

Effect of habitat complexity on biological control by the red imported fire ant (Hymenoptera: Formicidae) in collards

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Abstract

A potentially important and understudied biological control agent in US agroecosystems is the red imported fire ant, *Solenopsis invicta* Buren. Red imported fire ants may be particularly important biological control agents because we can manipulate their abundance with changes in habitat complexity. The effect of habitat complexity on biological control by fire ants was determined using plots of collards intercropped with white clover (complex habitat) and simple collard monocrops. The most economically significant pests of collards are larvae of the diamondback moth (DBM), *Plutella xylostella* (L.). Predation of DBM larvae by fire ants was more rapid and efficient in the intercrop than the monocrop. Red imported fire ants were 23% less abundant in the intercrop than the monocrop, however, suggesting that fire ants had a greater per capita effect on DBM survival in the complex habitat. Red imported fire ant predation of DBM larvae was significantly affected by larval density. Red imported fire ants also reduced the survival of leaf beetles, another economically significant pest taxa, by 45%. Furthermore, collard leaf damage tended to be inversely related to fire ant density and fire ants were more effective at reducing crop damage in the complex intercrop. Our study indicates the ability of red imported fire ants to be effective biological control agents and suggests that increasing habitat complexity can enhance red imported fire ant efficacy and herbivore control.

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1. Introduction

Collards (*Brassica oleracea* L. Brassicaceae) and other crucifers (*Brassica* spp.) are economically important crops throughout the world, but to maintain their economic benefits effective pest management is essential. Globally, the most economically damaging pest of collards is the diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) (Biever et al., 1994; Talekar and Shelton, 1993). Diamondback moth is primarily controlled with conventional pesticides; however, massive use of these chemicals causes health and food safety hazards. Furthermore, DBM has rapidly evolved resistance to many of these

conventional products, as well as biological alternatives like the bacterial insecticide *Bacillus thuringiensis* Berliner (Bt) (Perez et al., 1997; Shelton et al., 1993). In addition, many pesticides that are effective against DBM will be removed from the market as a result of changes in pesticide regulations (Food Quality Protection Act, 1996). Firmer regulations on pesticides also affect the control of other economically important pests such as several species of leaf beetles (Coleoptera: Chrysomelidae) (Adams, 1991; Latheef and Ortiz, 1984). Therefore, integrated pest management (IPM) and biological control are essential for the control of collard pests, particularly DBM, and to maintain the economic viability of collards and other crucifers (Biever et al., 1994; Talekar and Shelton, 1993; Verkerk and Wright, 1996).

A potentially important and largely unstudied biological control agent in US agroecosystems is the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), henceforth referred to as fire ants.

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Fire ants are one of the most abundant and voracious generalist predators in the southern US (Reagan, 1986; Vinson, 1997) and many studies have identified them as potential biological control agents (e.g., Hu and Frank, 1996; Vogt et al., 2001; Way and Khoo, 1992). In particular, fire ants prey upon a variety of lepidopteran pest species in cotton and sugarcane (Ali et al., 1984; Bessin and Reagan, 1989; Eubanks, 2001). These studies suggest that fire ants may be important biological control agents in collards and other crucifers.

Fire ants could be particularly effective predators of collard pests because we may be able to manipulate their abundance. Fire ant species tend to be more abundant in agroecosystems with increased habitat complexity (Risch and Carroll, 1982; Way and Khoo, 1992). For example, the abundance of fire ants was greater in complex sugarcane habitats that included broad-leaf weeds than in simple, weed-free monocrops (Ali and Reagan, 1985; Ali et al., 1984). As a result, predation of herbivores was greater in the mixed crop, which reduced pest abundance (Ali et al., 1984). This is likely to be important for biological control by fire ants in collards and other crucifers, because they are often grown in complex, mixed cropping systems (Andow, 1991; Itulya et al., 1997). Habitat complexity in agroecosystems is usually created by allowing weeds to accumulate (Ali and Reagan, 1985; Ali et al., 1984; Schellhorn and Sork, 1997) or by intercropping with a secondary crop (Finch and Collier, 2000; Itulya et al., 1997; Smith and McSorley, 2000). In intercropping a secondary crop is planted around and between rows of a focal crop making this method more desirable because the secondary crop may also be harvested (Smith and McSorley, 2000).

