

Behavior of *Solenopsis invicta* (Hymenoptera: Formicidae) in Pecan Orchards

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ABSTRACT Pecan, *Carya illinoensis* (Wangenh.) K. Koch, orchards provide an important habitat for the red imported fire ant, *Solenopsis invicta* Buren, and orchards from middle to southern Georgia were heavily infested. Honeydew produced by blackmargined aphids, *Monellia caryella* (Fitch), on pecans was an important source of carbohydrate food for *S. invicta*, which were found foraging at 9-m heights in trees. Mowing of orchard ground cover caused a change in the ratio of *S. invicta* on the ground to that in trees but was not correlated with outbreaks of *M. caryella* in trees. *S. invicta* was a major predator of eggs, larvae, and pupae of a green lacewing, *Chrysoperla rufilabris* (Burmeister), and of the pupae of *Allograpta obliqua* (Say) in pecans but had little effect on the eggs of *Hippodamia convergens* Guérin-Méneville. A close mutualistic relationship between *S. invicta* and the mealybug *Dysmicoccus morrisoni* (Hollinger) was discovered. *S. invicta* promoted the development of colonies of *D. morrisoni* on callus tissue located on the main stem of trees by covering the colony with soil and debris, by defending the colony, and by collecting honeydew.

KEY WORDS Insecta, *Solenopsis invicta*, behavior, biology

WHEELER (1926) cited a variety of mutualistic relationships between ants and other arthropods. Mutualism between ants and honeydew-producing Homoptera is common (Way 1963). Two well-known cases include mutualism between the ant *Anoplolepis custodiens* (Smith) and the citrus mealybug, *Planococcus citri* (Risso), on guava in South Africa (Samways 1983) and between the Argentine ant, *Iridomyrmex humilis* (Mayr), and the brown soft scale, *Coccus hesperidum* L., on citrus in California (De Bach et al. 1951). Both cases can cause economically important outbreaks of homopterans that can be averted by eliminating ants from the trees.

The red imported fire ant, *Solenopsis invicta* Buren, has not been associated with the outbreak of pest homopterans, but its mutualism with various homopterans has been reported. Whitcomb et al. (1972) reported that *S. invicta* tended unspecified mealybugs and soft scales on weeds and grass roots but not on soybeans. Sterling et al. (1979) reported "symphilism" between *S. invicta* and the cotton aphid, *Aphis gossypii* Glover, early in the season. Hays & Hays (1959) observed *S. invicta* tending aphids and scale insects on unspecified plants including "apple aphids" on branches placed on ant colonies in the laboratory. We found only one thor-

ough study (Scarborough 1984) of mutualism with homopterans, which included the corn leaf aphid, *Rhopalosiphum maidis* (Fitch), on sweet corn and johnsongrass; the buffalo treehopper, *Stictocephala bisonia* Kopp & Yonke, on green beans, blackeyed peas, and cowpea daisy; *A. gossypii* on okra, wild sunflower, and cotton; and a treehopper, *Thelia bimaculata* (F.), on wild sunflowers.

Reports of associations between *S. invicta* and tree-inhabiting Homoptera are rare. However, Wilkinson & Chellman (1979) reported *S. invicta* attending an outbreak of the pine tortoise scale, *Toumeyella parvicornis* (Cockerell), on 3-yr-old slash pine, *Pinus elliotii* Engelm. Mutualism between *S. invicta* and homopterans found on pecan, *Carya illinoensis* (Wangenh.) K. Koch, trees has not been reported. For this study, we use the term "mutualism" as defined by Way (1963): "an association between ants and other insects without necessarily implying obligate dependence or interdependence."

Solenopsis invicta is best known as an opportunistic predator that simplifies the ecosystem by displacing other ant species of the same trophic level (Whitcomb et al. 1972). On cotton, it is reported to be a beneficial predator of larval boll weevil, *Anthonomus grandis grandis* Boheman (Sterling 1978), and the eggs and larvae of *Heliothis virescens* (F.) (McDaniel & Sterling 1979). It is the most important predator of sugarcane borer, *Diatraea saccharalis* (F.), in Louisiana (Charpentier et al. 1967). Dutcher & Sheppard (1981) reported that it caused a 38% reduction of pecan weevil, *Curculio caryae* (Horn), larvae in a caged field test in Georgia. Also, it is suspected of preying

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on certain homopterans including the pea aphid, *Acyrtosiphum pisum* (Harris), on alfalfa (Morrill 1978). Hays & Hays (1959) concluded that, although it is omnivorous, *S. invicta* feeds mainly on living and dead insects. However, the full range of behaviors and their consequences in varied agricultural environments remain to be explored (Lofgren 1986).

In commercial orchards of pecan, mounds of *S. invicta* often interfere with orchard management, especially by damaging mowers. Growers regularly complain that *S. invicta* sting laborers hand-weeding around newly planted trees and workers grafting or topworking trees at heights up to 4.5 m. Several growers have suggested that outbreaks of aphids on pecans follow mowing operations. We suspected that it interfered with biological control experiments employing convergent lady beetle, *Hippodamia convergens* Guérin-Meneville, and a green lacewing, *Chrysoperla rufilabris* (Burmeister), against foliar-feeding pecan aphids (W.L.T., personal observation). Large numbers of ants were usually present when outbreaks of blackmargined aphids, *Monellia caryella* (Fitch), occurred on pecan trees. An additional honeydew-producing species, *Monelliopsis pecanis* Bissell, also occurs on pecan, but *Monellia caryella* is the greatest honeydew producer, excreting a total of 92 mg per aphid (Tedders 1978) (nine times more glucose-equivalents per aphid than *Monelliopsis pecanis* [Tedders & Wood 1987]). *Monellia caryella* honeydew produced on pecan contains about 24% glucose (Tedders et al. 1982).

