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Estimates of the Direct and Indirect Effects of Red Imported Fire Ants on Biological Control in Field Crops

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Red imported fire ants, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), are usually considered serious pests. *S. invicta* workers, however, are voracious predators and are frequently among the most abundant predators in agroecosystems within their range. Unfortunately, fire ant workers may also attack beneficial insects and arthropods. The goal of this study was to quantify the relationship between the abundance of fire ant workers and the abundance of insect pests and their natural enemies in cotton and soybean. In addition, I used path analysis to estimate the direct and indirect effects (potential loss of pest control due to suppression of other natural enemies) of fire ants. Densities of *S. invicta* workers were negatively associated with all 16 herbivore taxa sampled in cotton and 13 of the 16 herbivore taxa sampled in soybean. These data suggest that red imported fire ants are important predators of the major insect pests of these crops. The abundance of fire ants, however, was also negatively correlated with the densities of 22 of 24 natural enemy taxa in cotton and 14 of 16 natural enemy taxa in soybean. It appears that fire ants are significant intraguild predators of some of the most important biological control agents in these crops. These indirect interactions were often complex because fire ants not only suppressed populations of beneficial natural enemies (i.e., natural enemies that had negative impacts on pest populations), but also suppressed natural enemies that interfered with biological control (i.e., intraguild predators that had net positive effects on pest populations). Detailed experimental work is needed to determine whether the benefits of pest suppression by fire ants outweigh the negative impact of fire ants on natural enemies. © 2001 Academic Press

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INTRODUCTION

Red imported fire ants, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), are serious pests in the southern United States and are expanding their range westward and northward (MacKay and Fagerlund, 1997; Vinson, 1997; Anonymous, 1999). These ants are pests because they are aggressive, have a painful and often allergenic sting, reach extremely high densities, and have large, unsightly mounds (Adams, 1986; Vinson, 1997). Red imported fire ants, however, can be beneficial. *S. invicta* workers are voracious consumers of arthropods and are among the most active and abundant predators in many crops. Red imported fire ants have been reported as ecologically and economically significant predators of a wide variety of insects, including boll weevils in cotton (Sterling, 1978; Jones and Sterling, 1979), sugarcane borer in sugarcane (Negm and Hensley, 1967; Reagan *et al.*, 1972; Bessin and Reagan, 1993), horn flies in manure piles (Lemke and Kissam, 1988; Hu and Frank, 1996), velvetbean caterpillar larvae in soybeans (Lee *et al.*, 1990), and whiteflies in greenhouses (Morrill, 1977). In addition, several Texas studies suggested that red imported fire ants do not interfere with other economically important predators in cotton (Sterling *et al.*, 1979; Reilly and Sterling, 1983a,b). As a consequence, many growers within the southeastern United States regard fire ants as important beneficial insects.

Some studies, however, raise questions about the beneficial impact of red imported fire ants and suggest that benefits of *S. invicta* are inconsistent and difficult to predict (Vinson, 1994). Factors such as plant size, season, soil moisture, geography, and insecticide use can reduce the relative efficacy of fire ants as biological control agents (Negm and Hensley, 1967, 1969; Sterling, 1978; Sturm and Sterling, 1990; Sturm *et al.*, 1990). In addition, follow-up studies in sugarcane have

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questioned the conclusion of earlier studies that fire ants were key predators of the sugarcane borer (Negm and Hensley, 1969; Adams *et al.*, 1981).

Most importantly, red imported fire ant workers are relatively indiscriminant, omnivorous predators that attack beneficial insects in addition to pest species (Wilson and Oliver, 1969; Ricks and Vinson, 1970; Morrill, 1977; Lee *et al.*, 1990; Vinson, 1994). Red imported fire ant workers attack predators of horn flies and other pests in pastures (Hu and Frank, 1996) and predators of aphids and scales in the pecan agroecosystem (Bugg and Dutcher, 1989; Tedders *et al.*, 1990; Dutcher, 1998). There are also indications that red imported fire ants decrease the efficacy of parasitic wasps as biological control agents, primarily by consuming wasp larvae and pupae (Lopez, 1982; Sturm *et al.*, 1990; Vinson and Scarborough, 1991; Vinson, 1994).