Incorporating intercropping into crucifer IPM has reduced the abundance of many important pests (Endersby and Morgan, 1991; Latheef and Ortiz, 1984; Root, 1973; Talekar and Shelton, 1993). When compared with monocrops, crucifers intercropped with tomato (*Lycopersicon esculentum* Mill. Solanaceae), red and white clover (*Trifolium pratense* L. and *Trifolium repens* L. Fabaceae), and several herb species had significantly reduced populations of DBM (Åsman et al., 2001; Buranday and Raros, 1975; Endersby and Morgan, 1991).

The goal of our study was to assess how habitat complexity affects fire ant predation of DBM and other important defoliators and, in turn, to determine if fire ants affect collard damage and yield. To address this goal, we conducted a series of greenhouse and field experiments to answer five questions: (1) Do fire ants significantly reduce the survival of DBM larvae? (2) Does habitat complexity increase or decrease the effect of fire ants on DBM survival? (3) Does the density of DBM larvae affect the intensity of fire ant predation? (4) Does habitat complexity and fire ants affect the abun-

dance of other important defoliators? and (5) Do habitat complexity and fire ants interact to affect collard damage and yield?

2. Materials and methods

2.1. Effect of red imported fire ants on DBM survival in greenhouse mesocosms

The effect of fire ants on the survival of DBM larvae was quantified in a greenhouse mesocosm experiment using caged collard plants (var. Vates) and larvae from a laboratory colony. The laboratory colony was established and maintained on artificial diet following the procedures of Shelton and Collins (2000). Individual collard plants (7–10 leaf stage) were transplanted into 75 × 30 × 33 cm cages constructed with mosquito netting. Half the cages were connected to pans (53 × 43 cm × 13 cm) containing ca. 500 fire ant workers and a rounded shovel of mound material (and associated larvae) with 0.5 cm diameter plastic tubing (Eubanks et al., 2002). Remaining cages were left as controls. Inside edges of pans were coated with liquid Teflon to prevent ant escape. Fire ants were collected from the campus of Auburn University, Auburn, Alabama. Fire ants were allowed to forage in the cages for 12 h before plants were infested with DBM larvae. Two experiments were conducted with eight replicates each. In the first experiment 10 second- and third-instar larvae were randomly placed on each plant. In the second experiment seven fourth-instar larvae were randomly placed on each plant. Remaining larvae were counted after 9 h.

2.2. Effect of habitat complexity on red imported fire ant predation of DBM

To determine the effect of habitat complexity on fire ant predation of DBM, two field experiments were conducted at E.V. Smith Research and Experiment Center, Alabama Agricultural Experiment Station, Macon County, Alabama. In spring and fall 2001, collard plots (each ≈120 m²) were planted in two cropping systems to establish habitat complexity treatments. Ten plots were planted as a collard monocrop alongside (≈10 m apart) 10 corresponding plots planted as a collard-white clover intercrop. Each plot consisted of four rows of 25 collards (var. Vates; total 100 plants/plot). Collards were planted with 45 cm in row spacing and 90 cm between row spacing (Peet, 1991). White clover was planted in late fall 2000 to establish a healthy stand before collard planting.

To establish and maintain different fire ant abundances among collard plots, four plots in the monocrop and the corresponding plots in the intercrop were

treated with commercially available ant-specific bait (Amdro; 0.14 g/m²). The active ingredient in Amdro is hydramethylnon, comprising 0.73% of the bait. Hydramethylnon blocks the production of ATP, killing target ants by inhibiting energy production (Valles and Koehler, 1997). The remaining 99.27% of the bait consists of an inert, corn-grit granule treated with soybean oil, making it highly attractive to fire ants. The bait is readily picked up by foraging fire ants, leaves no residue in fields, and does not affect the survival of herbivores or other natural enemies (Eubanks et al., 2002; Hu and Frank, 1996). Amdro was applied to plots at the outset of each field season and re-applied approximately every 4 weeks to maintain fire ant suppression. Baited plots (low fire ants) were separated from controls (high fire ants) by at least 30 m. This generated a two-by-two factorial field experiment with cropping system (intercrop and monocrop) and fire ant abundance as the treatment effects.

To quantify fire ant abundance, pitfall traps (3/plot) were set for a 24-h period each week during both growing seasons. Pitfall traps consisted of a 266 ml cup seated in a 90 mm diameter PVC pipe coupling inserted flush with ground level. Each cup was filled with approximately 120 ml of ethylene glycol as an entrapment medium.