It is not clear what net effect *S. invicta* has on the population dynamics of aphids on pecan, so we decided to investigate. The objectives of the study were to determine the extent of infestations of commercial and noncommercial pecan orchards in Georgia; the height at which it forages in pecan trees; the effect of mowing on its activity in orchards; possible mutualism between *S. invicta* and *Monellia caryella* and *Monelliopsis pecanis*; and possible predation by *S. invicta* on *Monellia caryella*, *C. rufilabris*, *H. convergens*, and the aphidophagous syrphid, *Allograpta obliqua* (Say).

Materials and Methods

Casual Observations. From 1986 to 1988, commercial pecan orchards from middle to southern Georgia were observed for the presence and location of *S. invicta* mounds.

Systematic Observations and Tests on Mature Trees. During 1986 and 1987, we studied the activities of *S. invicta* each month in commercial orchards of 65–80-yr-old, sprinkler-irrigated 'Schley' and 'Stuart' trees at Albany, Ga., at the Southeastern Fruit and Tree Nut Research Laboratory, Byron, Ga., and in nonirrigated, noncommercial orchards of 65-yr-old 'Schley' and 'Moore' trees at Byron. The presence of workers in trees was determined using white index cards (7.62 by

12.7 cm) soaked in peanut oil (Dutcher & Sheppard 1981). These bait cards were fastened to the main stem or limbs of trees with thumb tacks. Actual numbers of *S. invicta* on cards were recorded.

Foraging Heights. Two experiments were conducted to determine foraging by *S. invicta* in mature trees as a function of height. In the first experiment, each of four 'Moore' trees was sampled for ants at heights of 1.5, 3.0, 6.0, and 9.0 m (10 oil-soaked cards at each height) on the morning of 28 August for a period of 1.5 h. For the second experiment, each of four 'Moore' trees was sampled at 9.0 m with 50 cards per tree on the morning of 2 September for a period of 1.5 h.

Systematic Observations and Tests on Young Trees. During 1987 and 1988, we studied the activities of *S. invicta* in 6-yr-old, drip-irrigated 'Cheyenne' and 'Desirable' trees at Albany (commercial) and at Byron (noncommercial). Other studies of activities during 1987 were in 12-yr-old water hickory, *Carya aquatica* (Michaux f.) Nuttall, 12-yr-old bitternut hickory, *Carya cordiformis* (Wangenh.) K. Koch, and hican (intraspecific cross of pecan × unidentified *Carya* sp.).

The presence of workers in trees or on the orchard floor was determined using index cards soaked in peanut oil. These bait cards were fastened to the ground with a nail or thumbtacked to the main stem or limbs of trees. When the number of *S. invicta* per card was about 25 or less, the actual numbers were recorded; larger numbers per card were estimated in 50-ant increments based upon previous knowledge of counts on cards up to 300 per card. Ants collected for identification and ants carrying insects or insect parts were aspirated into vials and stored in 70% ethanol for later study. Voucher specimens are stored in the insect collection in the USDA-ARS facility at Byron.

Mowing. One spring and one summer experiment were conducted to determine if mowing understory vegetation changed the relative numbers of *S. invicta* on the ground versus in trees, and whether such changes were accompanied by changes in aphid numbers. The two experiments were conducted in different parts of the same orchard in Albany. The first was conducted from 23 April to 12 June with mowings on 20 April, 12 May, and 9 June; the second from 31 July until 27 August with mowings on 12 and 18 August. The orchard was planted with 119 trees per ha and was heavily fertilized. Mowed and unmowed (control) plots were 0.3 ha square and each contained 36 trees; the design was a randomized complete block replicated four times. The four center trees of each plot were sampled weekly by examining five compound leaves per tree for aphid numbers. One oil-soaked card was tacked to each of two opposing sides of tree main stems at 1.5 m height, and one card was nailed to the ground on each of two opposing sides of the tree 1.5 m from the main stem (total 32 cards per main stem, 32 cards on ground per treatment per count). Cards were examined

after 1 h. The ground cover was a lush mixture of rye and bermudagrasses, various vetches and clovers, and various broadleaf weeds. Counts of *S. invicta* mounds indicated that there was approximately one per tree in the study areas. Data were analyzed by analysis of variance (ANOVA).

Mutualism. Studies of the seasonal activity of *S. invicta*, reducing sugar content in foraging ants, and radioactive tagging of aphid honeydew were conducted to determine the existence of mutualism between *S. invicta* and pecan aphids.

Seasonal Activity. We sampled 20 young trees for ants and aphids once weekly from the first of May until the end of November at Byron. One oil-soaked card was thumbtacked onto the two opposing sides of the main stem of each tree at about 1.5 m height, and one card was nailed to the ground on two opposing sides of the tree about 1.5 m from the main stem of the tree (40 cards on main stems, 40 on ground per week). Ants were counted after 1 h. Aphids were counted on 10 compound leaves per tree. The ground cover in this orchard was common bermudagrass, which was mowed frequently and closely and resembled a lawn. The fertility level of the orchard was normal to low.

Reducing Sugar. To verify that workers of *S. invicta* were collecting honeydew, we aspirated workers from their trails on young pecan, hickory, water hickory, and bitternut hickory trees and analyzed them for reducing sugars. Visual observations were made of the sizes of gasters of workers relative to their movement either upward or downward in the trees. Ants moving upward and ants moving downward were aspirated separately. Afterward, samples of ants were taken from the mounds that produced the trails on the trees by disturbing the mound with a shovel and aspirating attacking ants from the handle of the shovel. Major workers were removed from all samples, and 40 workers of similar size were weighed, placed in vials with 1 ml 80% ethanol, and macerated with a glass rod. The vials were sealed tightly and heated at 80°C for 18 h. The ant-ethanol solutions were centrifuged in a Beckman microfuge for 1 min, and the supernatants were pipetted off. Aliquots of the supernatants were placed in test tubes and dried at 80°C under streams of N₂. Next, 0.5 ml H₂O + 0.5 ml buffer (0.05 M sodium acetate, pH 4.7) was added to each sample, and the procedure of Nelson (1944) was used to assay glucose content, with glucose used as the standard. Absorbance at 500 nm was determined from triplicate samples with a (Spectronic 21, Milton Roy Company, Rochester, N.Y.) spectrophotometer.