Understanding the impact of red imported fire ants on biological control is essential to develop effective integrated pest management strategies in areas currently infested with fire ants. This information is also critical if we are to predict the impact of fire ants on agroecosystems as this invasive species expands its range in California and other key agricultural states. The goal of this study was to document the impact of red imported fire ants on insect pests and beneficial arthropods in cotton and soybean. By documenting the impact of *S. invicta* on both pests and beneficials, we can begin to partition the impact of fire ants on pests into direct effects (direct predation) and indirect effects (potential loss of biological control as a result of suppression of beneficial insects by fire ants). To address this goal, I asked three related questions in each crop: (1) what is the relative impact of red imported fire ants on pests (herbivorous insects)? (2) what is the relative impact of red imported fire ants on natural enemies? and (3) what are the relative strengths of the direct and indirect effects of red imported fire ants on biological control of insect pests?

MATERIALS AND METHODS

Field Data

Twelve 0.4-ha plots of cotton were randomly selected within three cotton fields (>20 ha each) at the E. V. Smith Substation of the Alabama Agricultural Experiment Station at Shorter, Alabama. Twelve 1.2-ha plots of soybean were randomly selected for the study within two large soybean fields (>40 ha each) in Talladega County, Alabama (6 plots per large field). Soybean and cotton plots were selected such that plots were at least 100 m apart. The foliage of soybean and cotton plants was sampled approximately every other week throughout the 1999 growing season (May through September). Foliage was sampled with a 40-cm-diameter sweep net (3 samples per plot of cotton, 9 samples per plot of soybean, 25 sweeps per sample in both crops). Samples were returned to the laboratory and arthropods were identified and counted. With the exception of tarnished plant bugs, *Lygus lineolaris* (Palisot de Beauvois), herbivorous insects were not identified to species but rather placed in a pest "group." For example, all foliage-feeding caterpillars were lumped into the "lepidopteran larvae" group. Most other groups represent family taxa (e.g., mirids (minus tarnished plant bugs), aphids, weevils, etc.). I split the nymphs/larvae and adults of a few taxa into separate groups because I hypothesized that red imported fire ants might impact young and adults of these animals differently. Most of the beneficial insects were identified to species, and young and adults of these insects were also considered separately in the analyses.

Statistical Analyses

All data were transformed (log $(n + 1)$) prior to the following analyses (Sokal and Rohlf, 1995). To quantify the relationship between red imported fire ants and insects and other arthropods in cotton and soybean, I regressed the density of fire ant workers foraging on plants on the density of each herbivore taxa and each natural enemy taxa for both crops.

I used path analysis to quantify the direct and indirect interactions among red imported fire ants, insect pests, and other natural enemies. Path analysis is a powerful statistical tool that was developed to help interpret observational data (Wright, 1920; Li, 1975; Sokal and Rohlf, 1995). In this study, path analysis was used to estimate the effectiveness of fire ants as biological control agents as constrained by the negative impact of these ants on other natural enemies. In a path model there are independent variables (the causal factors) and a dependent variable (the response variable). Because independent variables are frequently correlated, an independent variable can indirectly change a dependent variable as a result of its influence on additional independent variables. This is an indirect effect. One can follow a chain of causality from the independent, causal variable, through the intermediate independent variable, to the response variable.

Path coefficients quantify the strength of each direct effect on the response variable. A path coefficient is a standardized partial regression coefficient and is a statistical estimate of the change expected in the response variable for a given change in the causal variable (Li, 1975; Sokal and Rohlf, 1995). Because path coefficients are standardized, they represent a change in the response variable in standard deviation units for a one-standard-deviation increase in the causal variable. When the path of causality goes from a background variable through one or more intermediate variables and then on to the response variable, the net effect of

TABLE 1

The Effect of Red Imported Fire Ants on Herbivorous Insects in Cotton and Soybean

	Cotton			Soybean		
Herbivore taxa	Slope	R^2	*df*	Slope	R^2	*df*
Lepidopteran larvae	−0.38	0.27***	94	−0.50	0.03^{ns}	128
Tarnished plant bugs	−0.41	0.28***	115	−0.50	0.68***	28
Mirids	−0.38	0.30***	111	−0.47	0.21**	59
Aphids	−1.07	0.19***	110		Not estimable	
Stink bugs	−0.12	0.19***	88	−0.44	0.41***	25
Leafhopper adults	−0.21	0.05**	175	−0.29	0.05**	121
Leafhopper nymphs		Not estimable		−0.57	0.34***	23
Treehopper adults	−0.11	0.10***	87	−0.38	0.03*	94
Treehopper nymphs		Not estimable		−0.61	0.40***	34
Froghoppers	−0.08	0.05*	86	−0.27	0.27*	23
Stainers	−0.12	0.19***	88	−0.71	0.54***	40
Cucumber beetles	−0.38	0.30***	111	−0.47	0.21***	59
Flea beetles	−0.29	0.26***	98	−0.09	0.006^{ns}	89
Leaf beetles	−0.28	0.19***	94	−0.72	0.46***	74
Weevils	−0.28	0.12**	95	−0.50	0.40***	51
Scarab/chafer beetles	−0.28	0.06*	85	−0.59	0.28**	23
Click beetles	−0.16	0.11**	89		Not estimable	
Grasshoppers/crickets	−0.26	0.12***	143	0.18	0.02^{ns}	145

