

# Disruption of Cotton Aphid (Homoptera: Aphididae)—Natural Enemy Dynamics by Red Imported Fire Ants (Hymenoptera: Formicidae)

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**ABSTRACT** Red imported fire ants, *Solenopsis invicta* (Buren) (Hymenoptera: Formicidae), are an invasive species found in high densities throughout southeastern agricultural systems. We tested the hypothesis that fire ants tend cotton aphids, *Aphis gossypii* Glover (Homoptera: Aphididae), and thus release them from predation by lady beetle larvae, *Coccinella septempunctata* L. and *Hippodamia convergens* Guerin-Meneville (Coleoptera: Coccinellidae), and green lacewing larvae, *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae). Fire ants preferentially foraged on aphid-infested cotton, *Gossypium hirsutum* L., plants ( $\bar{x} = 103 \pm 47$  ants per plant) compared with plants without aphids ( $\bar{x} = 5 \pm 3$  ants per plant). In caged greenhouse experiments, fire ants reduced survival of lady beetle larvae by 92.9% and green lacewing larvae by 83.3%. Furthermore, strong mortality imposed on aphid predators by fire ants affected aphid survival. With the addition of fire ants to aphid-predator treatments, aphid survival approximately doubled. In a field experiment, predator larvae were more abundant in cotton plots with experimentally suppressed densities of fire ants ( $0.62 \pm 0.11$  lady beetle larvae per sample;  $0.06 \pm 0.02$  lacewing larvae per sample) than in plots with high fire ant densities ( $0.23 \pm 0.06$  lady beetle larvae per sample;  $0.01 \pm 0.01$  lacewing larvae per sample). Conversely, cotton aphids were more abundant in high fire ant density field plots ( $\bar{x} = 6.83 \pm 0.03$  aphids per leaf) than in low fire ant density plots ( $\bar{x} = 4.04 \pm 0.03$  aphids per leaf). These data suggest that red imported fire ants enhance cotton aphid survival and density in the field through predator interference.

**KEY WORDS** *Solenopsis invicta*, *Aphis gossypii*, *Chrysoperla carnea*, Coccinellidae, ant-aphid mutualism, predator interference

CERTAIN ANT SPECIES develop mutualistic relationships with members of the order Homoptera, such as aphids, whiteflies, and scale insects (Way 1963, Buckley 1987). The appeal of homopterans as mutualistic partners derives from their ability to produce honeydew, a sugary byproduct of herbivory excreted by phloem feeders. Honeydew is a solution that primarily comprises simple sugars mixed with various free amino acids (Mittler 1958, Douglas 1993). Consequently, honeydew is a very attractive food for ants because it satisfies nutritional requirements that are fundamental for colony growth and survival (Hölldobler and Wilson 1990). In exchange for honeydew, ants provide multiple services that benefit honeydew-producing homopterans. Primarily, ants protect homopterans from their natural enemies (Way 1963, Buckley 1987, Buckley 1990, Jiggins et al. 1993, Stechmann et al. 1996, Queiroz and Oliveira 2001). Tending ants may also reduce the density and abundance of interspecific competitors by attacking herbivores that feed on the same host plant (Messina 1981, Ito and Higashi 1991, Floate and Whitham 1994). Additionally, ant attendance may confer direct benefits to homopteran sur-

vival. For example, persistent honeydew removal by ants allows homopterans to attain maximal feeding rates, improving nutrient uptake and assimilation, without the threat of host plant contamination (Banks and Nixon 1958, Larsen et al. 2001).

