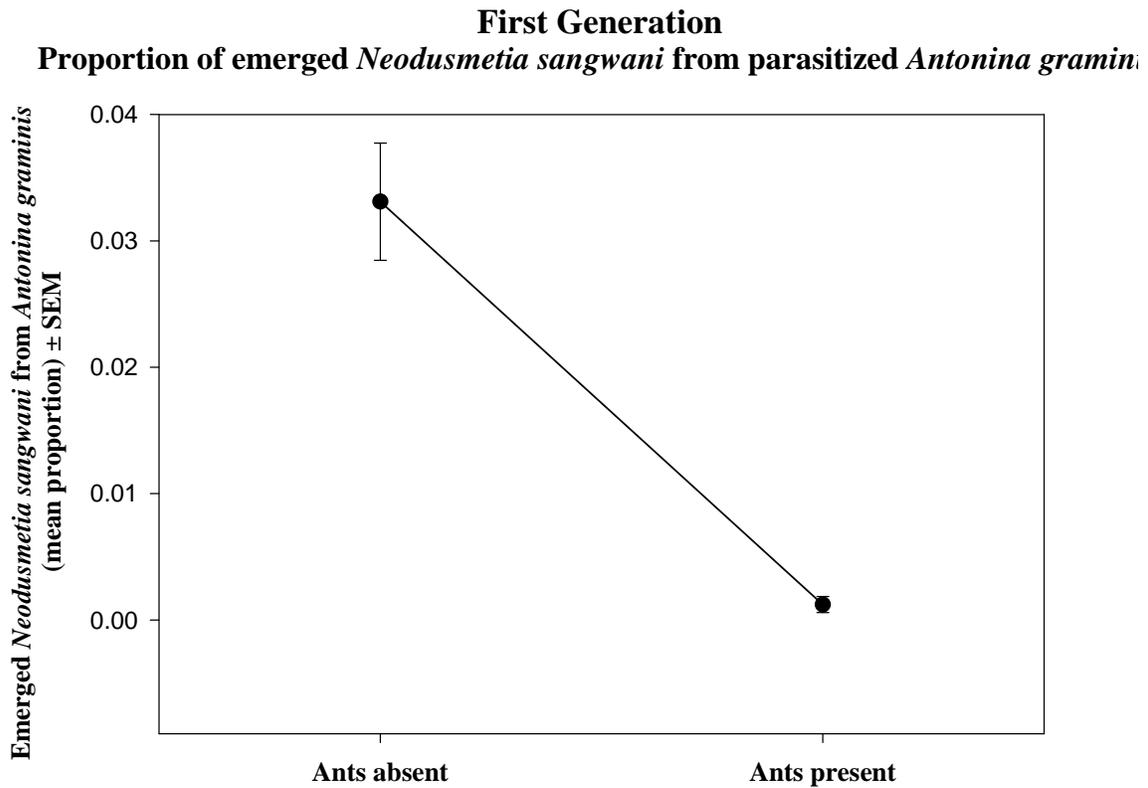


Fig. 2.2. First generation mean proportion of emerged *Neodusmetia sangwani* from parasitized *A. graminis*. *Solenopsis invicta* significantly reduced the proportion of emerged *Neodusmetia sangwani* from parasitized *Antonina graminis*.

