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Plant Resources and Colony Growth in an Invasive Ant: The Importance of Honeydew-Producing Hemiptera in Carbohydrate Transfer Across Trophic Levels

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ABSTRACT Studies have suggested that plant-based nutritional resources are important in promoting high densities of omnivorous and invasive ants, but there have been no direct tests of the effects of these resources on colony productivity. We conducted an experiment designed to determine the relative importance of plants and honeydew-producing insects feeding on plants to the growth of colonies of the invasive ant *Solenopsis invicta* (Buren). We found that colonies of *S. invicta* grew substantially when they only had access to unlimited insect prey; however, colonies that also had access to plants colonized by honeydew-producing Hemiptera grew significantly and substantially (≈50%) larger. Our experiment also showed that *S. invicta* was unable to acquire significant nutritional resources directly from the Hemiptera host plant but acquired them indirectly from honeydew. Honeydew alone is unlikely to be sufficient for colony growth, however, and both carbohydrates abundant in plants and proteins abundant in animals are likely to be necessary for optimal growth. Our experiment provides important insight into the effects of a common tritrophic interaction among an invasive mealybug, *Antonina graminis* (Maskell), an invasive host grass, *Cynodon dactylon* L. Pers., and *S. invicta* in the southeastern United States, suggesting that interactions among these species can be important in promoting extremely high population densities of *S. invicta*.

KEY WORDS *Antonina graminis*, *Cynodon dactylon*, honeydew, invasive species, *Solenopsis invicta*

The considerable importance of ants in ecological systems stems largely from their interactions with other organisms, which may often be determined directly or indirectly by diet. Many ants are generalist omnivores, opportunistically gathering animal tissues by predation and/or scavenging, and collecting plant exudates (nectar, sap) and honeydew produced by herbivorous insects (Carroll and Janzen 1973). There is strong evidence that animal tissues are important to omnivorous ants, whereas the importance of plant-based resources is less clear, suggesting that plant resources could be primarily important as supplemental food when animal tissues are limited (Tschinkel 2006). Comparisons of the nutritional composition of animal and plant tissues, however, indicate that plant resources could be more important than generally realized.

Animal tissues are rich in proteins (amino acids) that are important to developing ant larvae, whereas plant exudates and honeydew are rich in carbohydrates (sugars) important in fueling adult activity (Abbott 1978, Stradling 1978). Studies have show that proteins are fed primarily to developing brood and carbohydrates are fed primarily to adults (Abbott 1978, Sorensen and Vinson 1981). Because adult workers forage, rear the brood, and defend the colony, it is clear that carbohydrates acquired from plants could be important to colony function. Moreover, adult ants can ingest only liquids (Eisner 1957, Glancey et al. 1981), and animal tissues have a large solid component, suggesting that adult workers may rely to a significant degree on liquids from plant exudates and/or honeydew (Tobin 1994). The importance of plant-based foods in the ants is also suggested by the evolution of specialized digestive systems that facilitate utilization of plant exudates and honeydew in some ant subfamilies (Eisner and Brown 1958, Davidson et al. 2004).

The relative importance of animal- versus plant-based food has important consequences for ecological systems. Ants are often extremely abundant, and Tobin (1994) suggested that animal tissue is unlikely to support such populations, proposing that ants may often act as primary consumers by making extensive use of plant exudates and honeydew. Abundant ants are often those that specialize in acquiring plant-based foods, and the carbohydrates they acquire from plants may result in a positive feedback in resource acquisition by supporting extensive activity, facilitating the location and defense of more limited protein-rich foods (Davidson 1998, Grover et al. 2007).