Cotton aphids, *Aphis gossypii* Glover, are a polyphagous pest species found on a variety of crop plants including chrysanthemum, cotton, cucumber, okra, and tomato (Ebert and Cartwright 1997). High aphid populations can have negative impacts on cotton yield and result in economic losses (Andrews and Kitten 1989, Harris et al. 1992, Rosenheim et al. 1995). In 1991, the cotton aphid was the number one pest species in domestic cotton, causing a yield loss of >2% (Head 1992). Even small populations of late-season aphids are potentially damaging. Honeydew production during boll set may result in "sticky cotton" that can decrease cotton lint quality (Carter 1992). Additionally, cotton aphids can vector >50 plant viruses (Kennedy et al. 1962). For example, the cotton aphid was implicated in a multivirus epidemic affecting Alabama tomato production that, in some areas, resulted in 100% yield loss (Sikora et al. 1998).

In cultivated cotton systems, these aphids have only recently emerged as primary pests. It is theorized that

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this is because of their evolution of insecticidal resistance to novel classes of pesticides (Kerns and Gaylor 1992, O'Brien and Graves 1992). Furthermore, the application of broad-spectrum insecticides for control of pest species (e.g., boll weevil, *Anthonomus grandis* Boheman) has devastated natural enemy populations and contributed to cotton aphid outbreaks (Slosser et al. 1989). Natural enemies are fundamental in the control of cotton aphid outbreaks and regulation of seasonal population dynamics (Hardee and Herzog 1993, Hardee et al. 1994, Dreistadt and Flint 1996). Thus, any factor interfering with the control of cotton aphids by predators, parasitoids, or other biological control agents has the potential to cause economic harm.

Red imported fire ants, *Solenopsis invicta* (Buren), are an invasive species native to South America that arrived in the southeastern United States  $\approx 75$  yr ago. Since that time, they have spread throughout the southern states and continue to expand their range into other regions of the country, including the mid-Atlantic states and the Southwest (Callcott and Collins 1996, Sparks 1999). Red imported fire ants are aggressive, predatory generalists that can reach extremely high densities. They have been implicated in the decline of biodiversity and simplification of ecological communities in natural and managed systems (Vinson 1994, Wojcik et al. 2001). Agricultural systems permit fire ants to reach particularly high densities because of their disturbed nature and abundance of potential food items. Consequently, fire ants often dominate and severely alter arthropod food web dynamics in agroecosystems (Whitcomb et al. 1972, Lofgren et al. 1975, Eubanks 2001, Eubanks et al. 2002). For example, in Alabama soybean and cotton fields fire ant densities are negatively correlated with  $>90\%$  of beneficial natural enemies and herbivorous pest species (Eubanks 2001).

Despite their apparent pervasive impacts on arthropod food webs, it has yet to be resolved whether fire ants have a net beneficial or detrimental effect in agricultural systems. Fire ants may provide beneficial control of pest species (Negm and Hensley 1969, Morrill 1977, Sterling 1978, Eubanks 2001, Vogt et al. 2001). Alternatively, fire ants may act as higher-order predators of natural enemies and indirectly release pest species from regulation (Wilson and Oliver 1969, Tedders et al. 1990, Vinson and Scarborough 1991, Hu and Frank 1996, Eubanks et al. 2002).

Red imported fire ants have been observed tending mealybugs and soft scales on weeds and grass roots growing within soybean fields (Whitcomb et al. 1972). They also aggregate in areas with planthoppers (Homoptera: Cixiidae) (Sheppard et al. 1979) and cotton aphids (Reilly and Sterling 1983a, 1983b). Vinson and Scarborough (1989) suggested that fire ants directly interfere with cotton aphid predators. We expand on the work of Vinson and Scarborough (1989) by (1) documenting the numerical response of fire ants to aphid presence in the canopy of cotton plants; (2) performing greenhouse experiments to quantify cotton aphid survival in the presence and absence of fire

ants and aphid predators; and (3) conducting a large-scale field experiment to support our greenhouse experiments. We hypothesize that red imported fire ants protect cotton aphids from predators and that this results in larger aphid populations in cotton fields.

