

RED IMPORTED FIRE ANTS (HYMENOPTERA: FORMICIDAE) INCREASE THE ABUNDANCE OF APHIDS IN TOMATO

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ABSTRACT

Red imported fire ants, *Solenopsis invicta* (Buren) (Hymenoptera: Formicidae), are abundant in many agroecosystems in the southern United States and can affect the abundance of arthropods in these systems. We determined the effects of red imported fire ants on the abundance of aphids, other herbivorous insects, and beneficial arthropods in Alabama tomato (*Lycopersicon esculentum*) by manipulating the density of red imported fire ants in plots of tomato plants and by sampling fresh market tomato farms for two years (2003 and 2004). In both years of our study, aphid abundance was significantly greater in tomato plots with high densities of fire ants than in plots where fire ant densities were suppressed. Further, the abundance of fire ants was positively correlated with the abundance of aphids on intensely managed tomato farms in both years. These aphids included many species that are the primary vectors of economically-important plant viruses of tomato and other vegetable crops. The positive effect of fire ants on aphid abundance was likely due to facultative fire ant—aphid mutualisms. Other studies have demonstrated that fire ants protect honeydew-producing insects from natural enemies, and we found that fire ants reduced the abundance of beneficial arthropods in the second year of our field experiment. However, red imported fire ants did not significantly reduce the abundance of non-aphid herbivores in either year of our field experiment, suggesting that fire ants are not important biological control agents of these insects in tomato. Fire ants may disrupt biological control of aphids in tomato fields and suppression of fire ants on tomato farms may decrease the abundance of aphids.

Key Words: *Solenopsis invicta*, red imported fire ant, biological control, intraguild predation, *Lycopersicon esculentum*, tomato, ant-aphid mutualism

RESUMEN

La hormiga de fuego roja importada, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), es abundante en varios ecosistemas agrícolas en el sur de los Estados Unidos y puede afectar la abundancia de artrópodos en estos sistemas. Nosotros determinamos los efectos de la hormiga de fuego roja importada sobre la abundancia de áfidos, otros insectos herbívoros, y artrópodos benéficos en tomate (*Lycopersicon esculentum*) en el estado de Alabama por medio del manejo de la densidad de la hormiga de fuego roja importada en parcelas de plantas de tomate y por el muestreo de fincas que producen tomate fresco para el mercado por 2 años (2003 y 2004). En ambos años de nuestro estudio, la abundancia de áfidos fue significativamente mayor en las parcelas de tomate con densidades altas de la hormiga de fuego que en las parcelas donde la densidad de la hormiga de fuego fue suprimida. Además, la abundancia de la hormiga de fuego fue correlacionado positivamente con la abundancia de áfidos en fincas de tomate bajo el manejo intensivo para ambos años. Estos áfidos incluyeron muchas de las principales especies que son vectores de virus económicamente importantes en plantas de tomate y de otros cultivos de hortalizas. El efecto positivo de la hormiga de fuego sobre la abundancia de áfidos probablemente fue debido al mutualismo facultativo entre la hormiga de fuego y los áfidos. Otros estudios han demostrado que la hormiga de fuego protege insectos que producen sustancias azucaradas de sus enemigos naturales, y encontramos que la hormiga de fuego redujo la abundancia de artrópodos benéficos en el segundo año de nuestro estudio de campo. Sin embargo, la hormiga de fuego roja importada no redujo significativamente la abundancia de herbívoros que no son áfidos en ninguno de los años de nuestro experimento, ello indica que las hormigas de fuego no son agentes de control biológico importantes de insectos en tomate. La hormiga de fuego puede interrumpir el control biológico de áfidos en campos de tomate y la supresión de la hormiga de fuego en estos campos de tomate puede reducir la abundancia de áfidos.