Note. Regression results (slope estimate, R^2, and total degrees of freedom) are given for both crops.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
ns Nonsignificant.

that background variable on the response is estimated as a compound path coefficient. A compound path coefficient is the product of all coefficients along a pathway. If more than one pathway connects background and response variables, then the compound path coefficients are summed to estimate the entire effect coefficient (Li, 1975; Sokal and Rohlf, 1995).

RESULTS

Impact of Red Imported Fire Ants on Pests

S. invicta abundance was negatively correlated with all 16 herbivore taxa sampled in cotton and 13 of the 16 herbivore taxa sampled in soybean (Table 1). Only the abundance of lepidopteran larvae, flea beetles, and grasshoppers and crickets were unrelated to the density of foraging fire ants in soybean. The abundance of 11 herbivore taxa was negatively correlated with fire ant density in both crops (Table 1).

Impact of Red Imported Fire Ants on Natural Enemies

The abundance of fire ants on plants was negatively correlated with the densities of 22 of 24 natural enemy taxa sampled in cotton and 14 of 16 natural enemy taxa sampled in soybean (Table 2). In cotton, only *Stethorus* spp., ladybeetles, and syrphid larvae were not inversely correlated with fire ant abundance (these two predator taxa were not collected in soybeans) (Table 2). In soybean, the densities of adult big-eyed bugs (*Geocoris punctipes* (Say)) and spiders were not significantly correlated with fire ant density, even though their abundance was negatively affected by fire ants in cotton.

Assessing the Direct and Indirect Impacts of Red Imported Fire Ants on Biological Control

To fully assess the direct and indirect impact of *S. invicta* on the biological control of all herbivores collected during the study, a separate path analysis would have to be constructed for each herbivore taxon collected in cotton and each herbivore taxon collected in soybean (32 distinct analyses). To simplify and focus the analyses, I calculated path models for the five most economically important and abundant herbivore taxa: lepidopteran larvae (primarily *Helicoverpa zea* (Boddie) and *Spodoptera* spp. in cotton and *Plathypena scabra* (Fabricus), *Anticarsia gemmatalis* Hubner, *Pseudoplusia includens* (Walker), and *Trichoplusia ni* (Hubner) in soybean), tarnished plant bugs, other mirids (primarily *Neurocolpus nubilus* Reuter and *Psallus seraltus* Reuter), aphids (primarily *Aphis gossypii* Glover), and stinkbugs (*Nezara viridula* (Linnaeus), *Acrosternum hilare* (Say), and *Euschistus servus* (Say)). I calculated a separate path analysis for