Radio-Labeled Honeydew. An additional experiment using ¹⁴C radioactive labeling techniques was conducted to verify that honeydew excreted by *M. caryella* was the source of reducing sugar collected by *S. invicta*. A 2-yr-old pecan seedling growing in a clay pot was used for the labeling study. The foliage of the seedling was washed with tepid water to remove any traces of honeydew,

aphids, and other contaminants. The seedling was held under subdued light (about 1,000 moles m⁻² s⁻²) sealed inside a 3-mil plastic bag also containing a glass vial with 10 μCi aqueous NaH¹⁴CO₃ (56 mCi per mmole S.A.). Then 100 liters of 1 N HCl was added to the NaH¹⁴CO₃ to liberate ¹⁴CO₂. The seedling was allowed to assimilate the ¹⁴CO₂ for 8 h, after which the plastic bag was removed and allowed to air out for 24 h. Next, a nylon cage (79 mesh per cm) was placed over the seedling and infested with 300 field-collected *M. caryella* adults. The cage with seedling and aphids was kept in a greenhouse for 6 d. Afterward, the infested seedling was placed near a trail of foraging *S. invicta* under an open building, and the cage was removed.

After several hours, ants were observed on the seedling, and triplicate samples of each of the following were collected: 10 ants from the ¹⁴C-treated seedling foliage; 10 ants from the trail on the ground that was the source of ants; 10 ants from the trail of an untreated (control) ant colony; 10 fourth-instar aphids from ¹⁴C-treated seedling foliage; 10 fourth-instar aphids from an untreated (control) seedling; 1-ml aliquots of "wash" taken from 75 mm² of treated leaf tissue washed with 10 ml 80% ethanol; and leaf tissue disks (1.3 cm diameter) from treated seedling foliage with honeydew removed by washing. Samples of ants, aphids, and leaf tissue were digested separately in scintillation vials, each with 1 ml of tissue solubilizer (Beckman BT5-450, Beckman Instruments, Fullerton, Calif.) for 24 h, then liquid scintillation cocktail (Beckman Renty-Solv MP) was added to all samples. Disintegrations per minute (dpm) of ¹⁴C and control samples were counted with a Beckman LS-1800 Liquid Scintillation Counter.

Predation. A number of experiments were conducted in the field at Byron to determine the extent of predation by *S. invicta* on *M. caryella*, *C. rufilabris*, *H. convergens*, and *A. obliqua*.

Monellia caryella. In two experiments with *M. caryella*, pecan leaflets with numerous aphids on the lower sides and a heavy coating of honeydew on the upper sides were thumbtacked adjacent to vigorous ant trails on young trees. For each experiment, four leaflets were positioned with the aphid-carrying side away from the tree, and four leaflets were positioned with the honeydew-carrying side away from the tree. This provided foraging ants with a convenient choice of aphids or honeydew. The experiments were observed for 1 h.

Chrysoperla rufilabris. Three experiments were conducted with *C. rufilabris* eggs. Each experiment was periodically observed for *S. invicta*, and counts of predation were made at the end of each experiment. For the first experiment, 15 field-collected *C. rufilabris* eggs (laid on pecan leaflets) were thumbtacked adjacent to an ant trail on a young tree and left for 24 h. In the second experiment, *C. rufilabris* eggs laid on strips of brown paper (1 by 55 cm) from a laboratory colony were wrapped around the trunks of trees and across the

trail of foraging ant workers and thumbtacked in place. One strip was placed 1.5 m above the ground on each of five trees. Five strips carried 227–296 eggs each; strips averaged 261 eggs. Ant predation on the eggs was determined after 18 h. For the third experiment, *C. rufilabris* eggs laid on strips of paper (2 by 30 cm) taken from the laboratory colony were wrapped around the trunk and limbs of three trees having trails of foraging ant workers and around the trunk and limbs of three control trees without foraging ants. *S. invicta* colonies were previously eliminated from the control trees with applications of hydramethylnon bait (Amdro) (American Cyanamid Company, Wayne, N.J.). Strips were placed in each tree at 1-, 2-, 3-, and 4-m heights. Strips averaged 85 eggs each, and the strips were examined for ant predation after 18 h.

Two experiments were conducted with *C. rufilabris* larvae. Each experiment was observed periodically, and counts were made at the end of the experiments. In the first, living second and third instars were affixed with cyanoacrylate glue to each of six paper disks (2.54 cm diameter). Disks were thumbtacked at random to the limbs of a young tree with no consideration to the proximity of an ant trail; they were examined after 24 h. In the second experiment, open-topped styrene plastic containers (2.54 by 2.54 by 1.3 cm) were coated around the upper inner edge with a 2–3-mm band of Fluon AD-1 (Northern Products, Woonsocket, R.I.). Each container served as an inescapable cage for 20 first-instar, laboratory-produced *C. rufilabris*. The fluon band prevented lacewing larvae from leaving the cage, but the narrowness of the band allowed access of larger ants into and out of the containers. To reduce the incidence of cannibalism by the lacewing larvae, 0.5 ml of *Sitotroga cerealella* (Olivier) eggs was placed in each container as food. One container with larvae and *Sitotroga* eggs was affixed to each of the four cardinal sides of the main stem of a young tree at 0.3-m intervals from the ground to a height of 3.6 m. The containers were observed after 20 and 48 h for the presence or absence of lacewing larvae, *Sitotroga* eggs, and ants.