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Of ant species with large populations, some of the largest occur as invasive species. All are omnivorous and make extensive use of plant exudates and/or honeydew (Helms and Vinson 2002, Holway et al. 2002, Abbott and Green 2007). Because the negative impacts of invasive ants result from extreme abundance, it is important to determine the role of alternative food resources in determining their population sizes at introduced locations. Of the invasive ants, the diet of *Solenopsis invicta* in the southeastern United States is best studied. The importance of animal tissues is often emphasized (Vinson and Greenberg 1986, Tschinkel 2006); however, there is growing evidence that plant-based foods are important. *S. invicta* uses plant exudates and honeydew excreted by aphids, scales, and mealybugs, as well as some seeds (Tennant and Porter 1991, Helms and Vinson 2002, Tschinkel 2006). They also damage some agricultural food crops and presumably collect phloem from the wounded plants, suggesting that plant-based carbohydrates might also be acquired directly (Stewart and Vinson 1991, Tennant and Porter 1991). Tennant and Porter (1991) found that the majority of food acquired by foraging *S. invicta* workers was liquid, with a chemical profile consistent with plant phloem or honeydew, suggesting that most food collected by *S. invicta* is derived from plants. The generality of this conclusion has been questioned (Tschinkel 2006); however, other studies showed that *S. invicta* tend honeydew-producing Hemiptera extensively (Helms and Vinson 2002, Kaplan and Eubanks 2005). In addition, laboratory studies have shown that sucrose, one sugar common in honeydew and plant exudates, increases colony growth beyond that possible with insect prey (Porter 1989). The constituents of honeydew and plant exudates are complex, however, and there have been no experimental tests of their importance to colony growth and population size in *S. invicta* or other omnivorous ants. It is also unclear whether these ants can acquire significant plant resources directly from plants or whether honeydew-producing insects are necessary intermediaries. In this study, we experimentally tested for the relative importance of animals versus plants on the growth of colonies of *S. invicta* and determined whether the importance of plants is dependent on indirect transfer through honeydew-producing Hemiptera or alternatively whether those resources can be acquired directly from plants.

Materials and Methods

Our experiment was designed to determine the relative importance of insect prey, honeydew-producing Hemiptera, and the Hemiptera host plant to the growth of *S. invicta* colonies. The experiment was conducted during June and July of 2004 within a greenhouse on the campus of Texas A&M University, College Station, TX. Greenhouse temperatures were thermostatically controlled with a multistage cooling system engaging at 32, 35, and 37°C and a heating system engaging at temperatures <25.5°C. Although temperatures within the greenhouse varied according to external environment (temperature, sunlight), they remained within the range favorable to *S. invicta* colony growth and activity, i.e., 24–36°C (Porter 1988, Helms and Vinson 2005). In addition, treatments were arranged spatially such that replicates of each treatment were interspersed throughout greenhouse locations to control for any microclimate differences that might occur.

Plants used in the experiment were common Bermuda grass (*Cynodon dactylon*), a non-native, invasive, and widespread grass of agricultural importance in lawns and grazing pastures of the southern United States (Holm et al. 1977). The honeydew-producing insects used were *Antonina graminis*, an invasive mealybug that commonly uses *C. dactylon* as an important host plant (Chada and Wood 1960). Both *A. graminis* and *C. dactylon* are common throughout the range of *S. invicta* in the southeastern United States, and *A. graminis* is often associated with *S. invicta* (Holm et al. 1977, Helms and Vinson 2002).

Plants of *C. dactylon* were established in nursery containers from runners (stolons) collected from a single field site in Washington County, TX. The runners were first submerged for 2 h in a 2.0% solution of insecticidal soap to eliminate existing arthropods and rinsed thoroughly with water. Seven runners 18 cm in length were planted in the greenhouse in each of 51 nursery containers (2.5 liter) filled to within 2.5 cm of the top with commercial potting soil. At least one root node of each runner was planted beneath the soil surface; the soil was kept wet until rooting occurred, and runners resumed growth.

After 1 mo, plants in one third (19) of the containers were inoculated with first instars (crawlers) of the mealybug *A. graminis* by removing adult females from *C. dactylon* plants in the field and placing 10 in each container. The females produced first-instar nymphs (crawlers) that colonized the plants; adult females of *A. graminis* produce live crawlers for up to 60 d after removal from their host plant (Schuster 1967, Gerson et al. 1975). Within 2 mo, *A. graminis* were well established on the plants, producing honeydew, and ready for inclusion in the experiment.

Solenopsis invicta colonies were initiated from single foundress queens collected from a mating flight 1 yr before the start of the experiment. When queens produced their first workers, the colonies were fed frozen crickets [*Acheta domesticus* (Linnaeus)], live mealworms (*Tenebrio molitor* Linnaeus), and a 10% solution of honey mixed with water. In April 2004, the live mass of colonies (≈6–8 g) was reduced to 1.0 ± 0.1 g on a microbalance. Included was the single queen and adult workers, pupae, larvae, and eggs in the approximate proportions at which they occurred in the source colony. They were placed in 100 by 15-mm petri dish laboratory nests and fed as before. After 2 wk, the colonies were randomly assigned to the experimental treatments.