## Materials and Methods

**Greenhouse Experiments.** All greenhouse experiments used the same basic design. Cages were constructed of a polyvinyl chloride (PVC) pipe frame (75 cm  $\times$  30 cm  $\times$  33 cm), covered with fine-mesh mosquito netting and placed in 37-liter plastic containers filled with potting soil. All cages contained one cotton plant, *Gossypium hirsutum* L. ( $\approx 1$  m tall). Caged plants assigned to a fire ant treatment were connected to plastic pans (53 cm  $\times$  43 cm  $\times$  13 cm) containing a laboratory colony of  $\approx 500$  red imported fire ant workers. Colonies were started from local collections and were allowed to acclimate to greenhouse conditions for 24 h before the start of the experiment. Pans were connected to cages through plastic tubing (5 cm diam) that acted as a foraging tunnel. All pans were lined with liquid Teflon to prevent ant escape.

Ants were given a choice between plants with no aphids and plants infested with aphids (200–250 aphids per plant). Ants were allowed to forage for 24 h; and then plants were cut at their base, secured in plastic bags and frozen. Twenty-four hours later all ants in both treatments were counted. This experiment was replicated six times, and statistical analysis was performed using a one-way analysis of variance (ANOVA).

The impact of aphid predators on aphid survival in the presence and absence of fire ants was quantified in two greenhouse experiments similar to the previous one. One of four treatments was randomly assigned to each cage: 1, cotton aphids; 2, cotton aphids and fire ants; 3, cotton aphids and predator larvae (see below); 4, cotton aphids, fire ants, and predator larvae. Twenty apterous aphids of similar size and coloration were selected from a greenhouse colony and individually placed on leaves of each caged plant. Aphids were allowed to acclimate and initiate feeding for 24 h before ant exposure. Because of their high fecundity, aphids on every plant were recounted before ant exposure to obtain an initial aphid density.

In the first experiment, two lady beetle larvae (see below) were placed on caged plants that were assigned predators. In the second experiment, two green lacewing larvae (see below) were placed on caged plants that were assigned predators. Both types of larval predators were placed on caged plants  $\approx 24$  h after fire ants were given access. Lady beetle and green lacewing larvae were chosen because they are abundant predators that consume large numbers of aphids in southeastern cotton fields. Lady beetle larvae (late instar) were collected from local cotton fields, and green lacewing larvae, *Chrysoperla carnea* Stephens, (also late instar) were obtained from the Beneficial Insectary supply company (Redding, CA). The two most abundant lady beetle species in Alabama