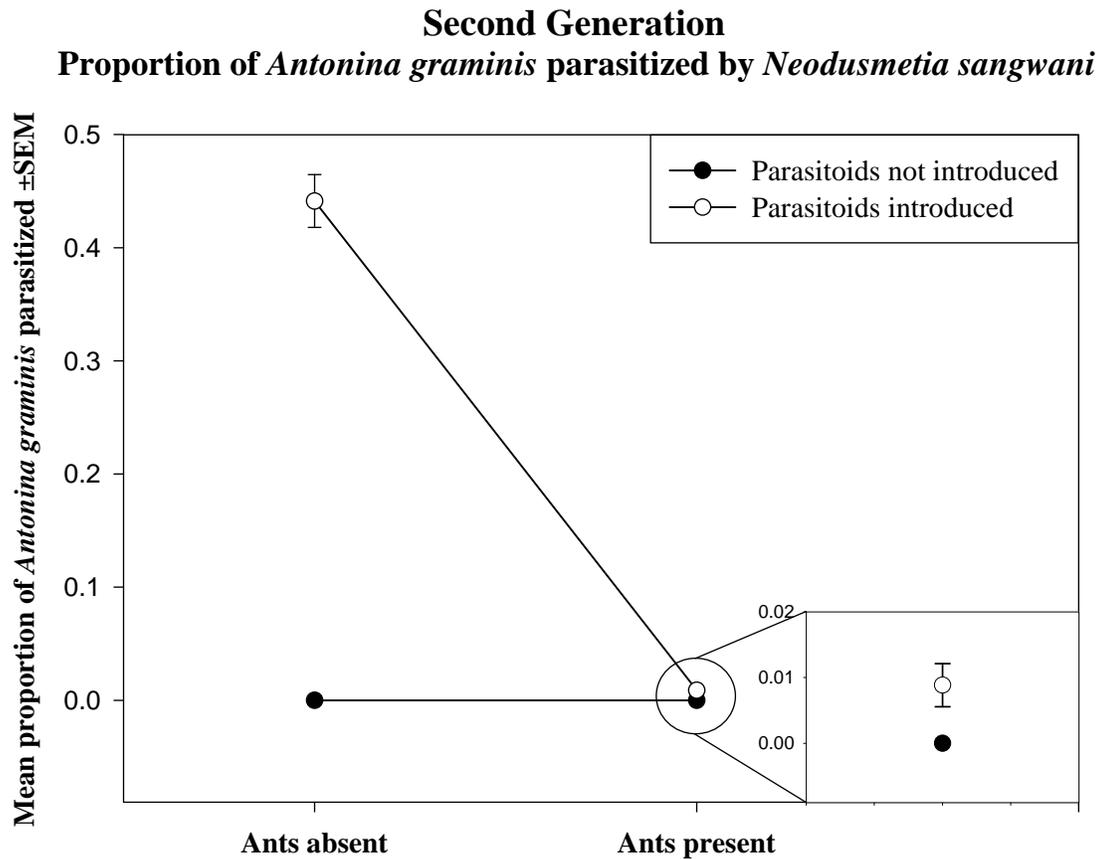


Fig. 2.3. Second generation mean proportion of *Antonina graminis* parasitized by *Neodusmetia sangwani* in the presence and absence of *Solenopsis invicta*. *Solenopsis invicta* significantly decreased second generation proportion of parasitized *Antonina graminis* by *Neodusmetia sangwani*.