INTRODUCTION

Tomatoes (*Lycopersicon esculentum*) are the second most important vegetable crop in the United States with over 8 million tons produced annually in the U.S. (Brunke et al. 2003). The economic viability of tomatoes is threatened by numerous insect pests, including lepidopteran larvae, thrips (Thysanoptera: Thripidae), stinkbugs (Hemiptera: Pentatomidae), whiteflies (Hemiptera: Aleyrodidae) and aphids (Hemiptera: Aphididae) (Nault & Speese 2002; Kemble et al. 2004). Aphids can be particularly serious pests of tomato because aphid feeding reduces the yield and fruit quality of tomatoes and, more importantly, aphids are the primary vectors for plant viruses that can devastate tomato production (Tomlinson 1987). For example, epidemics of *Cucumber mosaic virus* (CMV) have significantly reduced tomato production in the southeastern U.S. and in China, France, Italy, and Spain (Jorda et al. 1992; Kaper et al. 1990; Sikora et al. 1998). Plant viruses like CMV are often difficult to manage because they may have extremely large host ranges (Edwards & Christie 1991) and can be transmitted by dozens of species of aphid species in a nonpersistent manner (Palukaitis et al. 1992). Viruses transmitted by aphids in a nonpersistent manner are acquired in seconds by the aphid while probing an infected epidermal cell and are retained on the tip of the aphid's stylet. The virus can then be immediately transmitted in the same general process, i.e., a quick probe of a plant's epidermal cell by the aphid. Because virus transmission of nonpersistent viruses like CMV by aphids is rapid, chemical pesticides are ineffective because aphids transmit the virus before they are intoxicated. Additionally, some pesticides actually enhance the spread of plant viruses by increasing aphid probing and movement among plants (Lowery & Boiteau 1988; Perring et al. 1999). Because aphids are the primary vectors of most plant viruses, any factor that increases aphid abundance is likely to increase the spread of the virus and the potential for a virus epidemic (Madden et al. 2000; Hull 2002; Jeger et al. 2004). For example, the abundance of alate aphids is positively correlated with the incidence of *Beet mosaic virus* in sugar beet, *Beta vulgaris* (L.) (Dusi et al. 2000), with the incidence of *Barley yellow dwarf virus* in cereals (Power et al. 1991; Chapin et al. 2001; Fabre et al. 2003), and with the incidence of *Potato virus Y* and *Potato leafroll virus* in potato, *Solanum tuberosum* (Basky 2002).

Our work in southeastern agricultural systems has identified an important ecological interaction that may alter the abundance of virus vectors: fire ant—aphid mutualisms. Red imported fire ants, *Solenopsis invicta* (Buren) are widespread, invasive ants that are notoriously aggressive and voracious (Vinson 1997; Holway et al. 2002). They were

originally introduced through the port of Mobile, Alabama, in the early 1900s, spread across the southern United States from North Carolina to Arizona, and have recently invaded California (MacKay & Fagerlund 1997; Vinson 1997). Fire ants, like many ant species, readily form facultative mutualisms with honeydew-producing insects such as aphids, scales, and whiteflies (Reilly & Sterling 1983a, 1983b; Vinson 1997; Helms & Vinson 2002). Fire ants are attracted to plants infested with aphids and are effective at protecting aphids from predators. Fire ants, for example, preferentially forage on aphid-infested cotton plants compared with aphid-free cotton plants, and fire ant and cotton aphid abundances are positively correlated in the field (Kaplan & Eubanks 2002, 2005). Fire ant predation of lady beetle larvae is twice as high on aphid-infested plants as on aphid-free plants (Kaplan & Eubanks 2002) and predator larvae are more abundant in cotton fields with suppressed densities of fire ants than in control fields with large fire ant populations (Kaplan & Eubanks 2002, 2005; Diaz et al. 2004).

The positive effect of ants on aphid population density may affect the movement of aphids. Under low density conditions, developing aphids do not produce wings when they molt and become apterous or wingless adults. When crowded, however, nymphs develop wings as they molt and become alate or winged adults (Dixon 1977; Muller et al. 2001). Dispersing aphids typically search for new host plants with no or few aphids (Dixon 1977; Hodgson 1991). If fire ant protection of aphids results in a 3 to 5-fold increase in aphid population density (i.e., Kaplan & Eubanks 2002, 2005), then it is likely that fire ant protection will result in a 3 to 5-fold increase in the number of alates. This could result in an increase in the movement of aphids among different plant species and ultimately increase virus spread and incidence.

The effect of fire ants in agroecosystems is not always negative. For example, fire ants have been reported as predators of a wide variety of insect pests including the velvetbean caterpillar, *Anticarsia gemmatilis* Hübner (Lee et al. 1990), red-necked peanutworm, *Stegasta bosqueella* (Chambers) (Vogt et al. 2001), horn fly, *Haematobia irritans* (L.), boll weevil, *Anthonomus grandis* (Sterling 1978; Jones & Sterling 1979), cotton bollworm, *Helicoverpa zea* (Diaz et al. 2004); beet armyworm, *Spodoptera exigua* (Hubner) (Diaz et al. 2004), and the sugarcane borer, *Diatraea saccharalis* (Zehntner) (Adams et al. 1981; Fuller & Reagan 1988; Bessin & Reagan 1993). Thus, the suppression of fire ants in tomato may result in reduced aphid densities, but could increase the abundance of other insect pests of tomato.