Two experiments were conducted with laboratory-produced *C. rufilabris* pupae within cocoons as prey for *S. invicta*; both experiments were observed periodically. For the first, two cocoons were glued to each of six paper disks (2.43 cm diameter), which were in turn thumbtacked at random to the limbs of a young tree. No attempt was made to place them near an ant trail. Examinations for predation were made after 24 h. For the second experiment, two to four cocoons were glued onto similar paper disks and thumbtacked at random to the limbs of a young tree. A total of 42 cocoons was used; these were examined after 5 d for predation and adult lacewing emergence.

Hippodamia convergens. Two experiments were conducted with *H. convergens*. For the first, 52 clusters of laboratory-produced *H. convergens* eggs

laid on paper disks (2.54 cm diameter) were thumbtacked to the main stem and six limbs of a young tree during September. Egg numbers per cluster averaged 33 and ranged from 11 to 65. Egg clusters were placed at 15-cm intervals, beginning just above the ground and extending to 3.5 m along several limbs. During the experiment, the tree had an active *S. invicta* colony at the base, and the foliage supported a large population of *M. caryella* that was excreting honeydew. The eggs were left for 48 h, after which the following counts were made: unchanged egg clusters, hatched egg clusters with larvae gone, hatched egg clusters with first instars still present, and destroyed or missing egg clusters.

The second experiment evaluated predation by *S. invicta* on *H. convergens* pupae during late May. A total of 24 laboratory-produced pupae on seven paper disks (one to six pupae per disk) were thumbtacked to a tree 1.2 m high and examined every other day for 14 d. The numbers of pupae preyed upon by ants, the number of pupae missing, and the number of adult eclosions were recorded. An active *S. invicta* mound was located at the base of the experimental tree, but large numbers of aphids were not present.

Allograpta obliqua. One experiment was conducted on predation by *S. invicta* on *A. obliqua* puparia during September. Thirteen field-collected puparia were glued individually to paper disks (2.54 cm diameter) and thumbtacked adjacent to an ant trail on a young tree. Puparia were examined after 3 d for ant predation or fly emergence. The tree supported large numbers of *M. caryella* that were excreting honeydew.

Results and Discussion

Casual Observations. Commercial orchards from middle to southern Georgia, in which no deliberate attempts were made to control ants, were heavily infested with *S. invicta*. This species was the dominant ant present. Almost all mounds were located on the southern side of the trees. Mature pecan trees were observed with one mound at the base of each tree. It was evident that routine application of insecticides for various pecan pests did not eliminate *S. invicta* from pecan orchards and apparently had little effect on the numbers of colonies present.

Systematic Observations and Tests on Mature Trees. Because of the large overlapping scales of bark commonly found on 'Schley' and 'Moore,' as well as most other pecan cultivars, trails on 65- to 80-yr-old trees were difficult to locate irrespective of the time of the year. However, removal of scales of bark revealed trails during all months of the year. These trails were easily traced from mounds on the ground up into the tree crotch where part of the colony was usually nesting. Completely hid-

den trails often extended several meters upward along large scaly limbs of the trees.

In September 1986, 80-yr-old trees in Albany were observed with *S. invicta* nesting among the immature nut clusters at the ends of limbs. These nests each contained several hundred workers with eggs, larvae, and pupae, but no queens were observed. The ants used soil, debris, and dead insects to cover partially the nuts and nest. These nests were extensions of a large colony at the base of the tree and were located about 12 m from the mound. Ten to 20 such nests on nut clusters were seen on several trees. This phenomenon occurred during a severe drought situation and has not been previously reported.

Peanut oil-soaked cards were found to be a poor method to sample *S. invicta* activity on the lower half of mature trees because of the concealed nature of trails under bark. Cards were more effective on mature trees when displayed higher than 6 m where large overlapping scales of bark were less prominent and trails were exposed.

Foraging Heights. In the first experiment, after 1.5 h at 31°C and 45% RH, an average of 0.2 worker per card was collected at 1.5 m, none was collected at 3 m, 6.3 per card at 6 m, and none at 9 m. The reason for this variation is not understood, but it is probably associated with the intensity of ant foraging in the test tree at that time.

In the second experiment, after 1.5 h at 23°C and 92% RH, an average of 1.2 *S. invicta* per card was collected at 9 m (range, 0–50 per card). These two experiments demonstrated that ants do indeed forage high within mature pecan trees, although the experiments did not indicate excessive activity at these heights. Ant activity high in trees may be limited by distance from the mound and the time required to transmit information back to the colony.

Systematic Observations and Tests on Young Trees. Use of peanut oil-soaked cards was a good method for sampling *S. invicta* in young trees and on the ground. Foraging ants were collected weekly from the main stem of young smooth-barked trees from mid-April until the end of November. Easily observable foraging trails on young trees were noted from the first week of May, when significant aphid numbers were first noticed, until the end of October, just before most foliage had fallen. The rate of movement of ants up or down these trees ranged from 1.2 ants per minute to >30 ants per minute at temperatures ranging from 21 to 33°C. Ant activity relative to time of day, temperature, and humidity was not of particular interest, but it was obvious that activity was adversely influenced by high temperatures, direct sunlight, and by very low humidities. Large numbers of ants were collected on cards in the shade of the tree on the ground and on the main stem, even during periods when the temperature was near 33°C. Foraging ants were rarely collected from cards located on the ground in the sunshine on hot days. In com-

mercial orchards up to 15 yr old, trees were usually planted 119 trees per ha. These orchards were usually heavily fertilized, and in those where ant control was not practiced, ant mound counts often approached one per tree during the spring. Here too, routine applications of insecticides applied to control pecan pests had little effect on the number of ant colonies.