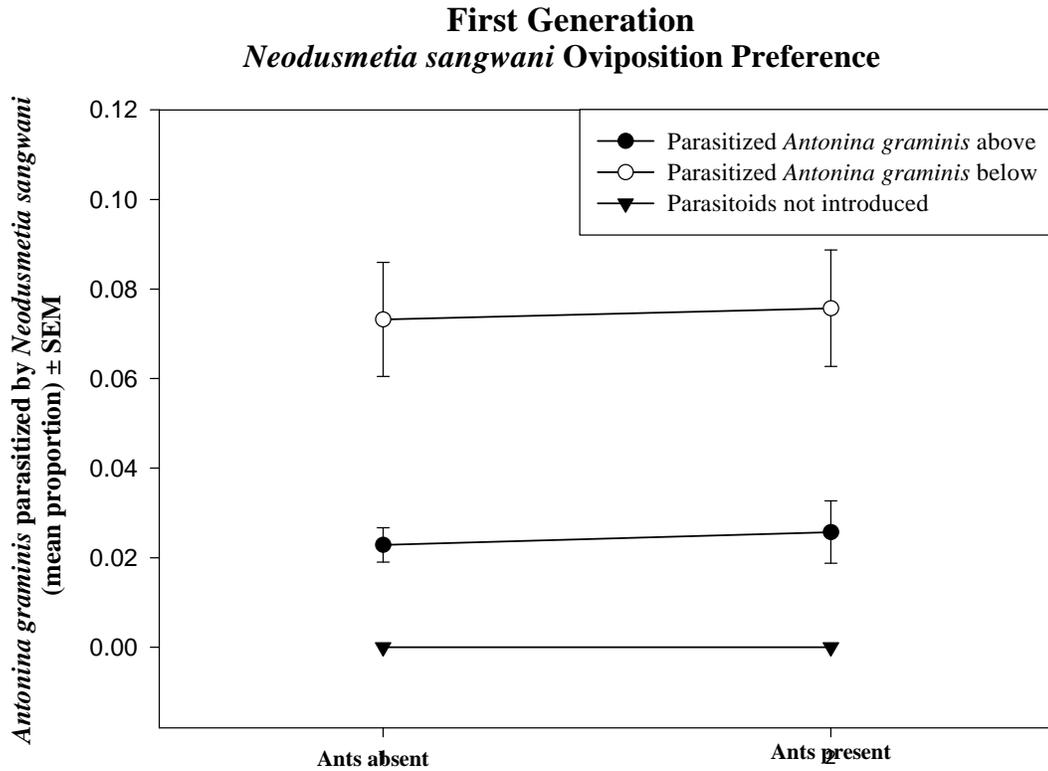


Fig. 2.4. First generation mean proportion of *Antonina graminis* parasitized above ground versus below ground by *Neodusmetia sangwani*. *Neodusmetia sangwani* displayed a significant preference toward below ground oviposition sites.

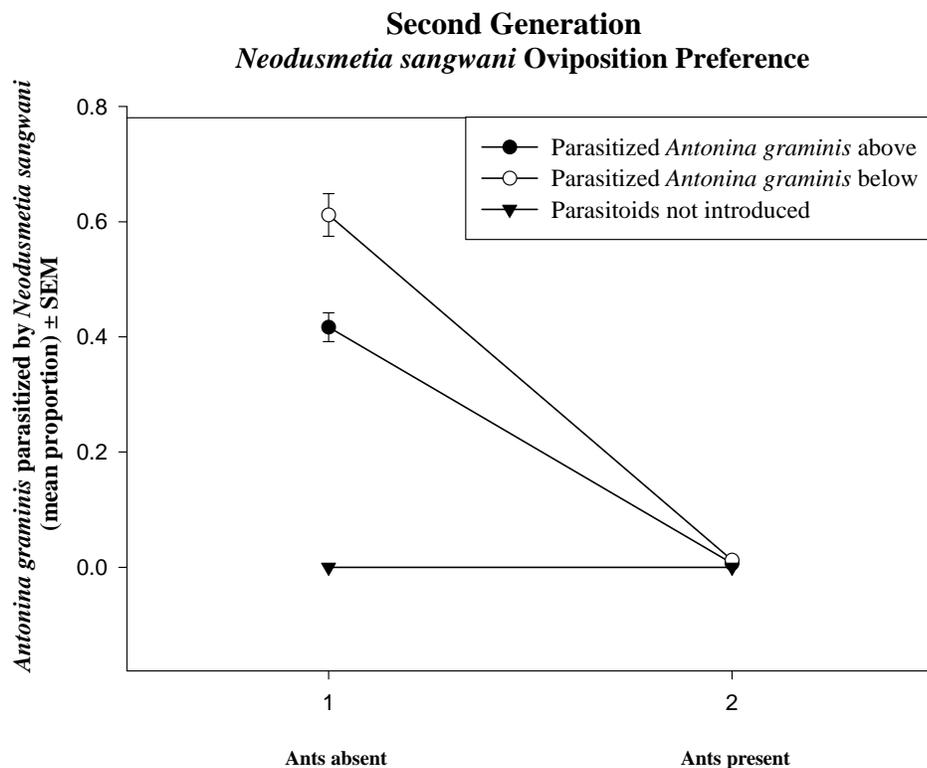


Fig. 2.5. Second generation mean proportion of *Antonina graminis* parasitized above ground versus below ground by *Neodusmetia sangwani*. *Neodusmetia sangwani* displayed a significant preference toward below ground oviposition sites in the absence of *Solenopsis invicta*. *Solenopsis invicta* significantly reduced the mean proportion of *Antonina graminis* parasitized by *Neodusmetia sangwani*.