2.2.1. Field experiment one

In the first field experiment, the abundance of fire ants and DBM larvae were manipulated and the survival of DBM larvae was quantified over a short time period. On three dates in spring and in fall 2001, one, random collard plant in each of the 16 plots was manually cleaned of all arthropods and seven DBM larvae were randomly placed on each plant. Seven larvae were used because this represents a larval density at economic threshold (action threshold). An assorted combination of second-, third-, and fourth-instars was used to mimic the range of larvae observed in the field. Surviving larvae were counted at 24, 48, and 72 h. Any larvae that pupated or emerged as adults were counted as surviving.

2.2.2. Field experiment two

In the second field experiment only fire ant abundance was manipulated and the abundance of DBM larvae and other caterpillars was monitored over two field seasons. Caterpillar abundance was estimated via weekly, visual searches of collard plants. In spring 2001, 50 random plants/plot (total 500 plants) was searched from March 22 to April 10. As collards grew, searches were decreased to 25 plants/plot from April 19 to May 1 and then to 20 plants/plot from May 8 to June 13 (Mitchell et al., 1997a,b). In fall 2001, 15 plants/plot were visually searched weekly from October 10 to November 19.

2.3. Effect of DBM density on red imported fire ant predation

The greenhouse experiment and first field experiment (detailed above) were conducted with high DBM densities. Because DBM larval densities do not always reach high levels (economic threshold) in the field, an additional experiment was conducted to determine if the density of DBM larvae affects the rate of predation by fire ants. In particular, we wanted to determine if fire ants were effective predators at relatively low DBM densities. In spring 2002, five plots (each ≈120 m²) were planted as a collard-white clover intercrop alongside five corresponding plots of collard monocrop at E.V. Smith Research and Experiment Center. Each plot consisted of four rows of 15 collards (var. Georgia) for a total of 60 plants/plot. Fire ant treatments were established with Amdro using the same procedures as 2001. Baited and control plots were separated by at least 15 m. All arthropods were removed from four randomly selected collard plants per plot. Two third-instar DBM larvae were randomly placed on two of those plants and seven third-instar DBM larvae were randomly placed on the other two plants. Remaining larvae were counted after 24 h.

2.4. Effect of habitat complexity and red imported fire ants on leaf beetle abundance

Leaf beetle abundance was monitored during the execution of the second field experiment. Leaf beetles are highly mobile, either flying or jumping (Alticinae) between plants, and were easily disturbed during visual searches, making assessment of their numbers difficult with this technique. Sticky traps were used to more accurately quantify leaf beetle abundance. Three, yellow, sticky traps (7.6 × 12.7 cm) per plot were clipped to metal stakes approximately 90 cm above the soil surface. Sticky traps were set for a 24-h period each week from April 17 to June 13 in the spring and from October 17 to November 20 in the fall.

2.5. Effect of habitat complexity and red imported fire ants on crop damage and yield

2.5.1. Collard damage

The effects of habitat complexity and fire ant abundance on crop damage were determined from harvested collards. In spring 2001, 10 collard plants were harvested from each plot approximately 90 days after planting. In fall 2001, eight collard plants were harvested per plot approximately 65 days after planting. Damage from herbivory was determined by use of a metal grid (1.25 cm² squares) to measure the missing leaf area of five, random leaves per plant. Total leaf area was

estimated by measuring length and width (at widest point) of each leaf. This estimation method yields a Pearson's correlation of 0.87 to actual leaf area (Schellhorn and Sork, 1997).

2.5.2. Crop yield

Plant aboveground biomass was used as a measure of crop yield. Harvested collards were weighed after drying in paper bags at $70 \pm 2^\circ\text{C}$ for 72 h.

2.5.3. Statistical analyses

All abundance data were $\log(n+1)$ transformed prior to analysis. Crop yield data were log transformed and proportions (crop damage and DBM mortality) were arcsine-square root transformed prior to analyses. Diamondback moth survival between treatment and control cages in the greenhouse experiment was analyzed with one-way analysis of variance (ANOVA) (SAS Proc GLM; Cody and Smith, 1997). Differences in fire ant, caterpillar, and leaf beetle abundance and DBM survival were compared with repeated measures ANOVA (SAS Proc Mixed with repeated statement; Khattree and Naik, 1999) with cropping system and fire ant abundance as treatment (fixed) effects. Plot was used as the unit of replication. To avoid pseudo-replication, sub-samples (data from individual plants, pitfall traps or sticky traps) were averaged to obtain a plot value for analysis. Treatment effects of crop damage and yield were analyzed with two-way ANOVA and treatment effects of the density experiment were analyzed with a three-way ANOVA (SAS Proc GLM).