The experiment was conducted in 68-liter (59 by 45 by 40 cm) fluon-lined (escape-proof) plastic storage boxes (arenas). Each arena received two of the soil-filled nursery containers. In three treatments, one of

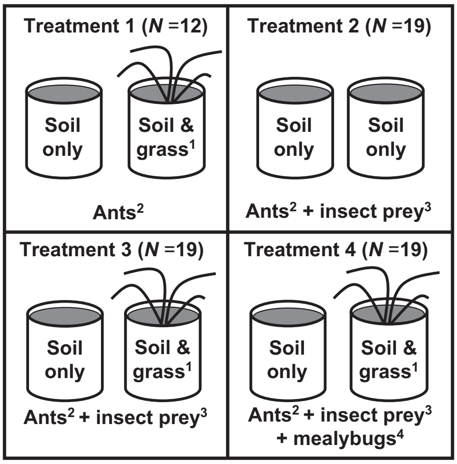

Fig. 1. Treatments used to test for the affects of insect prey and *A. graminis* and their host plant on the growth of *S. invicta* colonies. N = the number of replicates per treatment. (1) *C. dactylon* (Bermuda grass) plants. (2) *S. invicta* colony. (3) Frozen crickets (*A. domestica*) and live mealworms (*T. molitor*). (4) Honeydew-producing *A. graminis* on *C. dactylon* plants.

the two containers also had growing *C. dactylon* plants (treatments 1, 3, and 4; Fig. 1); in the remaining treatment, both containers were without plants (treatment 2; Fig. 1). Arenas receiving *C. dactylon* plants either had established *A. graminis* populations on the plants (treatment 4; Fig. 1) or *A. graminis* were absent (treatments 1 and 3; Fig. 1). All arenas received one of the randomly selected *S. invicta* colonies, which constructed a nest in the soil within 24 h. Initial live mass of colonies did not differ between treatments (mean ± SEM: treatment 1 = 1.037 ± 0.006 g, treatment 2 = 1.044 ± 0.007 g, treatment 3 = 1.014 ± 0.017 g, treatment 4 = 1.049 ± 0.006 g; $F = 2.25$, $P = 0.09$, one-way analysis of variance [ANOVA]).

Potential food sources available to each colony differed according to treatment. Those in treatment 1 had access to *C. dactylon,* those in treatment 2 had access to insect prey, those in treatment 3 had access to *C. dactylon* and insect prey, and those in treatment 4 had access to *C. dactylon,* insect prey, and honeydew-producing *A. graminis* (Fig. 1). Insect prey was provided at least three times weekly such that there was always an excess available to each colony that received them. Insect prey consisted of frozen crickets (*A. domesticus*) and live mealworms (*T. molitor*) and was provided in excess to test whether the acquisition of plant phloem, either directly from the plant, or indirectly from honeydew, has some nutritional benefit that cannot be provided for by insect prey. All experimental arenas were provided with water-filled test tubes plugged with cotton for a continuous water source. During the experiment, the soil in all containers (with and without plants) was watered at least bi-weekly to prevent drying.

After the experiment had progressed for 1 mo, we found that a small number of *A. graminis* had colonized *C. dactylon* plants in a minority of replicates of the *A. graminis* exclusion treatments (treatments 1 and 3). Presumably, this resulted from dispersal of crawlers from the treatment that included *A. graminis,* although *A. graminis* is also present on grasses in lawns adjacent to the greenhouse. Because we were unable to determine whether accidental colonization of plants had influenced results at that point in time, they were allowed to remain and we conducted posthoc regression analyses of colony growth as a function of the number of mealybugs colonizing the plants.

Duration of the experiment was 60 d, the approximate time period for two *S. invicta* worker production cycles (egg to adult) at greenhouse temperatures (Porter 1988). At the end of the experiment, the ants were anesthetized in their arenas with CO_2 for 2 min. In treatments with *C. dactylon* plants, the plants were separated from the soil and removed, and the numbers of *A. graminis* on plants were determined for each arena. In treatments without plants, the ants were also anesthetized and the soil was disturbed as in treatments where plants were removed. After ants had awoken and were fully active, the contents of each arena (soil-filled containers, debris, and any ants outside of the containers) were emptied into large buckets where the interior was coated with talcum powder to prevent escape. The colonies were allowed 2 d to reconstruct a nest, at which time the colony was recovered from the soil by dripping water into the bucket until the colony floated (Jouvenaz et al. 1977). The ants were removed and placed into fluon-lined plastic boxes with water tubes. After an additional 24 h, the live mass of each colony was measured to determine change in colony biomass according to experimental treatment. All statistical analyses of our results were conducted using Minitab 15 software (Minitab, State College, PA).