Discussion

Interactions between two invasive species, *S. invicta*, and *A. graminis* may be detrimental to suppression effects against both species. *Solenopsis invicta* significantly reduced the mean proportion of *A. graminis* parasitized by *N. sangwani* in the greenhouse experiment, which suggest that *S. invicta* may significantly reduce the effect of *N. sangwani* as a biological control agent of *A. graminis* in the field. Helms and Vinson (2003) reported that *A. graminis* densities increased with proximity to *S. invicta* mounds. Ants protect honeydew producing hemipterans from parasitoids and predators, frequently resulting in increased hemipteran populations (Barlett 1961; Way 1963; Buckley 1987; Stechmann et al. 1996; Gibernau and Dejean 2001). Prior studies showed that *A. graminis* is capable of providing up to 70% of honeydew gathered by *S. invicta* workers, providing an estimated 16 to 48% of the energy requirements of an average *S. invicta* colony (Helms and Vinson, 2003). Interactions between *S. invicta* and *A. graminis* may thus facilitate the success of both invasive species. Increased control of *A. graminis* populations may be a crucial step in reducing *S. invicta* colony numbers through diet regulation by the reduction of “free” carbohydrates and amino acids found in honeydew.

Solenopsis invicta significantly reduced the proportion of first generation *N. sangwani* emergence through predation of developing first generation *N. sangwani*. In most Apocrita, the midgut and hindgut end blindly during the first instars and lumens usually become fused, expelling the meconium, during the final instar (Quicke 1997).

Frass contained within parasitized *A. graminis* remains suggest that *S. invicta* detected developing *N. sangwani* following pupation.

Preliminary laboratory studies suggest that *S. invicta* may directly interfere with parasitism by attacking ovipositing *N. sangwani* females (Appendix 1). The greenhouse experiment did not address this issue because *S. invicta* were introduced following initial *N. sangwani* oviposition. Schuster and Boling (1971) reported native ants had little influence on the effectiveness of ovipositing *N. sangwani*.

Increased *N. sangwani* oviposition of *A. graminis* located below may have important field applications because *S. invicta* constructs shelters composed of soil and debris around *A. graminis* (Helms and Vinson 2002). The presence of unattended *A. graminis* located outside *S. invicta* colony boundaries may act as a source population of *N. sangwani*. Increased oviposition for hosts located below ground may increase the likelihood that *N. sangwani* will target *A. graminis* tended by *S. invicta*.

Although more work is needed, such as impacts on local biodiversity, to fully understand the impacts of the association of *S. invicta* and *A. graminis* is having on biological control, and surrounding arthropod and plant communities, our works further supports these interactions may be enhancing negative effects of both invasive species through facilitation of increased growth potential through food for protection interactions.

CHAPTER III
GENERAL SURVEY OF PARASITOIDS THAT UTILIZE
ANTONINA GRAMINIS AS A HOST

Introduction

Classical biological control has been a very important approach in controlling introduced insect pests throughout the world. Biological control is defined as “the action of parasites, predators, and pathogens in maintaining another organism’s population density at a lower average than would occur in their absence” (Stern and van den Bosch, 1959; Debach, 1964). Over the years, classical biological control, when carried out correctly, has proven to be a successful approach to providing permanent control of the target pest insects, returning pest populations to a “natural balance.”

Among the successful classical biological control programs are the southern green stink bug, *Nezara viridula*, in Hawaii (Davis, 1967); the olive scale, *Parlatoria oleae*, (Huffaker and Kennett, 1966), and the walnut aphid, *Chromaphis juglandicola*, in California (van den Bosch et al. 1970); the rhodesgrass mealybug, *Antonina graminis*, in Texas (Schuster and Boling 1971); and the carrot aphid, *Cavariella aegopodii*, in Australia and Tasmania (Stern and van den Bosch, 1959).

The Rhodes-grass mealybug, *Antonina graminis*, was described by Maskell in 1897 from specimens discovered in Hong Kong, China (Dean et al. 1979). *A. graminis* was considered a serious rangeland pest shortly after its discovery in 1942 throughout Texas and Mexico, where it could be found on approximately 70 different grass hosts through the Southern United States (Chada and Wood, 1960). An extensive biological

control effort of *A. graminis* was conducted in Southern Texas during the late 1940s through the 1950s by introducing three parasitoids of the pest: (1) *Anagyrus antoninae* Timberlake, in 1949, a Hawaiian import, (2) *Pseudectroma europaea* Mercet [= *Timberlakis europaea* (Mercet) in Bartlett, 1978] introduced from Europe, and (3) *Neodusmetia sangwani* Rao, from India in 1959 (Riherd, 1950; Schuster and Dean, 1976). *N. sangwani* was reported to reduce *A. graminis* populations by 68.8% in Texas, and, specifically in the Rio Grande Valley of Texas, scale numbers were reduced by 50 to 83% (Schuster and Dean, 1976).