Because the effect of Amdro on fire ant abundance varied among plots and within each season, there were not always statistically significant differences in fire ant abundance between baited and control plots. To more accurately quantify the effects of variation in fire ant abundance, an analysis of covariance (ANCOVA) with fire ant density as a covariate was conducted (SAS Proc GLM; Cody and Smith, 1997).

3. Results

3.1. Effect of red imported fire ants on DBM survival in greenhouse mesocosms

Exposure to foraging fire ants decreased survival of second-instar DBM larvae by 45% ($F_{1,14} = 39.16$; $P < 0.0001$). Mean survival (\pm SE) in control and treatment cages was $97.5 \pm 1.6\%$ and $53.8 \pm 4.9\%$, respectively. Fire ants reduced survival of fourth-instar larvae by 16% ($F_{1,14} = 8.46$; $P < 0.05$). Mean survival of fourth-instars was $98.3 \pm 1.9\%$ and $82.1 \pm 3.9\%$ in control and treatment cages.

3.2. Effect of habitat complexity on red imported fire ant predation of DBM

3.2.1. Fire ant abundance

In spring 2001, fire ant abundance was significantly reduced by the application of Amdro; however, differences in fire ant abundance varied among cropping systems and over the season (Date*Bait*Crop interaction; $F_{7,84} = 3.45$; $P < 0.01$). In general, fire ants were 49% less abundant in the intercrop than in the monocrop (Figs. 1A and B). Within cropping systems, fire ants were 78% less abundant in intercrop plots treated with Amdro (1.3 ± 0.2 ants/pitfall) than in intercrop controls (5.7 ± 1.0 ants/pitfall) and 84% less abundant in monocrop plots treated with Amdro (2.0 ± 0.3 ants/pitfall) than in monocrop controls (12.4 ± 1.7 ants/pitfall).

In fall 2001, application of Amdro also significantly reduced fire ant abundance ($F_{1,12} = 22.73$; $P < 0.001$). Fire ants were again less abundant in the intercrop and only this effect varied over the season (Date*Crop interaction; $F_{5,60} = 3.09$; $P < 0.05$). Overall, fire ants were 35% less abundant in the intercrop, averaging 1.0 ± 0.2 and 1.8 ± 0.3 ants/pitfall in the intercrop and 1.0 ± 0.2 and 3.2 ± 0.6 ants/pitfall in the monocrop in plots treated with Amdro and controls, respectively.

3.2.2. Field experiment one

In spring 2001, the effect of fire ants on DBM survival varied between cropping systems over the course of the experiment (Ant*Crop*Time interaction; $F_{2,24} = 3.41$; $P < 0.05$). Survival of DBM larvae was reduced by 73.2% over 24 h (0.9 ± 0.3 versus 3.4 ± 0.5 larvae/plant) and by 69.2% over 48 h (0.7 ± 0.3 versus 2.2 ± 0.3 larvae/plant) in intercrop plots with high fire ants densities compared to low fire ants densities, respectively (Fig. 2A). There was no difference in DBM survival between plots with suppressed fire ant densities and controls after 72 h (Fig. 2A). Conversely, in the monocrop, the effect of fire ants on DBM survival was less dramatic and took longer for the effect to be apparent. Fire ants did not significantly reduce DBM survival until 72 h in the monocrop (Fig. 2B).

In fall 2001, survival of DBM larvae was reduced by 30% (1.4 ± 0.2 versus 1.9 ± 0.2 larvae/plant) in plots with high fire ants densities compared to low fire ants densities, respectively. This effect of fire ants did not vary between cropping systems or with time (Ant*Crop interaction— $F_{1,12} = 0.05$; $P > 0.05$; Ant*Time interaction— $F_{2,24} = 0.03$; $P > 0.05$). Larval survival was significantly less in the intercrop than the monocrop over 48 h, but not over 72 h (Crop*Time interaction; $F_{2,24} = 5.53$; $P < 0.05$).

3.2.3. Field experiment two

In spring 2001, the abundance of DBM larvae was not significantly different between plots with suppressed