Our primary objective was to determine if fire ants increase the abundance of aphids in tomato. If fire ants do increase the abundance of aphids in

tomato fields, then the suppression of fire ants in and around tomato fields may reduce the abundance of aphids and potentially alter the spread of aphid-vectored viruses. A secondary objective of this study was to document the effect of fire ant suppression on the abundance of other insect pests in tomato so that any changes in pest abundance could be included in future decisions regarding the suppression of fire ants in tomato.

MATERIALS AND METHODS

Field experiments were conducted at the E.V. Smith Research Center in Macon County, Alabama, during 2003 and 2004. For both field seasons, tomatoes (*Lycopersicon esculentum* variety: Floralina) were grown from seeds in the greenhouse for 1 month or until they reached 20 cm in height. They were then placed outdoors for one week of acclimatization, and then transplanted into field plots. In 2003, twelve plots of tomato plants, separated by at least 10 m, were established on bare ground. Each plot consisted of 30 plants, spaced 45 cm apart and organized into three rows separated by 75 cm each. In 2004, tomatoes were transplanted into raised (15 cm) beds of white plastic mulch, following fresh market tomato production standards (Kemble et al. 2004). Twelve plots of tomato plants were established during 2004 with the same plant and row spacing as in 2003.

Plots were randomly divided into 2 treatments: natural or high fire ant density (control) or suppressed fire ant density. Suppression treatments were established with Amdro®, a commercially available, ant-specific bait. Foraging fire ant workers pick up the bait and return it to the colony. The active ingredient of Amdro® is hydramethylnon which blocks the production of ATP and kills ants by inhibiting energy production (Valles & Koehler 1997). Amdro® has very minimal effects on non-target arthropods (Hu & Frank 1996; Eubanks et al. 2002), and has been successfully used to suppress fire ants in similar sized and spaced plots in other studies (e.g., Harvey & Eubanks 2004; 2005). Amdro® was applied weekly to plots assigned to the fire ant suppression treatment, beginning 1 week prior to sampling, and fire ants were allowed to naturally colonize control (high fire ant) plots. Fire ant abundance was quantified weekly within each plot with traps consisted of a 2.5-cm piece of "hotdog" placed in a 50-ml plastic tube. One trap was placed in the center of each plot for \approx 45 minutes, after which they were collected, sealed, returned to the laboratory, and stored in a freezer until ants were counted. All plants within each plot were visually searched each week for aphids, fire ants, and other arthropods. All abundance data were $\log(n+1)$ transformed prior to analysis. Differences in the abundance of fire ants, aphids,

non-aphid herbivores, and natural enemies were compared between treatments with repeated measures ANOVA (SAS Proc Mixed with repeated statement; Khattree & Naik 1999). To avoid pseudo-replication (i.e., counting each plant within each plot as a replicate), data for each plot were averaged to obtain mean plot values for analysis.

In 2004, tomato plants in 4 fresh market tomato fields were sampled in Blount Co., Alabama for the presence of fire ants and other arthropods. Fields ranged from 5 to 7 acres and approximately 20 tomato plants per acre were visually searched for aphids, fire ants, and other arthropods weekly for 7 weeks. Additionally, "hotdog" traps were used to quantify the relative abundance of fire ants (1 trap per acre of tomato). In 2005 the same sampling procedures were repeated on 5 fresh market tomato fields in the same area of Blount County. We found very few non-aphid herbivores and natural enemies on tomato plants on the farms and, consequently, limited our analysis to a correlation of aphid abundance and fire ant abundance in commercial tomato fields with seasonal averages.

RESULTS

In both 2003 and 2004 the abundance of fire ants foraging on the ground in tomato plots was significantly reduced by the application of Amdro®, although fire ant suppression was better in 2003 (2003: 290.67 ± 48.13 fire ants per trap versus 39.1 ± 27.88 fire ants per trap, control versus Amdro® treated plots, respectively, $F_{1,20} = 27.51$; $P < 0.0001$; 2004: 355.83 ± 61.28 fire ants per trap versus 200.33 ± 31.41 fire ants per trap, control versus Amdro® treated plots, respectively, $F_{1,29} = 4.63$; $P = 0.04$).