Mowing. In the spring experiment, mowing did not cause an outbreak of aphids ($P = 0.93$; $CV = 75.2\%$). The aphid complex during this experiment was 95% *Monelliopsis pecan* and 5% *Monellia caryella*. However, mowing significantly changed the ratio of ants in trees to ants on the ground ($P < 0.01$) (Fig. 1). The ratio of tree to ground ants in the mowed treatment was 1:1.8, and that in the control treatment was 1:5.2. The total of average numbers of ants per card on tree and ground cards was 994 in the mowed area compared with 1,090 in the unmowed area; these were not significantly different ($P = 0.40$). Thus, mowing altered the foraging behavior of ants on the ground and caused increased foraging in trees.

In the summer experiment, the aphid complex was 99% *Monellia caryella* and 1% *Monelliopsis pecan*. Here too, we were unable to prove that mowing caused an outbreak in aphids ($P = 0.79$; $CV = 54.5\%$). *Monellia caryella* numbers increased dramatically about mid-August in mowed and control treatments, but as aphid numbers increased, ant numbers on ground and tree cards decreased sharply in both treatments (Fig. 2). The total of average numbers of ants per card on tree and ground cards in the mowed treatment was 36 less than that of the control and not significantly different ($P = 0.48$). The ratio of tree ants to ground ants in the mowed treatment was 1:3.1 compared with 1:4.6 in the control. Again there was a disproportionate number of ants on the ground in the mowed opposed to ants on the ground in the control, but this was statistically insignificant ($P = 0.48$). We believe the rapid decline of ant numbers in trees and on the ground was a result of honeydew dropping to the ground where it was easily accessible and abundant to foraging ants. This may have predisposed the ants to collect abundant honeydew rather than scarce peanut oil. The summer experiment was terminated after 4 wk because of the rapid buildup of aphids and the need for the grower to contain the outbreak with an aphicide.

Mutualism. Seasonal Activity. Large variations were found between numbers of ants on trees and on the ground during the entire season (Fig. 3A). From 7 May until 11 June, the dominance of ants on tree or ground cards varied almost weekly, but in weekly samples from 18 June to 25 August, ants were, on the average, twice as abundant per card on trees (92 ground versus 186 tree). From 25 August to the end of the season, the reverse was true; more than twice as many ants were found per card on the ground (87 ground versus 33 tree). Weekly percentages of ant numbers shifted significantly on

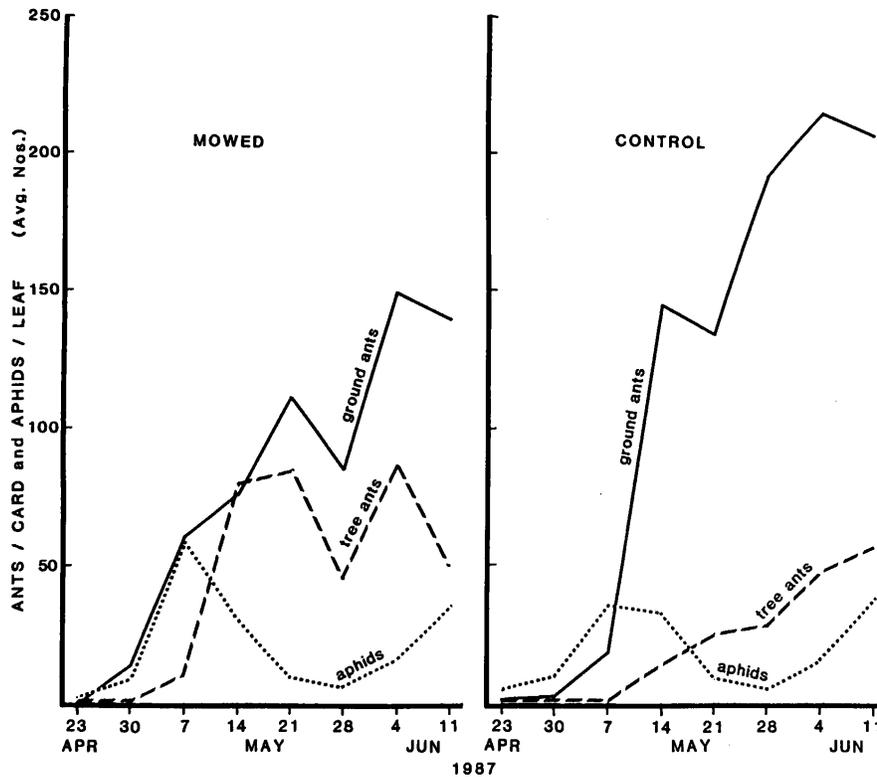


Fig. 1. Mean numbers of *S. invicta* on peanut oil-soaked index cards on trees and on the ground and mean numbers of *M. pecanica* on pecan foliage in mowed and control orchard habitat 23 April–11 June 1987, Albany, Ga.

23 May from the ground to the trees and then back to the ground on about 15 September (Fig. 3B). There was a negative correlation between aphids and ants on trees ($r = -0.49875$; $P < 0.01$). Data from ant collections after 15 September were similar to those obtained from the mowing experiment. Copious honeydew falling onto the ground cover eliminated the need for ants to climb trees. Again, our sampling technique used peanut oil; the ants were probably predisposed to collect honeydew. Ants were not observed to antennate *Monellia caryella* or *Monelliopsis pecanica* but simply gathered honeydew from leaf surfaces.

In this test, ants were never observed carrying aphids back to the mound when aphid numbers were low or increasing. Carrying aphids was common when aphid numbers were very large and the aphid population began to decline (crash). During one 30-min collecting period, 36 ants carrying prey back to the mound were aspirated from a trail. Examination of the prey revealed that 33 were first-instar-adult *M. caryella*, two were lacewing eggs, and one was an unidentifiable arachnid.