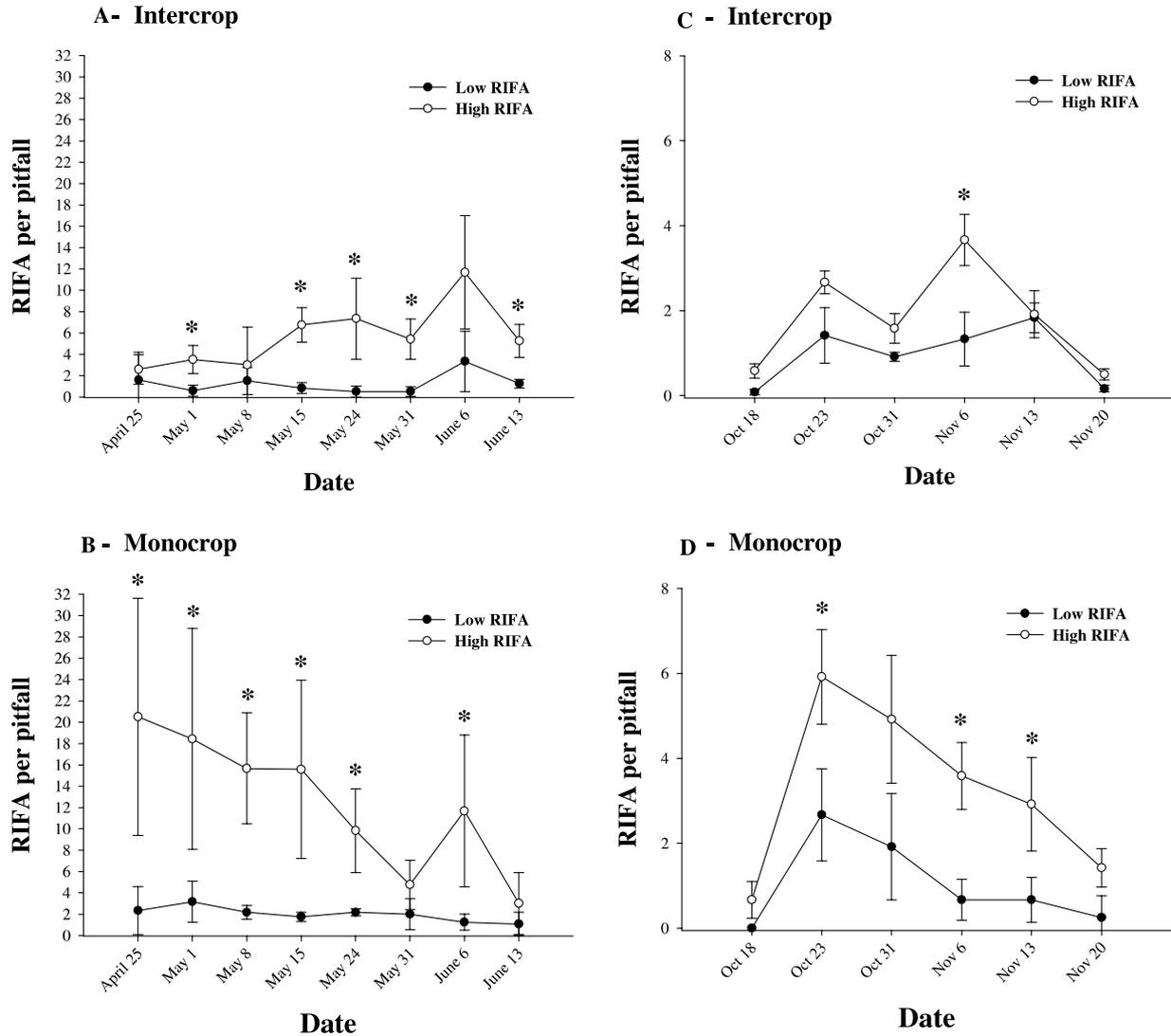


Fig. 1. Mean red imported fire ant (RIFA) abundance in plots baited with Amdro (low RIFA) and controls (high RIFA) in intercropped and monocropped collards for spring 2001 (A, B) and fall 2001 (C, D), respectively. Means were calculated from 3 pitfall traps/plot. Data were $\log(n + 1)$ transformed prior to analyses. Back-transformed data and 95% confidence intervals are presented. Significant differences between baited and control treatments are denoted with an asterisk (*).

fire ant densities and controls ($F_{1,12} = 0.02$; $P > 0.05$). Diamondback moth abundance averaged 0.19 ± 0.03 larva/plant in both fire ant suppressed-plots and control plots (Figs. 3A and B). Diamondback moth larvae were less abundant in the intercrop, but DBM abundance was only significantly different between crops in the middle of the season when abundance in the monocrop increased substantially (Date*Crop interaction; $F_{11,132} = 18.02$; $P < 0.0001$). Averaged over all dates in the spring, DBM larvae were 83% less abundant in the intercrop (0.32 ± 0.04 larva/plant) than in the monocrop (0.29 ± 0.05 caterpillar/plant; Figs. 3A and B). The same patterns were observed for total caterpillar abundance. There was a mean of 0.27 ± 0.04 caterpillar/plant in plots with suppressed fire ant densities and 0.29 ± 0.05 caterpillar/plant in control plots ($F_{1,12} = 0.84$; $P > 0.05$,

Figs. 3C and D). Overall, caterpillars were 88% less abundant in the intercrop (0.05 ± 0.01 caterpillar/plant) than in the monocrop (0.5 ± 0.05 caterpillar/plant), but caterpillar abundance between crops was not significant until the second half of the season when abundance in the monocrop greatly increased (Date*Crop interaction; $F_{11,132} = 12.58$; $P < 0.0001$, Figs. 3C and D).