We identified at least 6 different aphid species on tomato plants in our plots, including *Aphis gossypii*, *A. fabae*, *Aulacorthum solani*, *Macrosiphum euphorbae*, *Myzus persicae*, and *Uroleucon* spp. In 2003, aphid abundance was significantly different between treatments for apterous aphids ($F_{1,30} = 9.82$; $P = 0.004$) and for total aphids (apterous + alate) ($F_{1,30} = 8.57$; $P = 0.01$) (Fig. 1A). The abundance of alate aphids, however, was not statistically different between treatments ($F_{1,30} = 1.76$; $P = 0.19$). In 2004, however, the abundance of alate aphids ($F_{1,29} = 26.4$; $P < 0.0001$) and total aphids ($F_{1,29} = 27.2$; $P < 0.0001$) were significantly different between the two treatments (Fig. 1B). In contrast to 2003, alate aphids made up over 95% of total aphids in both control and suppression plots in 2004. Likewise, during our survey of fresh market tomato fields, the abundance of fire ants and aphids was positively correlated in 2004 (one-tailed test; $r = 0.09$; $P = 0.04$; $n = 4$) and during 2005 (one-tailed test; $r = 0.91$; $P = 0.02$; $n = 5$) and greater than 95% of these aphids were alates.

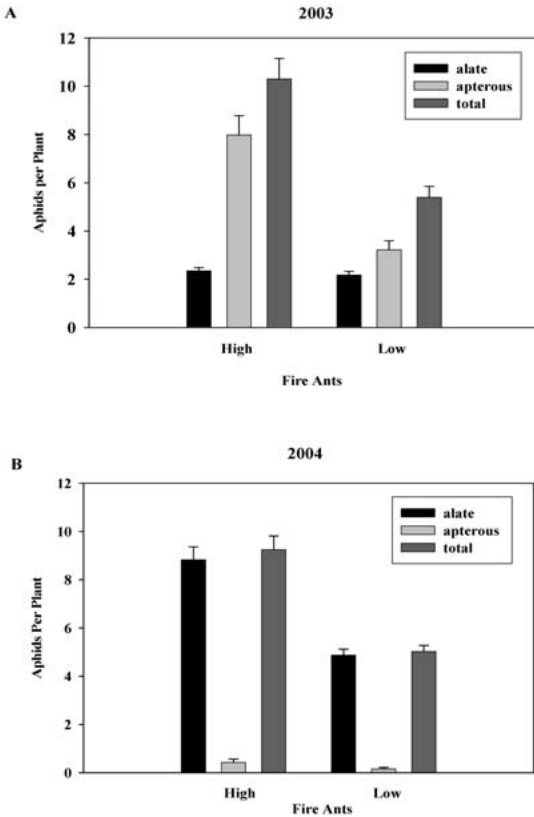


Fig. 1. The number of aphids per tomato plant in high fire ant plots and in low fire ant plots in 2003 (A) and 2004 (B). Means \pm one standard error plotted.

In 2003 and 2004, several non-aphid herbivores were found feeding on tomato plants (Table 1), although their overall densities were quite low, especially in 2004. Non-aphid herbivore abundance, however, was not significantly different between treatments in both 2003 (2.25 ± 0.2 per

plant versus 2.26 ± 0.2 per plant, control versus Amdro® treated plots, respectively) ($F_{1,24} = 3.89$; $P = 0.06$) and 2004 (0.32 ± 0.06 per plant versus 0.4 ± 0.05 per plant, control versus Amdro® treated plots, respectively) ($F_{1,23} = 0.00$; $P = 0.96$).

Several natural enemies also were present on tomato plants in our experimental tomato plots in 2003 and 2004 (Table 2). In 2003, the most abundant natural enemies were spiders and coccinellid larvae (Coccinellidae). Natural enemy abundance, however, was not significantly different between the 2 treatments (0.10 ± 0.02 per plant versus 0.09 ± 0.03 per plant, control versus Amdro® treated plots, respectively) ($F_{1,24} = 0.01$; $P = 0.93$). In 2004, the most abundant natural enemies were damsel bugs (Nabidae) followed by spiders and minute pirate bugs (Anthocoridae). There was a significant difference ($F_{1,29} = 4.31$; $P = 0.04$) in natural enemy abundance between suppressed fire ant plots and control plots with significantly more natural enemies on tomato plants in fire ant suppressed plots (0.13 ± 0.03 per plant versus 0.20 ± 0.03 per plant, control versus Amdro® treated plots, respectively).