TABLE 2

The Effect of Red Imported Fire Ants on Natural Enemies in Cotton and Soybean

	Cotton			Soybean		
Natural enemy taxa	Slope	R^2	*df*	Slope	R^2	*df*
Geocoris punctipes adults	−0.49	0.29***	160	0.07	0.004^{ns}	100
Geocoris punctipes nymphs	−0.36	0.27***	119	−0.60	0.35***	50
Spiders	−0.25	0.11***	158	−0.17	0.01^{ns}	124
Scymnus ladybeetle adults	−0.37	0.20***	137	−0.51	0.40***	44
Scymnus ladybeetle larvae	−0.26	0.29***	92		Not estimable	
Orius spp.	−0.40	0.20***	118	−0.67	0.45***	65
Damsel bugs	−0.28	0.04*	110	−0.35	0.12**	68
Harmonia axyridis adults	−0.32	0.22***	117	−0.57	0.63***	36
Harmonia axyridis larvae	−0.37	0.22***	98		Not estimable	
Hippodamia convergens adults	−0.25	0.25***	95	−0.31	0.44**	23
Hippodamia convergens larvae	−0.44	0.24***	103		Not estimable	
Stethorus ladybeetles	−0.04	0.005^{ns}	86		Not estimable	
Coccinella septempunctata adults	−0.22	0.18***	92	−0.60	0.70***	32
Coccinella septempunctata larvae	−0.34	0.30***	106	−0.31	0.42**	23
Coleomegilla maculata	−0.41	0.31***	98	−0.50	0.50***	28
Wasps	−0.25	0.18***	94	−0.47	0.52**	32
Ground beetles	−0.28	0.39***	100	−0.48	0.39***	33
Hemerobius and *Micromus* spp.	−0.19	0.20***	91		Not estimable	
Chrysoperla rufilabris adults	−0.09	0.08**	86		Not estimable	
Chrysoperla rufilabris larvae	−0.19	0.15**	90		Not estimable	
Assassin bugs	−0.10	0.11**	88	−0.73	0.62***	35
Rove beetles	−0.09	0.15***	87	−0.31	0.31**	23
Notoxus spp.	−0.34	0.30***	114	−0.52	0.55***	26
Syrphid larvae	0.0001	0.00^{ns}	84		Not estimable	

Note. Regression results (slope estimate, R^2, and total degrees of freedom) are given for both crops.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
ns Nonsignificant.

each herbivore taxon in each crop, except for aphids because they were collected only in cotton.

Figure 1 illustrates the path model for the direct and indirect effects of red imported fire ants on lepidopteran larvae in cotton. The analysis indicated that red imported fire ants were one of eight natural enemy taxa that had a significant affect on the abundance of lepidopteran larvae. Specifically, the analysis indicated that fire ants were the second most important biological control agent of lepidopteran larvae (−0.15). That is, a one-standard-deviation increase in the number of fire ants on cotton plants would result in a 0.15-standard-deviation decrease in the density of lepidopteran larvae. Only adult *Scymnus* spp. ladybeetles had a larger, negative impact on caterpillar abundance (−0.18). However, the path model suggested that red imported fire ants suppressed the abundance of other statistically important natural enemies. Several of these natural enemies, adult *Scymnus* spp., ladybeetles, big-eyed bug nymphs, brown lacewings (*Hemerobius* spp. and *Micromus* spp.), and seven-spotted ladybeetle (*Coccinella septempunctata* Linnaeus), significantly reduced the abundance of lepidopteran larvae in cotton. Thus, a reduction in their numbers by *S. invicta* interferes with biological control and provides an indirect benefit to lepidopteran larvae. Some natural enemies, however, seem to have a positive impact on the abundance of lepidopteran larvae. Increases in the abundance of spiders (+0.17), ground beetles (+0.12), and assassin bugs (+0.10) were all associated with significant increases in lepidopteran larvae. These natural enemies had positive effects on the abundance of lepidopteran larvae because their abundance was inversely correlated with the abundance of other natural enemies such as *Scymnus* spp., ladybeetles, and big-eyed bug nymphs (unpublished analyses). Thus, a reduction in the numbers of spiders, ground beetles, and assassin bugs by fire ants indirectly reduces the size of caterpillar populations. Even though *S. invicta* appears to have a strong, direct, negative effect on lepidopteran larvae (−0.15), the indirect effects of fire ants essentially cancelled out the direct effect.

The path analysis of the effects of fire ants on lepidopteran larvae in soybean suggested that fire ants have a weak and nonsignificant direct effect on lepidopteran larvae (+0.02) (Fig. 2). This was not surprising since fire ant abundance and caterpillar abundance