Although there have been many successful cases of biological control, the long-term follow-ups on the frequency and efficacy of biological control agents may go overlooked. Studies concerning the long-term establishment of biological control agents may provide beneficial information to maintaining pest suppression. Recently, *A. graminis* was recorded being tended, and housed in shelters by *Solenopsis invicta*, and ant tending has been linked with honeydew-producing hemipteran outbreaks resulting in detrimental effects on plant fitness. (Beattie 1985; Carter 1962; Buckley 1987; Delabie 2001; Holway et al. 2002). Information on the post-introduction efficacy of the biological control of *A. graminis* by *N. sangwani* will provide information on the impact *S. invicta* is having on an established successful biological control system.

In order to assess the current field rate of parasitism, and current range of *A. graminis* two surveys were conducted of parasitoids that utilize *A. graminis* as a host, first throughout Texas, and second in the southeastern United States.

Materials and Methods

In this study two separate surveys of parasitoids that utilize *A. graminis* as a host were conducted. The first was a fine scale study, ranging from Dallas to Brownsville TX in July and October 2005 of parasitoids that utilized *A. graminis* as a host. Sites were located primarily along Interstate 35, State Highway 6, and Highway 77 in 80 km intervals (Fig 3.1), and were labeled TX-1 through TX13. Each site was a roadside patch that was composed mainly of Bermuda grass and was surrounded by agricultural land, and disturbed habitats. A minimum of 75 *A. graminis* individuals were collected from each site; excess grass was removed, and *A. graminis* were placed into humid rearing chambers. Chambers containing samples were placed into an incubator at 30°C, and samples were checked daily for emerged parasitoids for a minimum of 30 days. Emerged individuals were cleared, counted, placed into 90% ETOH, and identified (Gibson et al. 1997).

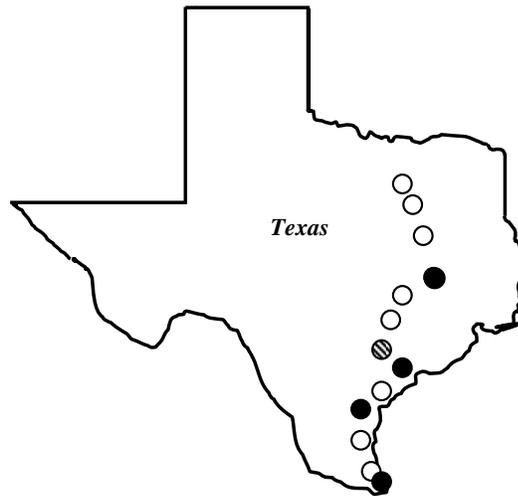
The second survey was a broader scale study across the southeastern United States from Louisiana east to Florida in October 2005. Sites were located along Interstate 10 and were labeled according to the state and site number. Sites were composed of Bermuda grass and crabgrass with *S. invicta* commonly present. In sites where *A. graminis* were present at least 100 individuals were collected, placed into rearing chambers and processed as outlined above.

Results

In the Texas survey the percent of *A. graminis* parasitized by *Pseudectroma* was relatively low, 0.97%, at site TX-7 in July, and was not collected in October (Table 3.1). *N. sangwani* was collected in sites TX-7, TX-8, and TX-10, at a low percent parasitism (<5%), and was collected at site TX-13 at a high percentage of 14.40% in July 2005 (Table 3.1). In the October collection percent parasitism increased by over 1% in sites TX-7, and TX-8. There was approximately a 1% decrease in percent parasitism in site TX-13 (Table 3.1). Site TX-10 was located between two agriculture fields that appeared recently treated, all grass in the surrounding area was severely damaged, and no data was collected from this site in October.

In the second survey throughout the southeastern United States, *N. sangwani* was collected in one site, FL-1, with a high percent parasitism of 10.08% (Table 3.2). *Acerophagus* sp. was collected at a high percent parasitism (>5%) in LA-4, and at low percent parasitism in site LA-1, and FL-5 (Table 3.2). *Antonina graminis* was collected in sites LA-1, LA-4, FL-1, and FL-5, and was not found in remaining sites.