In fall 2001, there was no significant effect of fire ant abundance on the abundance of DBM larvae or total caterpillars (DBM— $F_{1,12} = 0.08$; $P > 0.05$; total caterpillars— $F_{1,12} = 0.05$; $P > 0.05$). Mean abundance of DBM larvae was 0.07 ± 0.03 larva/plant in plots with suppressed fire ant densities and 0.06 ± 0.02 in control plots (Figs. 4A and B). Mean abundance of total caterpillars was 0.10 ± 0.04 caterpillar/plant in plots with suppressed fire ant densities and 0.09 ± 0.02 in control

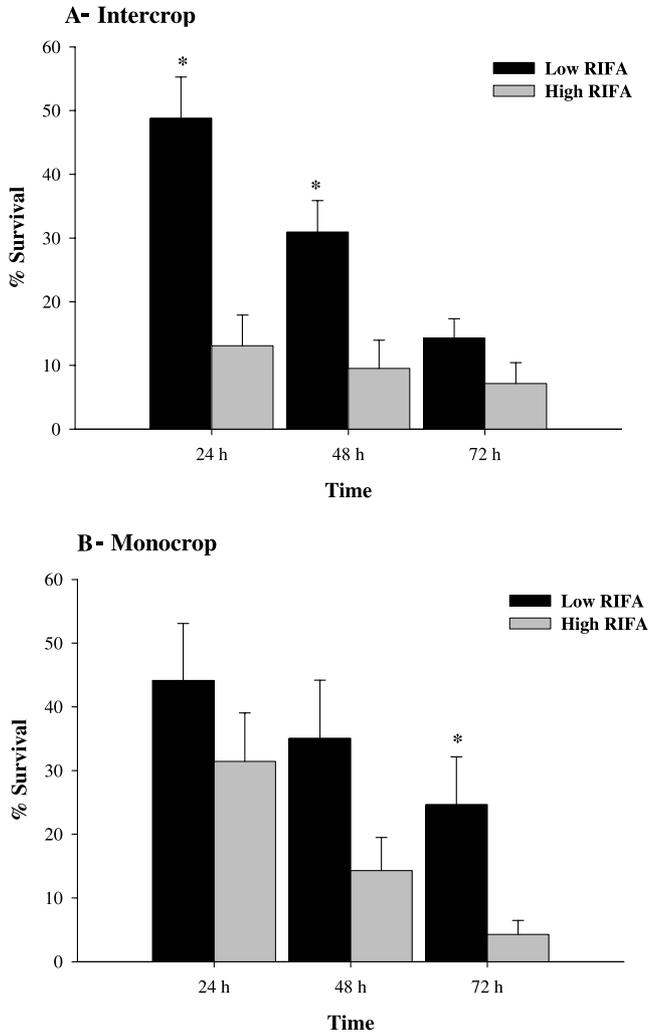


Fig. 2. Percentage of survival for diamondback moth (DBM) larvae (initial density 7 larvae/plant) over 24, 48, and 72 h in spring 2001. Effect of red imported fire ants (RIFA) on larval survival differed among intercropped (A) and monocropped collards (B). Significant differences between RIFA treatments are denoted with an asterisk (*).

plots (Figs. 4C and D). Caterpillars were again less abundant in the intercrop than the monocrop (DBM— 0.03 ± 0.01 versus 0.10 ± 0.03 larva/plant; total caterpillars— 0.03 ± 0.01 versus 0.16 ± 0.04 caterpillar/plant, respectively), but the difference was not significant until abundances in the monocrop increased late in the season (Date*Crop interaction; DBM— $F_{6,72} = 3.37$; $P < 0.05$; Figs. 4A and B; total caterpillars— $F_{6,72} = 5.24$; $P < 0.01$; Figs. 4C and D).