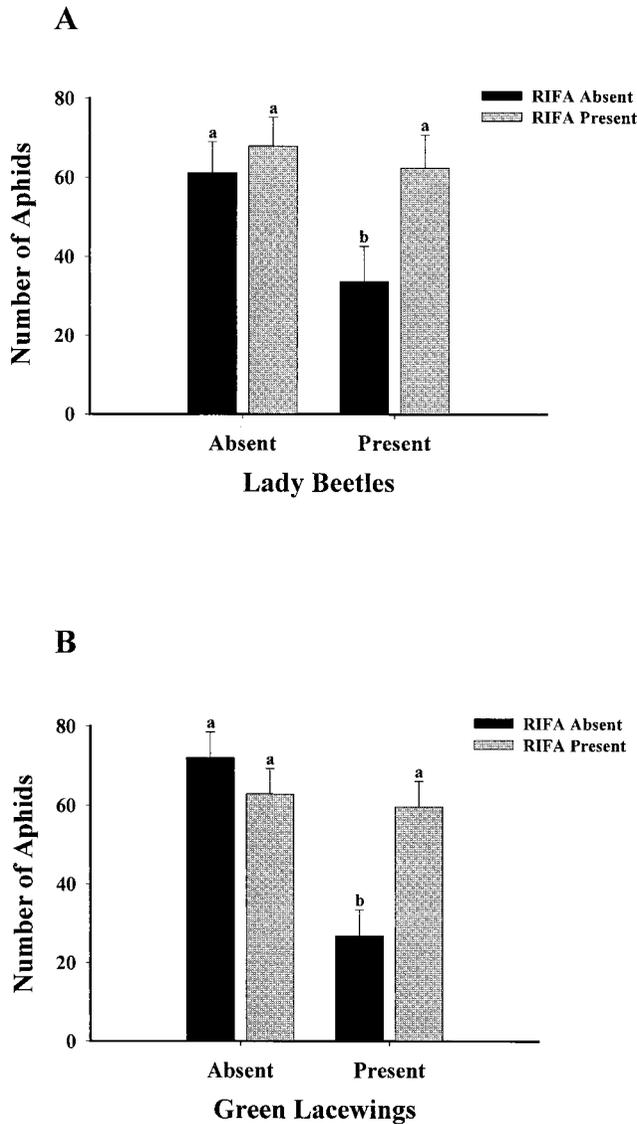


Fig. 1. The effect of fire ant, lady beetle larvae (A), and green lacewing larvae (B) presence on the survival of cotton aphids in caged greenhouse experiments; RIFA, red imported fire ant.

cotton fields were *Coccinella septempunctata* L. and *Hippodamia convergens* Guerin-Meneville (Eubanks 2001); these two species were used in our experiments. Predator larvae were randomly selected for experimental treatments from a group of similar sized larvae.

The densities of all insects used in greenhouse experiments—ants, aphids, and predators—are within the range commonly encountered in Alabama cotton fields (Eubanks 2001, Eubanks et al. 2002). Twenty-four hours after predators were added to cages, all cotton plants were cut at their base, secured in plastic bags and frozen. All ants, aphids, and/or predators were then counted and recorded. The experiment using lady beetle larvae was replicated 15 times, and the green lacewing experiment was replicated 10 times. Statistical analysis for predator survival was

performed using a one-way ANOVA. Statistical analysis for aphid survival was performed using a two-way analysis of covariance (ANCOVA) on the log-transformed data, with the presence and absence of fire ants and/or predators as main effects and initial aphid density as a covariate.

**Field Experiment.** Fire ants, predator larvae, and aphids were sampled approximately weekly from June through September 2000, in cotton fields at the E. V. Smith Research Station in Tallassee, AL. Fields were at least 20 ha and separated by 1–2 km. Four fields were used, each incorporating two 1.2-ha plots at opposite ends of the field. Plots were separated by at least 100 m. Plots were divided into two treatments: high fire ant density or low fire ant density. Treatments were assigned randomly and were established using Amdro, a

commercially available fire ant bait that significantly decreases fire ant abundance with little to no impact on nontarget arthropods. Amdro was applied  $\approx 1$  and 8 wk after planting at a rate of 5.5 kg/ha (granular bait, Hydramethylnon, 40.15 g active ingredient/ha, Wal-Mart, Auburn, AL).

Fire ants and predator larvae were sampled using beat cloth sampling (10 samples per field per week). We spread a 1-m<sup>2</sup> cloth on the ground between two rows of cotton. Six cotton plants, three from each row, were vigorously shaken over the cloth. All fire ants and predator larvae that fell on the cloth were identified and counted. Aphid sampling consisted of visually searching the upper six leaves of a cotton plant, counting all visible aphids on the top and bottom of each leaf. Ten random plants were searched per plot. Data were log ( $n + 1$ ) transformed, and we averaged samples collected from plots on each sampling date to avoid pseudoreplication. The densities of fire ants, predator larvae, and aphids were compared between untreated and experimental plots with repeated measures ANOVA with field as a blocking factor (SAS ProcMixed, Khattree and Naik 1999).

## Results

**Ant Tending Experiment.** In a choice experiment using caged cotton plants, we found that fire ants preferentially foraged on plants with aphids ( $F = 6.79$ ,  $df = 1$ ,  $P = 0.028$ ). Aphid-infested plants had a mean of  $103 \pm 47$  ants per plant, whereas aphid-free plants had a mean of  $5 \pm 3$  ants per plant. There was no apparent difference in aphid abundance on aphid-infested plants following ant exposure, and ants were never observed preying upon aphids. In addition, ants were observed palpating individual aphids with their antennae in apparent solicitation of honeydew (e.g., Way 1963).