- A.
- *Neodusmetia sangwani* present
 - ◐ *Neodusmetia sangwani* and *Pseudectroma*
 - *Antonina graminis* present
Parasitoids absent



- B.
- ◐ Acerophagus
 - Acerophagus and *Neodusmetia sangwani*
 - *Antonina graminis* absent

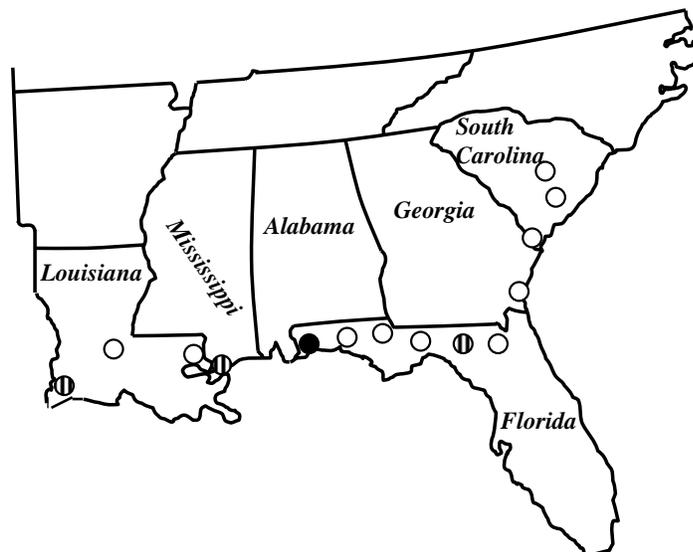


Figure 3.1. Distribution of parasitoids that utilize *Antonina graminis* as a host (A) Texas and (B) throughout the southeastern United States.

Table 1. Percentage parasitism *Antonina graminis* by parasitoid species at selected locations in Texas in July and October 2005.

Parasitoid Species	Site	Percent parasitism July 2005	N	Percent parasitism October 2005	N
-	TX-1	0%	108	0%	104
-	TX-2	0%	105	0%	113
-	TX-3	0%	98	0%	96
<i>Neodusmetia sangwani</i>	TX-4	2%	136	3%	94
-	TX-5	0%	100	0%	107
-	TX-6	0%	144	0%	123
<i>Neodusmetia sangwani</i>	TX-7	2.92%	206	4.06%	159
<i>Pseudectroma europaea</i>		0.97%		0%	103
<i>Neodusmetia sangwani</i>	TX-8	1.46%	249	3.14%	93
-	TX-9	0%	134	0%	122
<i>Neodusmetia sangwani</i>	TX-10	1%	224	*	0
-	TX-11	0%	282	0%	93
-	TX-12	0%	154	0%	103
<i>Neodusmetia sangwani</i>	TX-13	14.40%	153	13.14%	137

* Data not collected due to site alteration

- No parasitoids collected

N = Number of *Antonina graminis* collected

Table 2. Percentage parasitism *Antonina graminis* and parasitoid species name throughout Southeastern United States in October 2005.

Parasitoid Species	Site	Percent parasitism October 2005	N
<i>Acerophagus</i> sp.	LA-1	0.86%	116
-	LA-2	-	-
-	LA-3	-	-
<i>Acerophagus</i> sp.	LA-4	14.29%	7
-	MS-1	-	-
-	AL-1	-	-
<i>Neodusmetia sangwani</i>	FL-1	16.8%	119
<i>Acerophagus</i> sp.		3.4%	
-	FL-2	-	-
-	FL-3	-	-
-	FL-4	-	-
<i>Acerophagus</i> sp.	FL-5	2.67%	112
-	FL-6	-	-
-	GA-1	-	-
-	SC-1	-	-
-	SC-2	-	-
-	SC-3	-	-

- *Antonina graminis* absent

Discussion

Pseudectroma europaea was introduced from Europe to Texas in the late 1950's by Dean and Schuster in effort to control *A. graminis*, but was thought to have not established upon introduction. *Pseudectroma* was collected at site TX-7 in July 2005 at a percent parasitism of 0.97%. This is the first record of the establishment of *Pseudectroma* in South Texas, and may provide useful information into continued control of *A. graminis* populations.