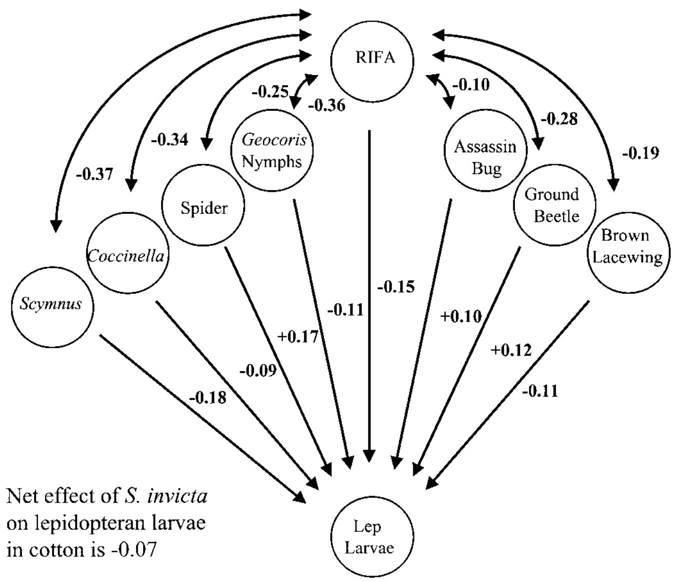

FIG. 1. Path analysis model of the direct and indirect effects of red imported fire ants (RIFA) on lepidopteran larvae in cotton. Single-headed arrows indicate direct effects of natural enemies on caterpillar abundance. Path coefficients in standard deviation units accompany these arrows. Double-headed arrows indicate interactions among natural enemies and are accompanied by the appropriate regression coefficients. Fire ants suppressed densities of lepidopteran larvae and other important natural enemies that affected lepidopteran larvae abundance: *Scymnus* ladybeetles, *Coccinella septempunctata* ladybeetles, spiders, *Geocoris* nymphs, assassin bugs, ground beetles, and brown lacewings.

were not significantly related in the simple regression analysis (Table 1). The path analysis further suggested that only two natural enemies significantly impacted caterpillar abundance in soybeans. Big-eyed bug nymphs had a negative effect (−0.13) and ground beetles had a positive impact (+0.15). The indirect effect of fire ants on lepidopteran larvae via the suppression of these two natural enemy taxa virtually eliminated their individual effects: the overall net effect of fire ants on caterpillar abundance in soybeans was a statistically insignificant +0.02.

Figure 3 illustrates the path model for the direct and indirect effects of red imported fire ants on tarnished plant bugs in cotton. Unexpectedly, the analysis indicated that the direct effect of fire ants on tarnished plant bugs was very weak, statistically insignificant, and positive (+0.01), even though the simple regression analysis indicated that there was a strong negative association between fire ants and tarnished plant bugs (Table 1). The direct effects of eight other natural enemies were statistically significant. Big-eyed bug nymphs (−0.10) and *Scymnus* ladybeetle larvae (−0.11) had direct negative effects on tarnished plant bug abundance. The remaining natural enemies all had positive effects on tarnished plant bugs. The effects of some of these natural enemies were large (e.g., convergent ladybeetle larvae, *Hippodamia convergens* Guerin-Meneville, had a +0.25 effect) (Fig. 3). However, because fire ants had large negative effects on all these natural enemies, most of the indirect effects of fire ants on tarnished plant bugs were negative. As a result, the overall net effect of fire ants on tarnished plant bug abundance was a relatively strong −0.22, suggesting that the powerful negative relationship indicated by the simple regression analysis (Table 1) is actually a result of indirect interactions.

The path analysis of the direct and indirect effects of fire ants on tarnished plant bug abundance in soybean indicated that fire ants had a huge, highly significant, direct negative effect on tarnished plant bug abundance (−0.72). The only other natural enemy that significantly affected the abundance of tarnished plant bugs in soybean was pink spotted ladybeetles (*Coleomegilla maculata* (DeGeer)). These beetles also had a relatively strong negative effect on tarnished plant bugs (−0.25). Although fire ants suppressed pink spotted ladybeetle abundance (Table 2) and, therefore, had a positive indirect effect on tarnished plant bug abundance (fire ants − pink spotted ladybeetles − tarnished plant bugs = +0.13), the overall net effect of fire ants on tarnished plant bug abundance in soybeans was −0.60.

Path analysis suggested that fire ants and antlike flower beetles (also called hooded beetles, *Notoxus* spp.) had relatively large, statistically significant, direct negative effects on mirid abundance (−0.46 for fire