**Aphid-Predator Survival Experiment.** The presence of fire ants alone did not have a significant effect on cotton aphid survival in caged greenhouse experiments (Fig. 1). Lady beetle and green lacewing larvae had significant negative effects on aphid survival in our caged greenhouse experiments (Table 1). Aphid populations were reduced by 44.8% in the presence of lady beetle larvae and 62.7% in the presence of lacewing larvae (Fig. 1).

Fire ants had a significant negative effect on the survival of lady beetle larvae ( $F = 15.00$ ,  $df = 1$ ,  $P < 0.001$ ) and green lacewing larvae ( $F = 7.46$ ,  $df = 1$ ,  $P = 0.014$ ) in greenhouse experiments (Fig. 2). Neither aphid predator demonstrated an ability to endure fire ant exposure and subsequent attack in caged experiments; both predators suffered a high degree of mortality ( $\approx 96\%$ ). Fire ant response to predator presence was similar between the two experiments, both predators were rapidly attacked by multiple ants upon detection (IK, unpublished data).

We found a significant predator-by-fire-ant interaction on aphid survival in lady beetle and lacewing experiments (Table 1). The addition of fire ants to the aphid-lady beetle treatment increased aphid survival

**Table 1.** Analysis of variance for the effects of fire ant and predator presence on aphid survival

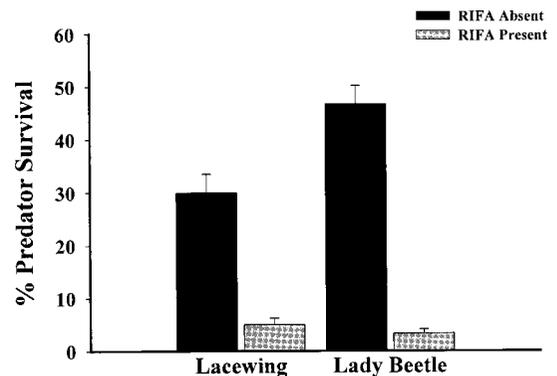
Source of variation	df	MSE	F
Lady beetle			
Block	2	18.54	39.5***
Fire Ant	1	2.47	5.32*
Lady Beetle	1	3.58	7.73**
Fire Ant $\times$ Lady Beetle	1	3.12	6.73*
Initial Aphid Density	1	6.42	13.84***
Error	46	0.46	
Green lacewing			
Block	1	14.54	103.12***
Fire Ant	1	1.56	11.03**
Lacewing	1	5.38	38.16***
Fire Ant $\times$ Lacewing	1	3.67	26.01***
Initial Aphid Density	1	3.81	27.03***
Error	34	0.14	

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

by 85.0% (Fig. 1A). Likewise, fire ants increased aphid survival by 121.9% in the aphid-lacewing experiment (Fig. 1B).

**Field experiment.** Fire ants were more abundant in untreated field plots than in Amdro-treated plots (Fig. 3; Table 2). Fire ants were approximately twice as abundant in high fire ant density plots ( $\bar{x} = 3.53 \pm 0.34$  ants per sample) than in low fire ant density plots ( $\bar{x} = 1.82 \pm 0.31$  ants per sample). Throughout the field season, fire ants gradually increased in abundance in untreated and treated plots, which likely reflects the reestablishment of local fire ant colonies following mound disruption during field tillage.