DISCUSSION

Total aphid abundance in both 2003 and 2004 was significantly greater in tomato plots with high densities of fire ants (control plots) than in plots with suppressed fire ant densities. In 2004 alate aphids were more than twice as abundant in high fire ant plots as in low fire ant plots and there was a positive correlation between the abundance of fire ants and alate aphids in commercial tomato fields in 2004 and 2005. Taken together, these results suggest that fire ants increase the abundance of important aphid pests of tomato. These results are consistent with studies conducted in other agricultural crops indicating that fire ants often increase aphid abundance. For example, fire ant ‘tending’ of aphids increases the

TABLE 1. MEAN NUMBER (\pm ONE STANDARD ERROR) OF NON-APHID HERBIVORES FOUND PER TOMATO PLANT IN CONTROL PLOTS (HIGH FIRE ANT PLOTS) AND AMDRO® TREATED PLOTS (LOW FIRE ANT PLOTS) IN 2003 AND 2004.

Herbivore Taxa	2003				2004			
	High fire ant	SE	Low fire ant	SE	High fire ant	SE	Low fire ant	SE
Aleyrodidae	2.25	0.20	2.24	0.20	0.027	0.013	0.038	0.01
Miridae	0.004	0.003	0.002	0.002	0.007	0.007	0.002	0.002
Coreidae	0.002	0.002	0	0	0	0	0	0
Lepidoptera larvae	0	0	0.007	0.007	0.17	0.03	0.23	0.04
Chrysomelidae	0	0	0	0	0.09	0.02	0.1	0.01
Gryllidae	0	0	0	0	0	0	0.002	0.002
Acrididae	0	0	0	0	0.007	0.007	0.008	0.004
Cercopidae	0	0	0	0	0	0	0.002	0.002
Pentatomidae	0	0	0	0	0	0	0.002	0.002

TABLE 2. MEAN NUMBER (\pm ONE STANDARD ERROR) OF NATURAL ENEMIES FOUND PER TOMATO PLANT IN CONTROL PLOTS (HIGH FIRE ANT PLOTS) AND AMDRO® TREATED PLOTS (LOW FIRE ANT PLOTS) IN 2003 AND 2004.

Natural enemy Taxa	2003				2004			
	High fire ant	SE	Low fire ant	SE	High fire ant	SE	Low fire ant	SE
Spiders	0.09	0.004	0.09	0.03	0.05	0.03	0.09	0.01
Coccinellidae adults	0	0	0	0	0	0	0.005	0.005
Coccinellidae larvae	0.004	0.01	0	0	0	0	0	0
Reduviidae	0	0	0	0	0.01	0.009	0.01	0.005
Nabidae	0	0	0	0	0.06	0.02	0.03	0.01
Chrysopidae larvae	0	0	0	0	0.007	0.07	0.03	0.01
Anthocoridae	0	0	0	0	0.04	0.02	0.02	0.007
Hymenoptera	0	0	0	0	0.007	0.007	0.008	0.004
Lygaeidae	0	0	0	0	0.007	0.007	0.005	0.003

abundance of cotton aphids (*Aphis gossypii*) in cotton (Kaplan & Eubanks 2002, 2005; Diaz et al. 2004) and brown citrus aphids (*Toxoptera citricida*) in citrus (Michaud & Browning 1999). By essentially doubling aphid abundance in tomato, fire ants may significantly reduce tomato yield and fruit quality, especially if these aphids are carrying plant viruses that infect tomato. All of the aphids that we identified in our field experiment (*A. gossypii*, *A. fabae*, *A. solani*, *M. euphorbae*, *M. persicae*, and *Uroleucon* spp.) have been identified as vectors of CMV and other plant viruses that can devastate tomato production (Sikora et al. 1998; Palukaitis et al. 1992). Our results suggest that suppression of fire ants in and around agricultural fields will significantly reduce the abundance of aphids and may reduce the spread of aphid-vectored plant viruses. We plan to test this hypothesis in the near future.

We found limited evidence that fire ants affected the abundance of non-aphid herbivores in tomato. This is surprising because many previous studies conducted in other crops have found that fire ants suppress herbivores (Eubanks, 2001; Vogt et al. 2001; Diaz et al. 2004; Harvey & Eubanks 2004). For example, Eubanks (2001) found that densities of *S. invicta* workers were negatively associated with densities of several herbivores in both cotton and soybean. Likewise, Diaz et al. (2004) found that fire ants destroyed significant numbers of bollworm (*Helicoverpa zea*) and beat armyworm eggs (*Spodoptera exigua* (Hübner)) in cotton. Additionally, Vogt et al. (2001) found that fire ants forage on many herbivores in peanut fields, suggesting that fire ants may have negative effects on many herbivorous taxa. One reason for the difference in our findings from other studies could be the composition of herbivores present or their relative abundance. The non-aphid herbivores in tomatoes were dominated by whiteflies and lepidopteran larvae (Table 1). Like aphids, whiteflies produce honeydew and are sometimes tended by fire ants (Queiroz & Oliveria