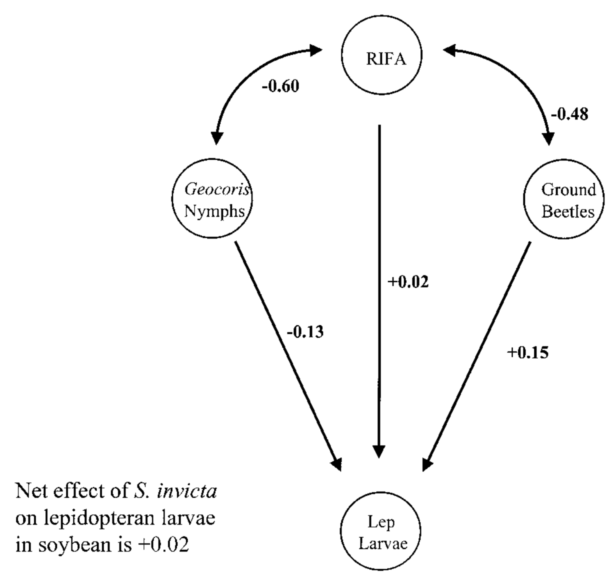

FIG. 2. Path analysis model of the direct and indirect effects of red imported fire ants (RIFA) on lepidopteran larvae in soybean. Single-headed arrows indicate direct effects of natural enemies on caterpillar abundance. Path coefficients in standard deviation units accompany these arrows. Double-headed arrows indicate interactions among natural enemies and are accompanied by the appropriate regression coefficients. Fire ants suppressed densities of lepidopteran larvae and *Geocoris* nymphs and ground beetles that also affected lepidopteran larvae abundance.

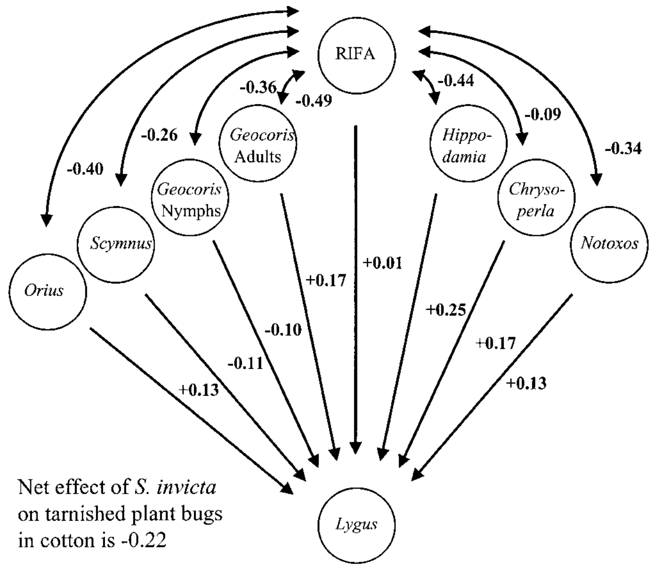

FIG. 3. Path analysis model of the direct and indirect effects of red imported fire ants (RIFA) on tarnished plant bugs in cotton. Single-headed arrows indicate direct effects of natural enemies on caterpillar abundance. Path coefficients in standard deviation units accompany these arrows. Double-headed arrows indicate interactions among natural enemies and are accompanied by the appropriate regression coefficients. Fire ants suppressed densities of tarnished plant bugs (*Lygus lineolaris*) and other important natural enemies that affected *L. lineolaris* abundance: *Orius* spp., *Scymnus* spp. ladybeetles, *Coccinella septempunctata* ladybeetles, *Geocoris punctipes* nymphs, *Geocoris punctipes* adults, *Hippodamia convergens* ladybeetles, *Chrysoperla rufilabris*, and *Notoxos* spp.

ants and −0.44 for antlike flower beetles). Fire ants, however, did suppress numbers of antlike flower beetles (Table 2), resulting in a positive indirect effect on mirid abundance (fire ant − antlike flower beetle − mirid indirect effect = +0.15). The overall net effect of fire ants on mirids, however, was still a relatively large −0.31.

The path analysis for the effects of fire ants on mirids in soybean was relatively straightforward. The analysis indicated that fire ants and big-eyed bug nymphs were the only natural enemies that significantly influenced mirid population size in this crop. Fire ants had a −0.21 direct effect and big-eyed bug nymphs had a −0.27 direct effect on mirid abundance. Again, the indirect effect of fire ants on mirids was positive (fire ants − bigeyed bug nymphs − mirids = +0.16), but the overall net effect of fire ants on mirids in soybean was still negative, although relatively small (−0.05).

Fire ants had a statistically significant, direct, negative effect on aphid abundance (−0.13). Big-eyed bug nymphs (−0.28) and seven-spotted ladybeetle larvae (−0.19) also had large, statistically significant, negative effects on aphids. Convergent ladybeetle larvae (+0.37) and green lacewing larvae (*Chrysoperla rufilabris* (Burmeister)) (+0.25) had large, statistically significant, positive effects on aphid populations. Because fire ants suppressed the densities of convergent ladybeetle and green lacewing larvae, fire ants had a relatively large overall net effect of −0.17.