Parasitism by *N. sangwani* has apparently dramatically decreased from a range of 22 - 45.7% on four different grasses in 1963-1965 (Schuster and Boling, 1971) to 1.5-4% in sites TX- 5, 7, 8, and TX-10 in 2005. This decrease is maybe due to a change in host densities from 1972 to 2005. As available *A. graminis* decreased it is likely that *N. sangwani* populations also decreased due to the limited host numbers. This apparent decrease may also be a result of site disturbance. Most sites were disturbed habitats, depending on dispersal of *N. sangwani* from long established populations. *N. sangwani*'s poor capability of dispersal, 0.8 km/yr (Dean et al. 1979), may account for the lower parasitism rate. In site TX-13, which may have remained undisturbed since the introduction of *N. sangwani*, percent parasitism was 14.40% in July and 13.14% in October 2005. This percentage is higher than found at other locations, supporting that site disturbance may play a role, but is still lower than previously reported illustrating that site disturbance may not be the only factor in the reduction in percent parasitism.

N. sangwani was released in Kingsville, Armstrong, and Encino, all in TX, and can now be found as far south as Brownsville, and north to College Station TX. *N.*

sangwani is not found in all regions between Brownsville and College Station, but rather appears to have a patchy distribution. This type distribution suggests that *N. sangwani* may have been accidentally brought into the area with *A. graminis* infested grass, instead of natural dispersal.

Currently *A. graminis* can easily be found on Bermuda grass in the Texas survey region, and throughout the region surveyed across the southeastern United States. Such abundance of *A. graminis* is likely due to its close association with *S. invicta*. *A. graminis* numbers have been reported to increase as proximity to *S. invicta* mounds decrease (Helms and Vinson, 2003), and ant tending has been linked with honeydew-producing hemipteran outbreaks which have detrimental effects on plant fitness through consumption of plant sap and increased transmission of plant pathogens (Beattie 1985; Carter 1962; Buckley 1987; Delabie 2001; Holway et al. 2002). The previously mentioned reduction in *N. sangwani* numbers may also be linked with the presence of *S. invicta*. In a large scale field manipulation, interactions between the cotton aphid (*Aphis gossypii*) and the red imported fire ant (*Solenopsis invicta*) resulted in a 27-33% reduction in herbivore taxa and a 40-47% reduction in predator taxa (Kaplan and Eubanks 2005). Because of *S. invicta*'s aggressive behavior, the efficacy of established biological control agents, such as *N. sangwani*, may be decreased due to increased predation.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Mutualistic interactions between ants and honeydew producing hemipteran has been a popular topic over the past 100 years, but little work has been directed toward the effects of ants tending honeydew producing Hemiptera on food webs, arthropod community structure, trophic interactions, and host plant fitness (Styrsky and Eubanks 2007). *A. graminis* and *S. invicta* are both invasive species that have become important pest in the Southern United States, and recent associations between *A. graminis* and *S. invicta* may be directly leading to increased population numbers and reduced control of both pest insects. Future work should be directed toward understanding whether interactions between *A. graminis* and *S. invicta* are aiding in the range expansion and population growth of these imported invasive species. Work should be directed toward a better understanding of interactions between *S. invicta* and *A. graminis* and the costs, benefits, and potential economic impact of resulting interactions on arthropod and plant communities.

***Antonina graminis* Population Density**

Ant tending has been linked with honeydew-producing hemipteran outbreaks, and these have been documented to have negative effects on plant fitness through consumption of plant sap and increased transmission of plant pathogens (Beattie 1985; Carter 1962; Buckley 1987; Delabie 2001; Holway et al. 2002). Ant-hemipteran

mutualisms are also thought to be detrimental to biological control due to increased aggression of hemipteran predators and parasitoids. This altered behavior may have a major effect in shaping food web dynamics and trophic interactions in agroecosystems (Vinson and Scarborough, 1991; Jiggins et al. 1993; Reimer et al. 1993; Stechmann et al. 1996; Dutcher 1998).

Helms and Vinson (2002) reported that *A. graminis* densities increased when proximity to *S. invicta* mounds decreased, but general field density numbers were not presented. Current field densities of *A. graminis* would permit comparison between post biological control densities of *A. graminis* (ca. 1960) and current densities allowing inferences to be made about *S. invicta*'s overall impact on *A. graminis* population densities.