Lady beetle larvae (Fig. 4A; treatment effect, Table 2) and lacewing larvae (Fig. 4B; treatment  $\times$  date effect, Table 2) were more abundant in field plots with low fire ant densities than in high fire ant density plots. Lady beetle larvae were almost three times more abundant in low fire ant density plots ( $\bar{x} = 0.62 \pm 0.11$  lady beetle larvae per sample) than in high fire ant density plots ( $\bar{x} = 0.23 \pm 0.06$  lady beetle larvae per sample). Lacewing larvae were approximately six times more abundant in low fire ant density plots ( $\bar{x} = 0.06 \pm 0.02$  lacewing larvae per sample) than in high



**Fig. 2.** The percent survival of lady beetle and green lacewing larvae in the presence and absence of fire ants after 24 h exposure in caged greenhouse experiments.

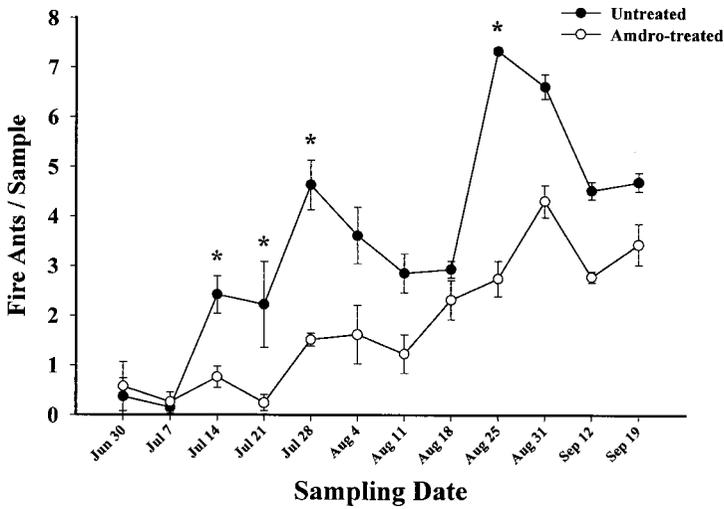


Fig. 3. The effect of high and low fire ant density treatments on fire ant abundance in the field. An asterisk indicates that means were significantly different on that sampling date (Bonferroni test).

fire ant density plots ( $\bar{x} = 0.01 \pm 0.01$  lacewing larvae per sample), although lacewings were relatively scarce in both treatments on most sampling dates.

Cotton aphids were more abundant in field plots with high fire ant densities ( $\bar{x} = 6.83 \pm 0.03$  aphids per leaf) than in low fire ant density plots ( $\bar{x} = 4.04 \pm 0.03$  aphids per leaf) (Fig. 5; treatment  $\times$  date effect, Table 2). We found a large early-season aphid outbreak, followed by a severe population decline during the middle season and a small late-season peak. This trend was consistent across both treatments. More than 90% of total aphids sampled were encountered early in the season, during three sampling dates (7, 14, and 21 July).

Discussion

In greenhouse experiments, fire ants preferentially foraged on aphid-infested plants. Observational evidence from this experiment and empirical data from aphid survival experiments (Fig. 1) indicate that the presence of fire ants does not have a direct impact on aphid survival. This suggests that fire ants found in the canopy of caged cotton plants were involved in honeydew retrieval rather than aphid predation. Furthermore, fire ants were frequently present in aphid-free cages, yet they rarely explored the foliage of these

plants, despite the presence of extrafloral nectaries. Aphids, therefore, may serve as a stimulus for fire ant foraging in the canopy of cotton plants.

Increased fire ant presence on cotton foliage is likely to result in enhanced survival of cotton aphids through interference with aphid predators (Figs. 1 and 5). Our greenhouse and field data support this assertion. Results from these experiments indicate that fire ants disrupt aphid predation by aphidophagous predators, such as lady beetle and lacewing larvae (Figs. 2 and 4). Intense interference of aphid predators by fire ants produced an apparent trophic cascade, whereby the impact of an organism of high trophic status (fire ants) indirectly benefits an organism of lower trophic status (cotton aphids). In a similar study, Rosenheim et al. (1993) found that predation of lacewing larvae by a community of generalist predators released aphid populations from predation in California cotton and resulted in higher aphid densities. These studies suggest that aphidophagous larvae are effective aphid predators yet are highly vulnerable to interference despite their relatively high trophic status.