The path analysis of the direct and indirect effects of fire ants on stinkbug abundance in cotton suggested that fire ants were the only natural enemy that significantly affected the abundance of this pest (−0.58). Because none of the other natural enemies had a statistically significant effect on stinkbugs, the overall net effect of fire ants on stinkbug densities is equal to the direct effect (−0.58).

The path analysis of the effects of fire ants on stinkbugs in soybean suggested that fire ants and adult seven-spotted ladybeetles significantly affected stinkbug abundance. Fire ants had a large negative direct effect on stinkbugs (−0.55) as did seven-spotted ladybeetle adults (−0.28). Because fire ants suppressed the abundance of seven-spotted ladybeetle adults (Table 2), the total net effect of fire ants on stinkbugs was less than the direct effect, but substantial (−0.38).

DISCUSSION

Red Imported Fire Ants as Biological Control Agents

Although correlative in nature, this study strongly suggests that red imported fire ants suppress the densities of many herbivorous insects, including some of the most important economic pests of cotton and soybean. Red imported fire ants were the third most abundant natural enemy in cotton and their abundance was negatively associated with the abundance of all 16 herbivore taxa collected in this crop (Table 1). Several of these herbivores, including lepidopteran larvae, tarnished plant bugs, and stinkbugs, are serious pests of cotton. Fire ants may maintain several of these pests below action thresholds and provide real economic benefits to growers. For example, if we examine the relationship between fire ant and bollworm/armyworm abundance in cotton (Fig. 4), we see that 11 of the 13 samples with no fire ants were above the action threshold. In contrast, only 1 of the 43 samples that contained fire ants also contained caterpillar densities above the action threshold. These results are consistent with other studies demonstrating that fire ants are economically important predators of insect pests in cotton (Sterling, 1978; Jones and Sterling, 1979; Sturm *et al.*, 1990).

Likewise, there was strong evidence that red imported fire ants suppressed populations of soybean pests. *S. invicta* abundance was negatively correlated with the abundance of 13 of the 16 herbivore taxa collected in soybean (Table 1). Affected herbivores included some of the most important pests of soybean in the southeastern United States, including stinkbugs and treehoppers (threecornered alfalfa hopper, *Spissistilus festinus* (Say)). Fire ants, however, did not have a

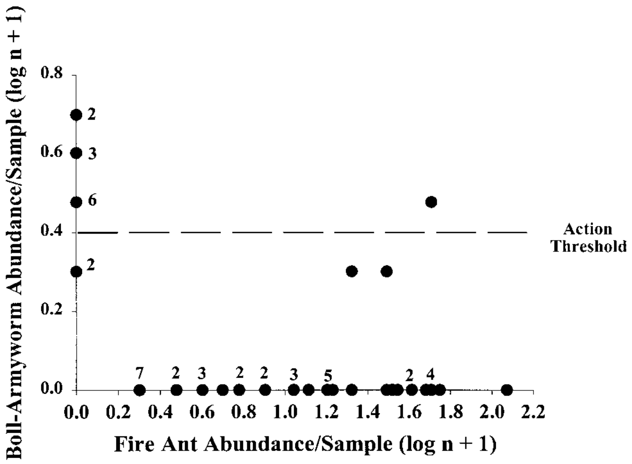

FIG. 4. Relationship between the abundance of red imported fire ants and bollworms (*Helicoverpa zea*) and armyworms (*Spodoptera* spp.) in cotton. The number beside each circle denotes the number of samples represented by that circle. Circles without numbers represent single samples. The action threshold is indicated by the dashed line.

significant effect on the abundance of lepidopteran larvae (Table 1). There was a general trend between increasing fire ant abundance and decreasing caterpillar abundance, but caterpillar abundance was highly variable. Some caterpillar species may be more susceptible to fire ant predation than others and seasonal variation in the abundance/mixture of caterpillar species may underlie variation in fire ant impact.