Results

At the end of the experiment, colony biomass differed significantly among treatments (one-way ANOVA: $F = 51.69$, $P < 0.001$). Analyses of individual treatments showed that presence of the grass *C. dactylon* had no positive affect on colony growth. Colonies with access to only *C. dactylon* (treatment 1) decreased significantly in size over the course of the experiment (one-way ANOVA: $F = 654.15$, $P < 0.001$), and the growth of colonies with access to the grass *C. dactylon* and unlimited insect prey (treatment 3) did not differ from the growth of colonies with access to only unlimited insect prey (treatment 2; Fig. 2; Tukey test for pairwise multiple comparisons, $P > 0.05$).

Colony biomass in the treatments receiving unlimited insect prey increased substantially and significantly over their initial size (one-way ANOVA: treatment 2: $F = 162.21$, treatment 3: $F = 101.48$, treatment 4: $F = 368.79$; $P < 0.001$ in all cases; Fig. 2). However, the increase was greatest when colonies also had access to the mealybug *A. graminis* feeding on *C. dactylon.* Colonies with access to *A. graminis* (treatment 4) grew significantly and substantially (≈50%) larger

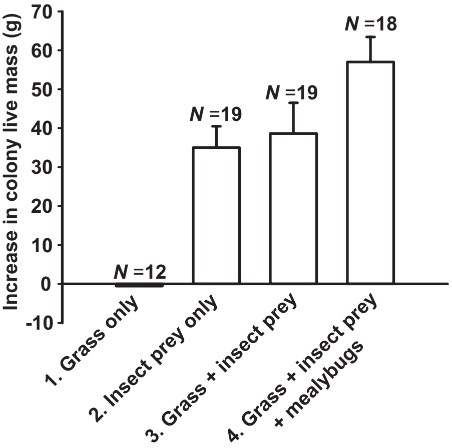

Fig. 2. Experimental treatments differed in how they affected the growth of *S. invicta* colonies. Data are treatment means with 95% CIs. *N* = the number of replicates per treatment.

than those in other treatments with access to unlimited insect prey (Tukey test for pairwise multiple comparisons, $P < 0.05$ in all cases; Fig. 2).

Where accidental colonization of *C. dactylon* by *A. graminis* occurred, the numbers of *A. graminis* were small relative to the treatment where *A. graminis* was intended. Accidental colonization in treatment 1 resulted in 6 of 12 replicates with *A. graminis* (mean number ± SEM = 11.92 ± 4.97) and in treatment 3, 9 of 19 replicates had *A. graminis* (94.3 ± 37.2). In treatment 4, where colonization of plants by *A. graminis* was intended, all 18 replicates had *A. graminis,* and their numbers were much higher (663.5 ± 54.2). Although the numbers of *A. graminis* per replicate were low when accidental colonization occurred, colony biomass increased with increasing numbers of *A. graminis* in both treatments (treatments 1 and 3; Fig. 3). In treatment 4, where colonization by *A. graminis* was intended, colony biomass did not increase with increasing numbers of *A. graminis* (Fig. 3).

Discussion

This study seems to be the first conducted with an omnivorous ant that tests experimentally for the importance of honeydew-producing Hemiptera to colony growth. We found that colonies of *S. invicta* grew substantially larger when they had access to *A. graminis* and unlimited insect prey than when they had access to only unlimited insect prey (Figs. 2 and 3), consistent with *A. graminis* providing resources not available in insect prey. *A. graminis* were tended extensively for honeydew by *S. invicta,* and the effect of *A. graminis* on colony growth presumably resulted from honeydew consumption. Common for Hemiptera honeydews (Way 1963), the primary nutritional components of *A. graminis* honeydew are carbohydrates; by dry mass, 98% of the nutritional content (carbohydrates and total amino acids) available in *A. graminis* honeydew are sugars (K. R. Helms and S. B. Vinson, unpublished data). Thus, increased colony growth is likely to result from the acquisition of plant-based carbohydrates. In addition to our study, the importance of carbohydrates to omnivorous ants is further supported by studies showing that sucrose significantly increases the growth of *S. invicta* and *Tetramorium caespitum* (Linnaeus) laboratory colonies, even when insect prey is abundant (Porter 1989, Kay et al. 2006).