Reducing Sugar. Ants were obviously carrying large amounts of unidentified substances back to the colony as indicated by the numerous ants foraging in the trees. Also, the swollen gasters of ants traveling downward on trees indicated feeding. Ants moving downward always weighed more than those

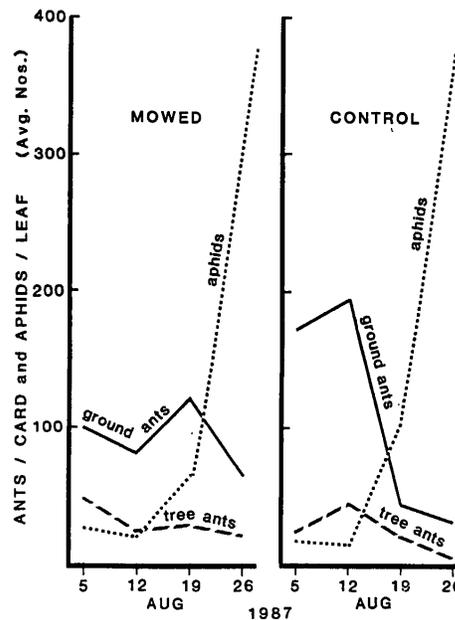


Fig. 2. Mean numbers of *S. invicta* on peanut oil-soaked index cards on trees and on the ground and mean numbers of *M. caryella* on pecan foliage in mowed and control orchard habitat 5–26 August 1987, Albany, Ga.

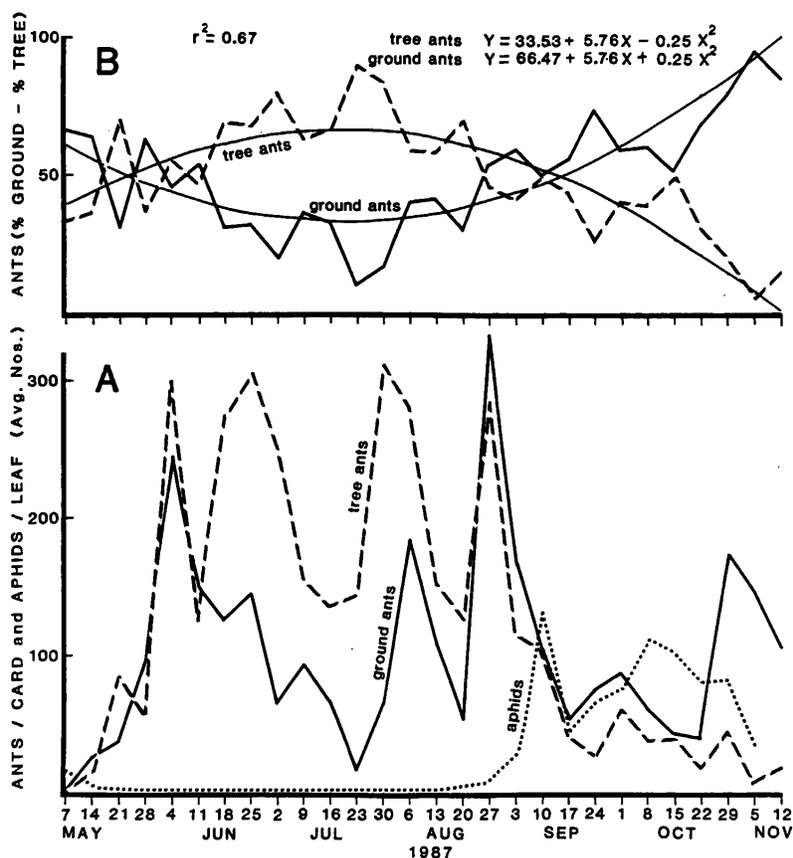


Fig. 3. (A) Mean numbers of *S. caryella* on peanut oil-soaked index cards on trees and on the ground and mean numbers of *Monelliopsis pecanica* and *Monellia caryella* on pecan foliage in closely mowed orchard habitat 7 May–12 November 1987, Byron, Ga. (B) Numbers of *S. invicta* (same as Fig. 3A) converted to percentages on each date and smoothed by computer-generated curves. $R^2 = 0.67$; tree ants ($Y = 33.53 + 5.76x - 0.25 \times 2$); ground ants ($Y = 66.47 + 5.76x + 0.25 \times 2$).

moving upward or those taken from mounds (Table 1.) Mean weights of ants moving toward the mound ranged from 5.8 mg (*C. aquatica*) to 26.3 mg (*C. cordiformis*) more than mean weights of those moving upward. Mean weights of ants from mounds ranged from about equal (pecan) to 5.7 mg heavier (hican) than mean weights of upward-moving ants, indicating that food was being transferred to ants in the mound. Mean amounts of reducing sugar (glucose) in ants moving toward the mound were always greater than those moving upward or in the mound (Table 1). Mean measurements of reducing sugar content in ants moving toward the mound ranged from 4.25 μg (pecan) to 18.70 μg (*C. cordiformis*) more than the sugar content in those moving up into the trees. As was expected, slightly more reducing sugar was found in ants from the mound than in those moving away from the mound.

Radio-Labeled Honeydew. Many *M. caryella* progeny were produced in the greenhouse; these excreted copious honeydew on the upper surfaces of leaves. Within 12 h, foraging ants located the seedling, aphids, and honeydew, all of which were now radio-labeled with ^{14}C . Samples of *M. caryella*

expressed the highest radioactivity ($30,545 \pm 2,647$ dpm), and honeydew measured a close second (Table 2). Ants taken from foliage were twice as radioactive as those from the trail, and leaf tissue was roughly twice as radioactive as ants from foliage. Control ants and control aphids expressed only a trace of radioactivity (background). This experiment leaves little doubt that ants use large amounts of honeydew produced by *M. caryella*.

Predation. During periods preceding honeydew flows, ant workers were often seen carrying various insects or insect parts back to the mound, but they rarely carried aphids.