Our findings are of great significance for biological control in southeastern agricultural fields that harbor both fire ants and honeydew-producing homopterans. Fire ants are top predators that are unlikely to be challenged by most natural enemies found in agro-

Table 2. Sources of variation, F-statistics, degrees of freedom (numerator, denominator), and probabilities for the effects of fire ant suppression on fire ants, lady beetle larvae, lacewing larvae, and aphids

Source	Species											
	Fire ants			Lady beetle larvae			Lacewing larvae			Aphids		
	F	df	P	F	df	P	F	df	P	F	df	P
Field	21.96	3,3	0.015	21.22	3,3	0.016	0.77	3,3	0.584	0.26	3,3	0.849
Treatment	25.17	1,3	0.015	120.16	1,3	0.002	8.98	1,3	0.058	5.27	1,3	0.105
Date	10.37	11,66	0.001	16.62	11,66	0.001	4.12	11,66	0.001	137.32	11,66	0.001
Trt $\times$ date	1.14	11,66	0.345	3.35	11,66	0.001	3.82	11,66	0.001	4.43	11,66	0.001

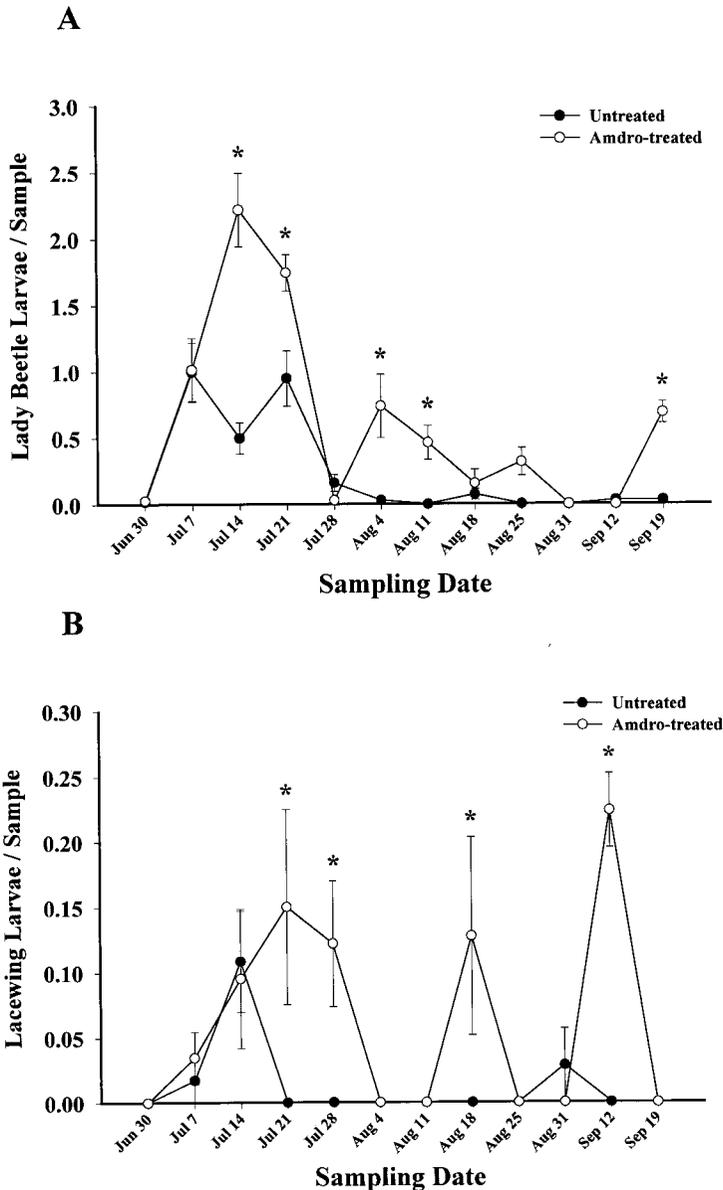


Fig. 4. The effect of fire ant density on lady beetle larvae (A) and lacewing larvae (B) abundance in the field. An asterisk indicates that means were significantly different on that sampling date (Bonferroni test).