3.3. Effect of DBM density on red imported fire ant predation

Fire ant predation of DBM larvae was significantly greater at high DBM densities (Ant*Density interaction; $F_{2,24} = 4.77$; $P < 0.05$; Fig. 5). Diamondback moth mortality was 49% greater in the intercrop than the

monocrop ($F_{1,24} = 9.35$; $P < 0.01$), but larval density did not affect the difference in mortality between crops (Density*Crop interaction; $F_{1,24} = 0.17$; $P > 0.05$).

3.4. Effect of habitat complexity and red imported fire ants on leaf beetle abundance

In the spring, leaf beetles (mainly *Microtheca ochroloma* Stål (Galerucinae), *Phyllotreta cruciferae* Goeze (Alticinae) and *Diabrotica undecimpunctata howardi* Barber (Galerucinae) with other occasional species) were significantly more abundant in intercropped plots with suppressed fire ant densities. In the monocrop, however, leaf beetles were significantly more abundant in high fire ant density plots on sampling dates near the beginning and near the end of the season (Date*Ant*Crop interaction; $F_{8,90} = 2.79$; $P < 0.05$; Fig. 6). Averaged over the season, leaf beetles were 8% more abundant in plots with suppressed fire ant densities (0.32 ± 0.05 beetle/sticky trap) than in control plots (0.30 ± 0.05 beetle/sticky trap) and 58% more abundant in the monocrop (0.4 ± 0.1 beetle/sticky trap) than in the intercrop (0.19 ± 0.04 beetle/sticky trap).

In the fall, leaf beetles (same species as spring, but fewer Alticinae) were 24% more abundant in plots with suppressed fire ant densities (1.9 ± 0.3 beetles/sticky trap) than in control plots (0.9 ± 0.1 beetle/sticky trap; $F_{1,12} = 11.13$; $P < 0.01$, Fig. 6C). There was no difference in the effect of fire ants on the abundance of leaf beetles between habitat complexity treatments (Ant*Crop interaction; $F_{1,12} = 4.72$; $P > 0.05$), even though leaf beetles were overall 35% more abundant in the monocrop (1.7 ± 0.4 beetles/sticky trap) than the intercrop (1.1 ± 0.2 beetles/sticky trap).

3.5. Effect of habitat complexity and red imported fire ants on crop damage and yield

3.5.1. Collard damage

In spring 2001, fire ants did not significantly reduce crop damage ($F_{1,12} = 3.23$; $P > 0.05$); however, leaf damage was 33% higher in plots with suppressed fire ant densities ($1.60 \pm 0.01\%$) than in controls ($1.12 \pm 0.02\%$). Crop damage was greater in the intercrop than the monocrop ($F_{1,12} = 7.36$; $P < 0.05$) and the greatest leaf damage ($4.04 \pm 0.04\%$) occurred in intercrop plots with suppressed fire ant densities.

In fall 2001, the effect of fire ants on damage varied between the two cropping systems (Ant*Crop interaction; $F_{1,12} = 13.06$; $P < 0.01$). In the intercrop, the greatest percentage damage was observed in plots with suppressed fire ant densities ($2.93 \pm 0.02\%$). In the monocrop, however, the greatest damage occurred in plots with high fire ant densities ($5.68 \pm 0.02\%$).

The ANCOVA did not reveal a significant effect of field season on crop damage ($F_{1,24} = 1.07$; $P > 0.05$),