The effect of accidental colonization of plants by *A. graminis* on the growth of *S. invicta* colonies in *A. graminis* exclusion treatments (Fig. 3) strengthens the conclusion that *A. graminis* has a significant positive effect on *S. invicta* colony growth. When accidental colonization occurred, colony growth increased proportional to the number of *A. graminis.* Seemingly at odds, however, was that colony biomass in treatment 4, where *A. graminis* were present by design, did not increase with increasing numbers of mealybugs (Fig. 3). The most likely explanation for this result is that *A. graminis* were abundant in treatment 4 throughout the experiment, and honeydew was available in excess of that which would increase colony growth. Grover et al. (2007) found recently that, although carbohydrates

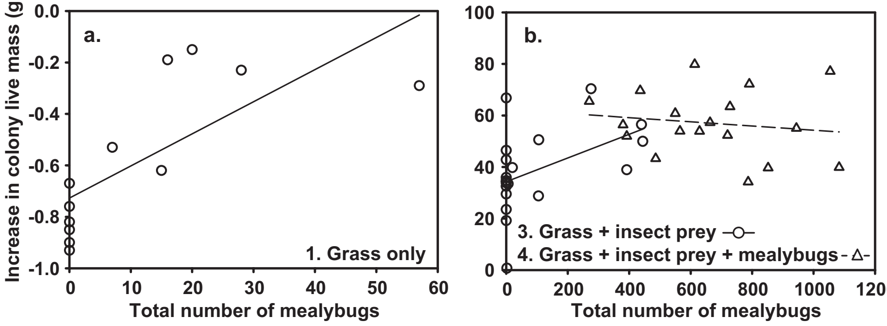

Fig. 3. Accidental colonization of *C. dactylon* by *A. graminis* resulted in increased colony growth with an increasing number of *A. graminis*, whereas intentional colonization did not. (a) Accidental colonization in treatment 1. ANOVA (regression): $F = 11.65$, $P = 0.007$, $r^2 = 0.538$. (b) Accidental colonization in treatment 3 versus intentional colonization in treatment 4. ANOVA (regression): treatment 3: $F = 4.52$, $P = 0.049$, $r^2 = 0.210$; treatment 4: $F = 0.34$, $P > 0.5$, $r^2 = 0.021$.

(sucrose) were important in fueling worker aggression and activity in the Argentine ant, *Linepithema humile* Mayr, artificially high levels decreased worker activity and apparently longevity, which could be responsible for the threshold level of increased colony growth from honeydew found in our experiment.

A surprising result from the accidental colonization of plants by *A. graminis* is that more *A. graminis* occurred on plants when *S. invicta* had access to grasses and insect prey (treatment 3) than when *S. invicta* had access to grasses alone (treatment 1; Fig. 3). It is possible that the absence of insect prey stimulated *S. invicta* to capture and consume *A. graminis* crawlers (first-instar nymphs) in treatment 1 while not in treatment 3. Crawlers could be consumed without discernible evidence remaining on plants because this is the mobile phase where plants are colonized. Crawlers find a suitable location on the plant, and lose their legs during the first molt, when their protective wax covering is produced (Chada and Wood 1960). An alternative answer for the differences in the numbers of *A. graminis* between treatments 1 and 3 is that *S. invicta* has some positive effect on *A. graminis* populations, with that effect increasing with increasing *S. invicta* abundance.

Our study does not directly test the effect of honeydew alone on colony growth; however, by itself, it is unlikely to be sufficient for colony growth in many if not most omnivorous ants. Comparison of the growth of *S. invicta* colonies in treatments 1 and 3 where *C. dactylon* was colonized inadvertently by small numbers of *A. graminis* is consistent with this conclusion. With *A. graminis* in the absence of insect prey, colony biomass decreased, whereas the biomass of colonies with *A. graminis* and insect prey increased (Fig. 3). Laboratory studies of the importance of insect prey versus sucrose showed consistent results, showing that insect prey alone is sufficient for at least limited colony growth, whereas sucrose alone is not (Porter 1989, Kay et al. 2006). Because amino acids necessary for brood development are rare in honeydew, it cannot facilitate substantial brood development, precluding increases in colony size. In addition, limited carbohydrates should be available to ants in the hemolymph of arthropod prey (Wyatt and Kalf 1957) and perhaps in the stomach contents of herbivorous arthropods consumed. If carbohydrates are necessary for colony growth to occur, they are likely to be available in limited quantities in insect prey.