Red Imported Fire Ants as Intraguild Predators

Intraguild predation occurs when one species in the natural enemy guild consumes another member of the natural enemy guild (Polis *et al.*, 1989; Rosenheim *et al.*, 1995). The results of this study suggest that intraguild predation involving red imported fire ants is widespread in cotton and soybeans. The abundance of fire ants on plants was negatively correlated with the densities of 22 of 24 natural enemy taxa found in cotton and 14 of 16 natural enemy taxa found in soybean (Table 2). These results are consistent with studies conducted in pasture and pecan agroecosystems that report significant levels of predation on other natural enemies by *S. invicta* workers (Bugg and Dutcher, 1989; Tedders *et al.*, 1990; Hu and Frank, 1996; Dutcher, 1998). Most studies of fire ants in cotton assert that fire ants do not interfere with other biological control agents (but see Lopez, 1982 and Vinson and Scarborough, 1989). For example, Sterling *et al.* (1979) suggested that most predator taxa were unaffected by the removal of fire ants and Reilly and Sterling (1983b) found no evidence of negative interactions between fire ants and other predators when they examined predator distributions within cotton fields. I believe that a more thorough examination of the impact of fire ants in other systems (Vinson, 1994) combined with the results of this study indicate that fire ants are major intraguild predators.

Indirect Effects of Fire Ants on Biological Control

Path analyses suggested that the impact of red imported fire ants on pests was mediated by relatively complex indirect interactions. These interactions were complex because fire ants suppressed populations of beneficial natural enemies that reduced pest populations and those of natural enemies that ultimately increased pest populations. For example, path analysis revealed that fire ants were one of eight important natural enemies of lepidopteran larvae in cotton (Fig. 1). However, the analysis also revealed that fire ants suppressed the abundance of all the other important predators. In some cases the indirect effect of fire ants relaxed predation pressure, positively affecting caterpillar abundance (e.g., fire ants − *Scymnus* ladybeetles − caterpillar indirect interaction). This result suggests that *Scymnus* ladybeetles are important predators of lepidopteran eggs or larvae. Fire ants, however, also suppressed the abundance of spiders, assassin bugs, and ground beetles that were positively associated with caterpillar abundance. These taxa have been identified by other studies as major intraguild predators (Shough, 1940; Sluss, 1967; Howell and Pienkowski, 1971; Nyffeler *et al.*, 1987a,b, 1992; Guillebeau and All, 1989, 1990; Rosenheim *et al.*, 1993, 1995; Snyder and Wise, 1999). Additional analyses indicated that the abundance of predators such as ladybeetles was inversely related to the abundance of spiders, assassin bugs, and ground beetles (M. D. Eubanks, unpublished data). Thus, I interpret the positive effects of spiders, assassin bugs, and ground beetles on caterpillar abundance as the ultimate effects of intraguild predation by these arthropods.

Some of the indirect interactions suggested by path analysis are harder to explain. An example is the path model of the effects of fire ants on tarnished plant bugs in cotton (Fig. 3). The analysis indicated that the direct effect of fire ants on tarnished plant bugs was weak, statistically insignificant, and positive (+0.02), even though the regression analysis indicated that there was a strong negative relationship between fire ants and tarnished plant bugs (Table 1). The direct effects of the other eight natural enemies were all statistically significant. Big-eyed bug nymphs (−0.10) and *Scymnus* ladybeetle larvae (−0.11) had negative effects on tarnished plant bug abundance. The remaining six natural enemies all had positive effects on tarnished plant bugs. The effects of some of these natural enemies were relatively large (e.g., convergent ladybeetle larvae had a +0.25 effect and green lacewings had a +0.17 effect) (Fig. 3). Because fire ants had large negative effects on all these natural enemies, most of the indirect effects of fire ants on tarnished plant bugs were negative and several were fairly large. As a result, the overall net effect of fire ants on tarnished plant bug abundance was a relatively strong −0.22. It is challenging to explain the positive effects of six natural enemies on tarnished plant bug abundance as the results of intraguild predation by these predators. Although many of these predators have been documented as intraguild predators (e.g., convergent ladybeetles and adult big-eyed bugs), it seems likely that several of these predators are tracking the same plant resources as tarnished plant bugs. Adult big-eyed bugs, minute pirate bugs, and antlike flower beetles consume pollen and nectar, and previous studies have shown that the density of flowers affects their abundance more than changes in prey density (Coll and Bottrell, 1991; Eubanks and Denno, 1999).

CONCLUSIONS AND FUTURE RESEARCH

The results of this study, although correlative in nature, support the conclusion that red imported fire ants are important predators of key pest species, but that red imported fire ants are also major intraguild predators. Manipulative experiments are needed to test the statistical models of complex trophic interactions involving red imported fire ants developed in this study. Because of the high densities of red imported fire ants in many parts of the United States and their continued range expansion into California and other key agricultural states, understanding the impact of fire ants on biological control is critical.

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