2001), so it is unlikely that fire ants are significant predators of whiteflies in tomato. In 2004 the most abundant herbivores were first and second instar lepidopteran larvae, but they were present at relatively low densities. Predation of caterpillars by fire ants has been shown to be density-dependent and to some extent size-dependent in other crops (e.g., collards (Harvey & Eubanks 2004) and soybean (Styrsky et al. 2006)) and their low densities in tomato may have resulted in low fire ant predation during our plot experiments.

The number of natural enemies was not significantly different between treatments in 2003. These results are inconsistent with results published by Bugg & Dutcher (1989), Eubanks et al. (2002), Kaplan & Eubanks (2002), and Vogt et al. (2001). The conflicting results may be attributed to the low density of natural enemies present and the behavior of the natural enemies. In 2003, only 2 kinds of natural enemies, spiders and lady beetle larvae (Coccinellidae), were found during visual searches and spiders were much more abundant than lady beetle larvae. Some spiders can avoid predation by foraging fire ants by rapidly moving to other parts of the plant, dropping off of the plant on silk lines, or stretching to reduce contact with the plant surface (Eubanks et al. 2002). In 2004, however, fire ants did negatively affect the abundance of natural enemies. A greater diversity of natural enemies was found during visual searches in 2004 than in 2003. Other studies have shown that damsel bugs and minute pirate bugs, the first and third most abundant natural enemies in our tomato plots in 2004, were much more susceptible to fire ants than spiders (Eubanks 2001; Eubanks et al. 2002). Thus, the difference in natural enemies among the 2 years of the study may explain the greater impact of fire ants on beneficial insects in 2004.

In conclusion, fire ants had strong, positive effects on aphid abundance and insignificant effects on non-aphid herbivores. Taken together, the results of this study suggest that fire ants may dis-

rupt biological control of aphids in this crop and the suppression of fire ants will decrease aphid populations in tomato.