Arthropod Community Structure

In a large scale field manipulation, interactions between the cotton aphid (*Aphis gossypii*) and the red imported fire ant (*Solenopsis invicta*) resulted in a 27-33% reduction in herbivore taxa, and a 40-47% reduction in predator taxa (Kaplan and Eubanks 2005). Tending ants can also change the abundance and distribution of generalist and specialist predators and parasitoids, and multiple species of herbivores in several feeding guilds, resulting in the changes to local species diversity (Strysky and Eubanks 2007).

A field study should be conducted to account for potential differences in local species diversity in the presence and absence of *S. invicta* in turf and rangeland

environments. Such a study would evaluate if the presence of *S. invicta* alters turf and rangeland pest and predator populations, demonstrating the beneficial or detrimental effects *S. invicta* may have on the yield of rangeland grasses. This study would also provide information on the potential reduction of honeydew producing hemipteran predators. The presence of *S. invicta* has been reported to significantly decrease the percent parasitism of *A. graminis* by *N. sangwani* (Chapter II), potentially reducing the effects of *N. sangwani* as a biological control agent of *A. graminis*. Changes in predator and parasitoid populations could increase the densities of economically important rangeland pests, such as *A. graminis*.

Behavioral Characteristics

Mutualistic relationships between ants and honeydew producing Hemiptera may increase the effects of ants as predators by altering tending-ant behavior such that ants become increasingly aggressive and attack insects that they might otherwise ignore, including predators as well as herbivores (Way 1963). An experiment containing *S. invicta* in the presence and absence of *A. graminis* with introductions of common turf and rangeland predators and herbivores would quantify the effects of *A. graminis* on *S. invicta* as a predator. Such a study would indicate alterations in behavioral characters, increased aggression, that may enhance the success of *S. invicta* colony establishment in the presence of *A. graminis*.

Invasive ants are increasingly attracted to hemipteran aggregations, and exploitation of honeydew and plant extrafloral nectar is hypothesized to enhance the

ecological dominance of invasive ants (Holway et al. 2002; Lach 2003; Ness and Bronstein 2004). Defense of foraging territories by abundant and aggressive hemipteran-tending ants has been reported to reduce the density and diversity of other ants resulting in a 'mosaic' distribution of subdominant and dominant ant species (Bluthgen et al. 2000, 2004; Dejean and Corbara 2003). A greenhouse experiment including grasses infested with *A. graminis* and uninfested grasses with a combination of native ants only, *S. invicta* only, and native ants coupled with *S. invicta* could demonstrate and quantify the advantage *S. invicta* may gain in outcompeting native ant fauna by tending *A. graminis*. Such an experiment could provide evidence that *S. invicta*'s association with *A. graminis* maybe facilitating the ability of *S. invicta* to defend colony territories and displace native ant fauna. Decreased *S. invicta* colony numbers, coupled with increased native ant populations may reduce *S. invicta* populations densities.

In summary, the recent association between *S. invicta* and *A. graminis* may benefit both imported invasive pest, while having an unknown impact on the arthropod, and plant communities. Future research should be directed toward a better understanding of the potential economic impact on rangeland and turf systems resulting from interactions between *A. graminis* and *S. invicta* by examining the arthropod community structure, behavior of *S. invicta* in the presence of *A. graminis*, and host plant yield. Disruption of interactions between *S. invicta* and *A. graminis* maybe the key to colony number reduction of *S. invicta*, maintained populations of *A. graminis*, and facilitate increase in the native ant fauna.

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APPENDIX A

A preliminary laboratory study was conducted to investigate if *Solenopsis invicta* would actively attack adult *N. sangwani* during host searching and/or oviposition. A sample of 5 *A. graminis* were placed into a 20 x 150 mm glass culture tube with 10 *S. invicta* workers for one hour. Five adult female *N. sangwani* were placed in to the culture tube with *A. graminis* and *S. invicta*, and observations for *S. invicta* predation of *N. sangwani* were recorded for one hour, five replicates were conducted. *Solenopsis invicta* was observed to actively attack $48 \pm 0.51\%$ (SEM) of *N. sangwani*. This high percentage may be due to the artificial conditions of the experimental design, but it is important to note that *S. invicta* will actively attack adult *N. sangwani*. Schuster and Boling (1971) reported that native ants had little impact on the effectiveness of *N. sangwani*. The interactions between *S. invicta* and *A. graminis* are likely interfering with the biological control of *A. graminis* by reducing the proportion of parasitized *A. graminis* through predation on developing and adult *N. sangwani*.

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