Monellia caryella. In both experiments, given a choice of *M. caryella* as prey or honeydew as a food source, *S. invicta* always collected honeydew and ignored aphids. Ant preference for honeydew also was displayed by attempts of workers to collect honeydew from between the leaflets and the tree while ignoring easily available aphids on the outer side of the same leaflet. Ants were occasionally observed carrying all three species of aphids down the tree, but this occurred only when aphid numbers began to decline when very high densities

Table 1. Reducing sugar content of *S. invicta* from foraging trails on selected species of *Carya* and from the source mound

Heading of and source of ants	Wt per 40 ants, mg	Reducing sugar per ant, μg^a
<i>Carya illinoensis</i>		
Upward	21.2	20.40
Downward	43.6	24.65
Mound	21.6	17.85
<i>Carya aquatica</i>		
Upward	15.6	11.90
Downward	21.4	20.42
Mound	19.4	11.09
<i>Carya cordiformis</i>		
Upward	17.3	15.11
Downward	43.6	34.00
Mound	21.6	21.25
<i>Carya illinoensis</i> × <i>Carya</i> sp. (hican)		
Upward	21.1	19.55
Downward	35.6	38.25
Mound	26.8	20.45

^a Means of three samples per treatment.

existed on trees. It was not determined if these aphids were used as food or if the ants were trying to relocate the aphid onto suitable foliage.

Chrysoperla rufilabris. In the first experiment after 24 h, only 1 of 15 eggs of *C. rufilabris* was missing. Because the egg stalk was also missing, we concluded that ants were not responsible for this loss. The results of the first test were not convincing because of the small numbers of eggs used and because of a previous observation (by W.L.T.) of workers carrying eggs believed to be those of lace wings. In the second experiment, a total of 18 eggs (<2% of original number) remained on the five strips (range, 2–16 eggs per strip). The stalks of the eggs were left intact because eggs had been excised from the tops of the stalks. In the third experiment, on strips on the three trees with foraging ants, after 18 h an average of 1.5% eggs remained at 1 m, 0.8% remained at 2 m, 0.4% at 3 m, and 13.3% at 4 m. In the control trees where ants were not present, an average of 44.7% of the eggs remained at 1 m, 65.9% at 2 m, 68.2% at 3 m, and 62.4% at 4 m. Thus, ants prey heavily on *C. rufilabris* eggs, but there are obviously other egg predators present in pecan trees where ants are not present.

In the first experiment after 24 h, the lacewing larvae on two paper disks had been attacked and only pieces of the larval exoskeletons remained. Ant workers continued in their attempt to remove these remains. The larvae on four other disks were unmolested and ants were not present. This experiment suggests that ants likely prey to some extent on *C. rufilabris*. In the second experiment after 20 h, all *C. rufilabris* and *S. cerealella* eggs had been removed from containers up to 1.5 m high, but foraging by ants gradually diminished up to 2.7 m (Table 3). There was no foraging at 3.0–3.6 m after 20 h. After 48 h, ants had removed

Table 2. Radioactivity in ¹⁴C radio-labeled pecan seedling leaf tissue, *M. caryella*, honeydew, *S. invicta*, and background radioactivity in nonlabeled *M. caryella* and *S. invicta*

Source	Treatment	Disintegration per min, $\bar{x} \pm \text{SD}$
Leaf tissue ^a	Labeled	2,604 ± 79
Honeydew ^b	Labeled	25,691 ± 4,392
<i>M. caryella</i> ^c	Labeled	30,545 ± 2,647
<i>S. invicta</i> (foliage) ^c	Labeled	1,290 ± 92
<i>S. invicta</i> (trial) ^c	Labeled	552 ± 58
<i>M. caryella</i> ^c	Control	39 ± 3
<i>S. invicta</i> ^c	Control	19 ± 1

^a 1.4 cm diameter.

^b 1-ml aliquot from 10 ml ethanol wash.

^c 10 individuals.

most *C. rufilabris* larvae and all *S. cerealella* eggs up to 3.6 m and by this time had virtually abandoned all containers at all heights. The use of *C. rufilabris* larvae combined with *S. cerealella* eggs as prey is not ideal methodology, but the experiment clearly demonstrates the expanding foraging behavior of ants in trees as a function of time, distance, and abundance of prey and satisfies us that *C. rufilabris* larvae are important prey of *S. invicta*.

After 24 h, the first experiment using *C. rufilabris* pupae in cocoons as prey revealed that ants had preyed on the pupae on two of the six paper disks. At that time, workers were observed attempting to open four of the cocoons, but they had succeeded in removing only the loose surrounding silk, in effect "polishing" the cocoon. Cocoons thus attacked by ants were seen easily and frequently during these studies.

In the second experiment after 5 d, 13 (31%) of the cocoons were missing and 22 (52%) of the cocoons had been successfully torn open by ants and the pupae were removed. The remaining seven (17%) had been polished by ants. Ants were the

Table 3. Total numbers of *C. rufilabris* larvae and *S. invicta* workers found in sets of four cages placed at each of 12 heights above the ground in a pecan tree

Cage height, m ^a	No. at beginning		After 20 h		After 48 h	
	<i>C. rufilabris</i>	<i>S. invicta</i>	<i>C. rufilabris</i>	<i>S. invicta</i>	<i>C. rufilabris</i>	<i>S. invicta</i>
0.3	80	0	0	0	—	—
0.6	80	0	0	2	—	0
0.9	80	0	0	2	—	0
1.2	80	0	0	7	—	0
1.5	80	0	0	18	—	0
1.8	80	0	1	19	0	0
2.1	80	0	22	18	0	0
2.4	80	0	45	10	0	0
2.7	80	0	50	6	0	0
3.0	80	0	35	0	1	0
3.3	80	0	80	0	0	2
3.6	80	0	80	0	0	8

^a Sets of four cages were placed at 0.3-m intervals; each cage originally contained 20 first-instar *C. rufilabris*.

predators because they were observed attacking the cocoons before the test ended. Of the seven polished cocoons, adults later emerged from three and four pupae failed to emerge as adults. It is doubtful that ants killed the pupae in polished cocoons; however, this question needs additional study. We concluded that after 5 d, ants destroyed 83% of the pupae (*C. rufilabris* pupae require about 9 d at 27°C to develop and emerge as adults).