ecosystems. Therefore, fire ants may prey upon many natural enemies that they encounter, regardless of their trophic position. Predators that consume homopterans as their focal prey may be at greatest risk of fire ant predation. Studies have indicated that aggressive, predatory ant species may be more successful at protecting homopteran populations because of their inherent tenacity (Buckley and Gullan 1991, Bishop and Bristow 2001). Red imported fire ants are notorious for their voracious tendencies and may be unsurpassed in their aggressive behavior among North American ant species. Consequently, fire ants may be the "ultimate" protection for homopteran populations

and are likely to be highly detrimental to their biological control.

In this report, we have documented the large-scale impact of a fire ant-homopteran mutualism in agricultural fields. Our results concur with other studies demonstrating that ant-homopteran mutualisms are prevalent in agricultural systems and may be detrimental for the biological control of Homoptera (Vinson and Scarborough 1991, Jiggins et al. 1993, Reimer et al. 1993, Stechmann et al. 1996, Dutcher et al. 1999, Queiroz and Oliveira 2001). These collective works suggest that ants can be a major force in shaping food web dynamics and complex trophic interactions in

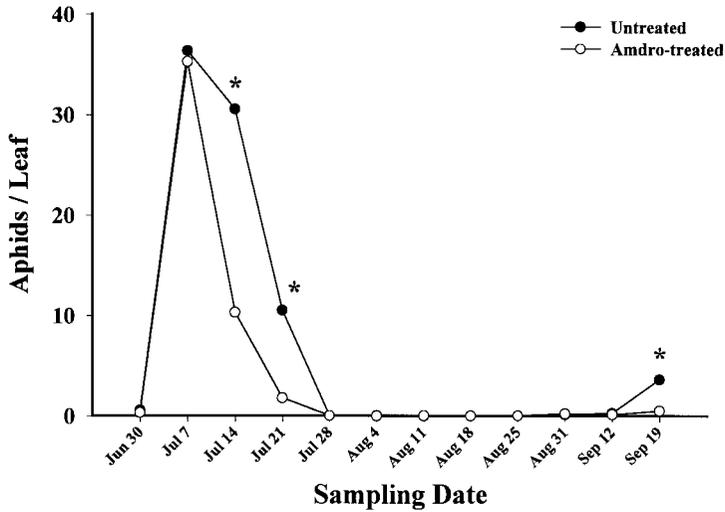


Fig. 5. The effect of fire ant density on aphid abundance in the field. An asterisk indicates that means were significantly different on that sampling date (Bonferroni test).

agroecosystems. Furthermore, our results contrast earlier studies (Sterling et al. 1979; Reilly and Sterling 1983a, 1983b) that suggest red imported fire ants do not interfere with other natural enemies, although these studies were based mainly on adult predators, whereas our study reports on larval predators.

Documenting the beneficial and deleterious effects of fire ants on agricultural systems is essential for making informed decisions on their management. Methods currently exist for fire ant control, but the economic implications of such control are unclear because of conflicting reports of fire ant impact on biological control. We have shown that fire ants have pervasive impacts on arthropod food webs that strongly influence the population dynamics of many key components in agroecosystems. These include direct effects, consuming pest species, and indirect effects, consuming beneficial natural enemies (e.g., Eubanks 2001). Fire ants currently range over a large percentage of agriculturally significant states and are likely to expand their range in the near future (Vinson 1997). Consequently, research aimed at quantifying the community-wide impacts of fire ants in agricultural systems will continue to be of interest until a better estimate of their cumulative effects is ascertained.

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