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REFERENCES CITED

- ADAMS, C. T., T. E. SUMMERS, C. S. LOFGREN, D. A. FOCKS, AND J. S. PREWITT. 1981. Interrelationship of ants and sugarcane borer in Florida sugarcane fields. *Environ. Entomol.* 10: 415-418.
- BASKEY, Z. 2002. The relationship between aphid dynamics and two prominent potato viruses (PVY and PLRV) in seed potatoes in Hungary. *Crop Prot.* 21: 823-827.
- BESSIN, R. T., AND T. E. REAGAN. 1993. Cultivar resistance and arthropod predation of sugarcane borer (Lepidoptera: Pyralidae) affects incidence of dead-hearts in Louisiana sugarcane. *J. Econ. Entomol.* 86: 929-932.
- BRUNKE, H., M. CHANG, AND C. STANFORD. 2003. Commodity profile: tomatoes, fresh. *Agricultural Issues Center*, University of California.
- BUGG, R. L., AND J. D. DUTCHER. 1989. Warm-season cover crops for pecan orchards: horticultural and entomological implications. *Biol. Agric. Hort.* 6: 123-148.
- CHAPIN, J. W., J. S. THOMAS, S. M. GRAY, D. M. SMITH, AND S. E. HALBERT. 2001. Seasonal abundance of aphids (Homoptera: Aphididae) in wheat and their role as *Barley yellow dwarf virus* vectors in the South Carolina coastal plain. *J. Econ. Entomol.* 94: 410-421.
- DIAZ, R., A. KNUTSON, AND J. S. BERNAL. 2004. Effect of the red imported fire ant on cotton aphid populations and predation of bollworm and beat armyworm eggs. *J. Econ. Entomol.* 97: 222-229.
- DIXON, A. F. G. 1977. Aphid ecology: life cycles, polymorphisms, and population dynamics. *Annu. Rev. Ecol. Syst.*
- DUSI, A. D., D. PETERS, AND W. VAN DAR WERF. 2000. Measuring and modeling the effects of inoculation date and aphid flights on the secondary spread of *Beet mosaic virus* in sugar beat. *Ann. Appl. Biol.* 76: 131-146.
- EDWARDSON, J. R., AND R. G. CHRISTIE. 1991. Cucumoviruses, pp. 293-319 *In* CRC Handbook of Viruses Infecting Legumes. CRC Press, Boca Raton, FL.
- EUBANKS, M. D., S. A. BLACKWELL, C. J. PARRISH, Z. D. DELAMAR, AND H. HULL-SANDERS. 2002. Intraguild predation of beneficial arthropods by red imported fire ants in cotton. *Environ. Entomol.* 31: 1168-1174.
- EUBANKS, M. D. 2001. Estimates of the direct and indirect effects of red imported fire ants on biological control in field crops. *Biol. Contr.* 21: 35-43.
- FABRE, F., C. A. DEDRYVER, J. L. LETERRIER, AND M. PLANTEGENEST. 2003. Aphid abundance on cereals in autumn predicts yield losses caused by *Barley yellow dwarf virus*. *Phytopathology* 93: 1217-1222.
- FULLER, B. W., AND T. E. REAGAN. 1988. Comparative predation of the sugarcane borer (Lepidoptera: Pyralidae) on sweet sorghum and sugarcane. *J. Econ. Entomol.* 81: 713-717.
- HARVEY, C. T., AND M. D. EUBANKS. 2004. Effect of habitat complexity on biological control by the red imported fire ant (Hymenoptera: Formicidae) in collards. *Biol. Contr.* 29: 348-358.
- HARVEY, C. T., AND M. D. EUBANKS. 2005. Intraguild predation of parasitoids by *Solenopsis invicta* (Hymenoptera: Formicidae): a non-disruptive interaction. *Entomol. Exp. Appl.* 114: 127-135.
- HELMS, K. R., AND S. B. VINSON. 2002. Widespread association of the invasive ant *Solenopsis invicta* with an invasive mealybug. *Ecology*. 83: 2425-2438.
- HODGSON, C. 1991. The dispersal of apterous aphids (Homoptera: Aphididae) from their host plants and its significance. *Bull. Entomol. Res.* 81: 417-427.
- HOLWAY, D. A., L. LACH, A. V. SUARES, N. D. TSUTSUI, AND T. J. CASE. 2002. The causes and consequences of ant invasions. *Annu. Rev. Ecol. Syst.* 33: 181-233.
- HU, G. Y. AND J. H. FRANK. 1996. Effect of red imported fire ant (Hymenoptera: Formicidae) on dung-inhabiting arthropods in Florida. *Environ. Entomol.* 25: 1290-1296.
- HULL, R. 2002. *Mathews Plant Virology*. Academic Press, John Innes Center, Norwich, U.K.
- JEGER, M. J., J. HOLT, F. VAN DEN BOSCH, AND L. V. MADDEN. 2004. Epidemiology of insect-transmitted plant viruses: modeling disease dynamics and control interventions. *Physiol. Entomol.* 29: 229-304.
- JONES, D., AND W. L. STERLING. 1979. Manipulation of red imported fire ants (*Solenopsis invicta*) in a trap crop for boll weevil (*Anthonomus grandis*) suppression. *Environ. Entomol.* 8: 1073-1077.
- JORDÁ, C., A. ALFARO, M. A. ARANDA, E. MORIONES, AND F. GARCIA-ARENAL. 1992. Epidemic of *Cucumber mosaic virus* plus satellite RNA in tomatoes in Eastern Spain. *Plant Dis.* 76: 363-366.
- KAPER, J. M., D. GALLITELLI, AND M. E. TOUSIGNANT. 1990. Identification of a 334-ribonucleotide viral satellite as principal aetiologiocal agent in a tomato necrosis epidemic. *Res. Virol.* 141: 81-95.
- KAPLAN, I., AND M. D. EUBANKS. 2002. Disruption of cotton aphid (Homoptera: Aphididae) natural enemy dynamics by red imported fire ants (Hymenoptera: Formicidae). *Environ. Entomol.* 31: 1175-1183.
- KAPLAN, I., AND M. D. EUBANKS. 2005. Aphids alter the community-wide impact of fire ants. *Ecology*. 86: 1640-1649.
- KEMBLE, J. M., T. W. TYSON, AND L. M. CURTIS. 2004. *Guide to Commercial Staked Tomato Production in Alabama*. Alabama Cooperative Extension System ANR-1156.
- KHATTEE, R., AND D. N. NAIK. 1999. *Applied multivariate statistics with SAS software*, second ed. SAS Institute Inc, Cary, NC.
- LEE, J. S., J. JOHNSON, AND V. L. WRIGHT. 1990. Quantitative survivorship analysis of the velvetbean caterpillar (Lepidoptera: Noctuidae) pupae in soybean fields in Louisiana. *Environ. Entomol.* 19: 978-986.
- LOWERY, D. T., AND G. BOITEAU. 1988. Effects of five insecticides on the probing, walking, and settling behavior of the green peach aphid and the buckthorn aphid (Homoptera: Aphidae) on potato. *J. Econ. Entomol.* 81: 208-214.
- MACKAY, W. P., AND R. FAGERLUND. 1997. Range expansion of the red imported fire ant, *Solenopsis in-*