Hippodamia convergens. Examination of the 52 *H. convergens* egg clusters after 48 h revealed that 18 egg clusters were unchanged, 22 had hatched and the larvae were gone, 10 had hatched and first instars remained on the egg chorions, and 2 at 0.6 and 0.9 m height had been destroyed by an unknown predator. Foraging ants were present in large numbers on the tree; under these conditions they obviously preferred honeydew over *H. convergens* eggs or first instars still on the egg chorions. The two missing egg clusters may have resulted from ant attraction to one or more damaged *H. convergens* eggs in each cluster or possibly from the work of some other egg predator. Other observations indicate that damaged coccinellid eggs may elicit predation. Thus, *H. convergens* eggs and larvae appear to have some resistance to ant predation, or the foraging ants were preoccupied with the collection of honeydew or some other food source on the tree.

In the second experiment after 14 d, 5 of the original 24 pupae were missing and 19 had emerged as adults. There were no indications that ants preyed upon the missing pupae; these could have been dislodged by other animals that also use pecan trees. *H. convergens* pupae also appear to have some natural resistance to ant predation. Ant predation on eggs, larvae, and pupae needs additional study under variable conditions.

Allograpta obliqua. Upon examination of *A. obliqua* pupae, ants were observed devouring one puparium. The remaining puparia had been completely removed except for a small portion of cuticle that remained glued to the paper disk. Ants obviously prey heavily on *A. obliqua* puparia.

Additional Observations. A close mutualistic relationship was discovered between *S. invicta* and the mealybug *Dysmicoccus morrisoni* (Hollinger). Infestations of *D. morrisoni* were found on callus tissue associated with healing wounds located on the main stem of vigorous young trees. Ants were observed antennating these mealybugs and collecting the excreted honeydew. Infestation sites of *D. morrisoni* were usually covered with a canopy of soil and other debris that was constructed by the ants. Ants also were observed moving all stages of *D. morrisoni* and were especially protective of *D. morrisoni* when the debris canopy was disturbed. *D. morrisoni* has not been reported previously as a pest on pecan; it may be limited by a shortage of proper feeding habitat. Fortuitous counts of *D. morrisoni* numbers were made in an orchard experiment designed to evaluate insecticidal control

of *S. invicta* at Byron. The trees were young and of the same cultivar and age. The ground area of a single 1.2-ha block of trees was treated with hydramethylnon bait at the rate of 1,134 g/ha on 21 and 28 April and 18 and 28 May. The treatments eliminated ants from the orchard during the 1987 growing season. Twenty trees were selected at random for *D. morrisoni* counts. An adjacent section of orchard of similar age and cultivar was left untreated as a control, and 20 trees were also randomly selected for examination. Thus there was only one replication, and the trees were examined only for positive or negative infestation of *D. morrisoni*. Pretreatment infestation counts were not taken. Trees were examined on 11 September and again on 21 September by a different technician. On the first examination, *D. morrisoni* were found infesting two ant-free trees and 14 control trees. The second technician found no mealybug infestations on 20 ant-free trees, but 17 control trees were infested. These data and our previous observations strongly suggest a close mutualistic relationship between *S. invicta* and *D. morrisoni*. On 6 October, 15 *D. morrisoni* colonies averaged 40 mealybugs per colony (range, 3–200).

The main stems of young trees in orchards heavily infested with ants at Albany also were found to be heavily infested with a nonhoneydew-producing armored scale, *Hemiberlesia diffinis* (Newstead). Excessive activity by *S. invicta* on tree main stems may affect predation by the scale-feeding species *Chilocorus stigma* (Say) and *Eurychiloptera luridula* Reuter, which are common on pecan.

Other species of ants were collected from trees in orchards infested with *S. invicta*, but none was particularly abundant. At Albany, *Paratrechina vividula* Nylander and *Brachymyrmex obscurior* Forel were common under the bark of mature trees. At Byron, *Crematogaster ashmeadi* Mayr were collected at heights of 4.6–13.7 m in mature trees, and *Forelius analis* (Andre) and *Conomyrma bureni* Trager were fairly common on young trees; the last-named two species appear to use honeydew produced by aphids, and all three coexist at Byron in relatively low numbers with large numbers of *S. invicta*.

Conclusions

All commercial and noncommercial pecan orchards observed from middle to southern Georgia appeared to be good habitat for *S. invicta*. Ants foraged for honeydew and insects as high as 9 m in the trees, but they appeared to take advantage of honeydew that dropped to the ground. Mowing the pecan orchards changed the ground-to-tree ratio of foraging ants, but there was no statistical evidence that ants caused outbreaks of *Monellia caryella* or other aphids. The behavior of *S. invicta* in the presence of *Monellia caryella* or *Monelliopsis pecanis* appeared to be affected by the volume of honeydew produced by the aphids, the

number of aphids present, and whether aphid numbers were increasing or decreasing. The strength of ant-*Monellia caryella* mutualism was probably regulated by existing conditions and needs of the ant colony. We now know that *S. invicta* is a major predator of the eggs, larvae, and pupae of *C. rufilabris* and of the pupae of *A. obliqua*; both species are major predators of the three species of foliar-feeding aphids on pecan. This, along with use of honeydew by *S. invicta* and the effect of mowing on vertical distribution, probably contributes to the outbreak of aphids on pecans. Honeydew produced by *Monellia caryella* is probably a major source of carbohydrates for *S. invicta*. There is a close mutualistic relationship between *S. invicta* and *D. morrisoni* and possibly some mutualism with *H. diffinis*. These relationships need additional study.

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