Although animal-based nutritional resources are clearly important to colony growth, our results show that honeydew can increase growth substantially over that possible with animal resources alone, suggesting that both animal- and plant-based nutritional resources are necessary to achieve optimal colony growth. We also note that carbohydrates are likely to be more important than our experiments suggest because they serve as energy to fuel worker activities (Abbott 1978, Stradling 1978, Grover et al. 2007). In our arenas, available food resources were easily accessible and often abundant near the colony, and there were no competitors for those resources. In nature, workers are likely to expend significantly more energy engaged in long-range foraging, and they would occur in an environment where they engage in territorial interactions and compete for and defend food resources. The full importance of carbohydrates may only be shown in situations where workers are engaged in energetically expensive activities that occur under natural conditions (Davidson 1998, Kay et al. 2006, Grover et al. 2007).

A number of studies have noted that invasive ants such as *S. invicta* are often associated with honeydew-producing Hemiptera and that those associations may often be with Hemiptera that are also introduced or invasive (Simberloff and Von Holle 1999, Helms and Vinson 2002, Holway et al. 2002, O'Dowd et al. 2003). Because the impacts of invasive ants increase with increasing population size, our results suggest that honeydew-producing Hemiptera, and thus their host plants, may be important in facilitating those impacts. This conclusion is, however, dependent on the degree that invasive ants can use alternative carbohydrate-rich resources. *S. invicta* often reaches its greatest densities in the United States in open pasturelands where grasses are dominant plants, and our results show that it is unlikely to acquire significant nutritional resources directly from grasses. Colonies with access to the grass *C. dactylon* as their sole nutritional resource (treatment 1) lost substantial mass, whereas colonies in all other treatments gained considerable mass (Fig. 2). More important, growth did not differ between colonies with access to insect prey (treatment 2) and colonies that had access to *C. dactylon* in addition to insect prey (treatment 3; Fig. 2). These results strongly suggest that *S. invicta* cannot acquire significant amounts of carbohydrates from *C. dactylon* plants.

Although it has been proposed that *S. invicta* may acquire significant carbohydrates directly from plant phloem, our results suggest that they are unlikely to acquire them directly from grasses. Studies of the responses of plants to injury by herbivorous insects further suggest that the apparent inability of *S. invicta* to acquire significant carbohydrates directly from the phloem of grasses may apply to many other plants as well. Although honeydew-producing Hemiptera have evolved mechanisms to directly access sieve tubes that transport plant phloem and maintain the flow of sap, ants must either chew on or locate wounded plants to directly access the phloem. Plants, however, often have physical barriers that limit mechanical damage, such as the cuticle and hardened or woody barriers, as well as wound-activated responses directed to healing damaged tissues and activating chemical defenses (Walling 2000, León et al. 2001). Although *S. invicta* may acquire some carbohydrates directly from plant wounds, it may not be of general importance. Alternatively, carbohydrates might be acquired directly from plants as nectar; however, nectar availability is likely to vary substantially and according to season as well as plant community (Rico-Gray and García-Franco 1998), and its importance remains to be determined.

Our experimental design is a simplified version of an ecological system common in the southeastern United States. In this system, tritrophic interactions occur among three common and often abundant invasive species: *A. graminis*, *C. dactylon*, and *S. invicta*. *C. dactylon* is often an abundant perennial grass in open habitats in the range of *S. invicta* in the United States, and it is a preferred host grass for *A. graminis*, on which it can reach tremendous densities (Chada and Wood 1960). In addition, *A. graminis* is present on *C. dactylon* and other perennial and annual grasses throughout the year, reaching its greatest densities in summer through fall, when other honeydew-producing Hemiptera become relatively rare (Chada and Wood 1960, Helms and Vinson 2000, 2002, 2003). A field study has estimated that *A. graminis* can supply *S. invicta* with a substantial proportion of it energy budget (Helms and Vinson 2002). This study goes further in showing that it may not only result in increased available nutritional resources, but rather it may also result in increased colony growth and larger population sizes than otherwise possible.

Acknowledgments

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