- victa* Buren (Hymenoptera: Formicidae), into New Mexico and extreme western Texas. Proc. Entomol. Soc. Washington. 99: 757-758.
- MADDEN, L. V., M. J. JEGER, AND F. VAN DEN BOSCH. 2000. A theoretical assessment of the effects of vector-virus transmission mechanism on plant virus disease epidemics. Phytopathology 90: 576-593.
- MICHAUD, J. P., AND H. W. BROWNING. 1999. Seasonal abundance of the brown citrus aphid *Toxoptera citricida*, (Homoptera: Aphidae) and its natural enemies in Puerto Rico. Florida Entomol. 82: 424-447.
- MULLER, C. B., I. S. WILLIAMS, AND J. HARDIE. 2001. The role of nutrition, crowding, and interspecific interactions in the development of winged aphids. Ecol. Entomol. 26: 330-340.
- NAULT, B. A., AND J. SPEESE III. 2002. Major insect pests and economics of fresh-market tomato in eastern Virginia. Crop Prot. 21: 359-366.
- PALUKAITIS, P., M. J. ROOSSINCK, R. G. DIETZGEN, AND R. I. B. FRANCKI. 1992. *Cucumber mosaic virus*. Adv. Virus Res. 41: 282-348.
- PERRING, T. M., N. M. GRUENHAGEN, AND C. A. FARRAR. 1999. Management of plant viral diseases through chemical control of vectors. Annu. Rev. Entomol. 44: 457-481.
- POWER, A. G., A. J. SEAMAN, AND S. M. GRAY. 1991. Aphid transmission of *Barley yellow dwarf virus*—inoculation access periods and epidemiologic implications. Phytopathology 81: 541-548.
- QUEIROZ, J. M., AND P. S. OLIVEIRA. 2001. Tending ants protect honeydew-producing whiteflies (Homoptera: Aleyrodidae). Environ. Entomol. 30: 295-297.
- REILLY, J. J., AND W. L. STERLING. 1983a. Dispersion patterns of the red imported fire ant (Hymenoptera: Formicidae), aphids, and some predaceous insects in east Texas cotton fields. Environ. Entomol. 12: 380-385.
- REILLY, J. J., AND W. L. STERLING. 1983b. Interspecific association between the red imported fire ant (Hymenoptera: Formicidae), aphids, and some predaceous insects in east Texas cotton fields. Environ. Entomol. 12: 541-545.
- SIKORA, E. J., R. T. GUDAUSKAS, J. F. MURPHY, D. W. PORCH, M. ADRIANIFAHANANA, G. W. ZHENDER, E. M. BAUSKE, J. M. KEMBLE, AND D. F. LESTER. 1998. A multivirus epidemic of tomatoes in Alabama. Plant Dis. 82: 117-120.
- STERLING, W. L. 1978. Fortuitous biological suppression of the boll weevil by the red imported fire ant. Environ. Entomol. 7: 564-568.
- STYRSKY, J. D., I. KAPLAN, AND M. D. EUBANKS. 2006. Plant trichomes indirectly enhance predation by a generalist predator, the red imported fire ant. Biol. Contr. 36: 375-384.
- TOMLINSON, J. A. 1987. Epidemiology and control of virus diseases of vegetables. Ann. Appl. Biol. 110: 661-681.
- VALLES, S. M., AND P. G. KOEHLER. 1997. Insecticides used in the urban environment: mode of action. Florida Cooperative Extension Services, Institute of Food and Agricultural Sciences, University of Florida, ENY282.
- VINSON, S. B. 1997. Invasion of the red imported fire ant (Hymenoptera: Formicidae): spread, biology, and impact. Am. Entomol. 42: 23-39.
- VOGT, J. T., R. A. GRANTHAM, W. A. SMITH, AND D. C. ARNOLD. 2001. Prey of the red imported fire ant (Hymenoptera: Formicidae) in Oklahoma peanuts. Environ. Entomol. 30: 123-128.