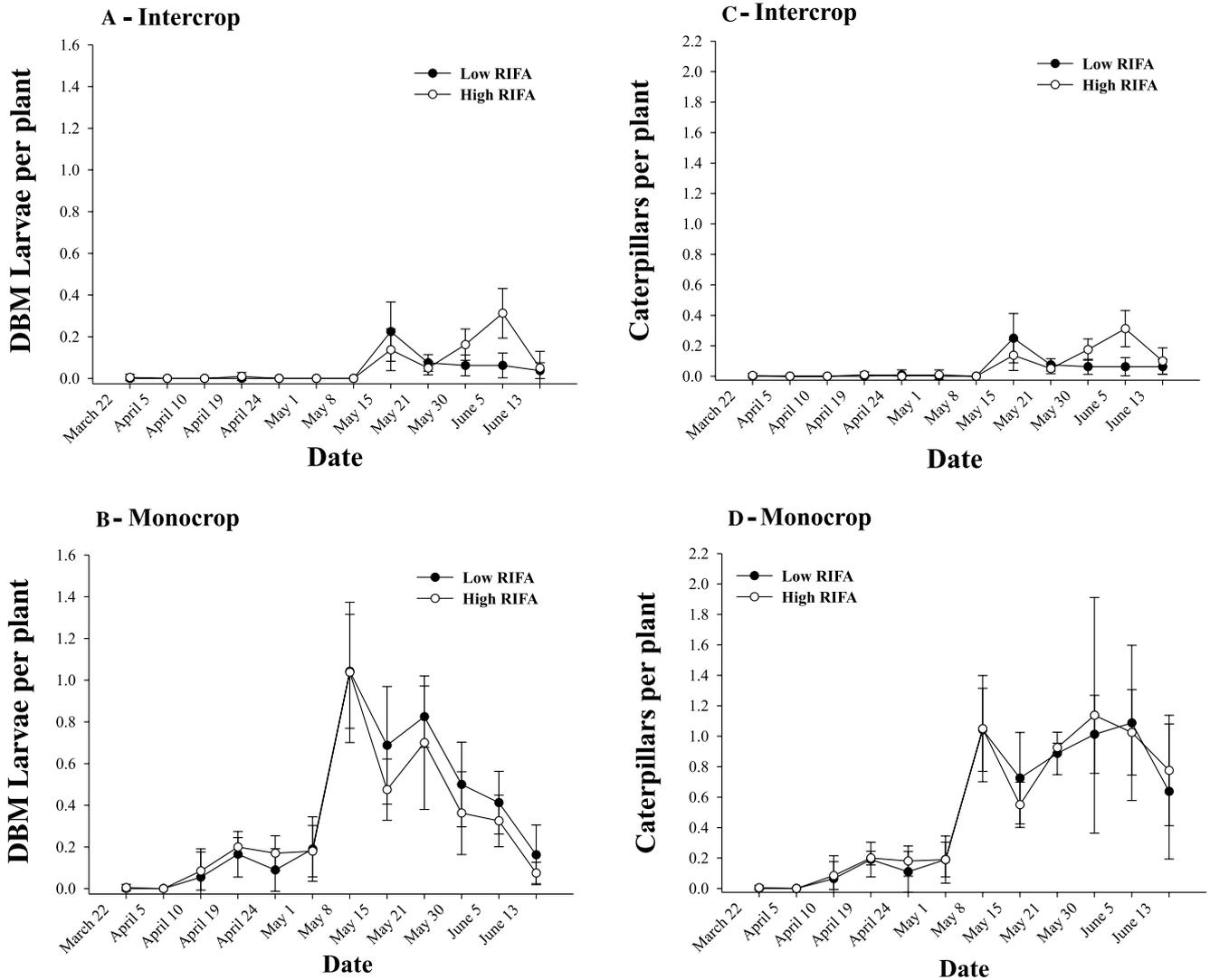


Fig. 3. Mean abundance of diamondback moth (DBM) and total lepidopteran larvae for spring 2001 in baited (low red imported fire ant (RIFA)) and control (high RIFA) treatments in intercropped (A, C) and monocropped collards (B, D). Means were calculated from weekly visual searches of collard plants. Data were $\log(n + 1)$ transformed prior to analyses. Back-transformed data and 95% confidence limits are presented. Visual searches incorporated 50 plants/plot March 22 to April 19, 25 plants/plot April 19 to May 1 and 20 plants/plot May 8 to June 13 as plants grew over the season.

which suggests the spring and fall results were consistent. As fire ant density increased, there was a concomitant decrease in crop damage and the magnitude of this effect was greater in the intercrop than the monocrop (Fig. 7). Thus, fire ants were associated with a reduction in crop damage in the intercrop to a greater extent than in the monocrop (Ant*Crop interaction; $F_{1,24} = 5.62$; $P < 0.05$; Fig. 7).

3.5.2. Crop yield

In spring 2001, crop yield (plant biomass) was approximately 28% less in collard plots with suppressed fire ant densities ($F_{1,12} = 9.74$; $P < 0.01$). There was no fire ant effect on crop yield in the fall. Crop yield was reduced in the intercrop in both field seasons (spring— $F_{1,12} =$

87.52; $P < 0.0001$; fall— $F_{1,12} = 68.88$; $P < 0.0001$). Plant biomass was 86% and 70% less in the intercrop (11.0 ± 1.4 and 19.0 ± 3.0 g) than in the monocrop (81.4 ± 10.8 and 62.9 ± 3.9 g) in spring and fall, respectively.

4. Discussion

In this study we found evidence that red imported fire ants are important biological control agents of DBM and other significant herbivores in collards. Fire ants significantly reduced the survival of DBM larvae and the abundance of leaf beetles, collard damage was inversely related to fire ant density, and collard yields were overall greater in plots with high densities of fire ants than in

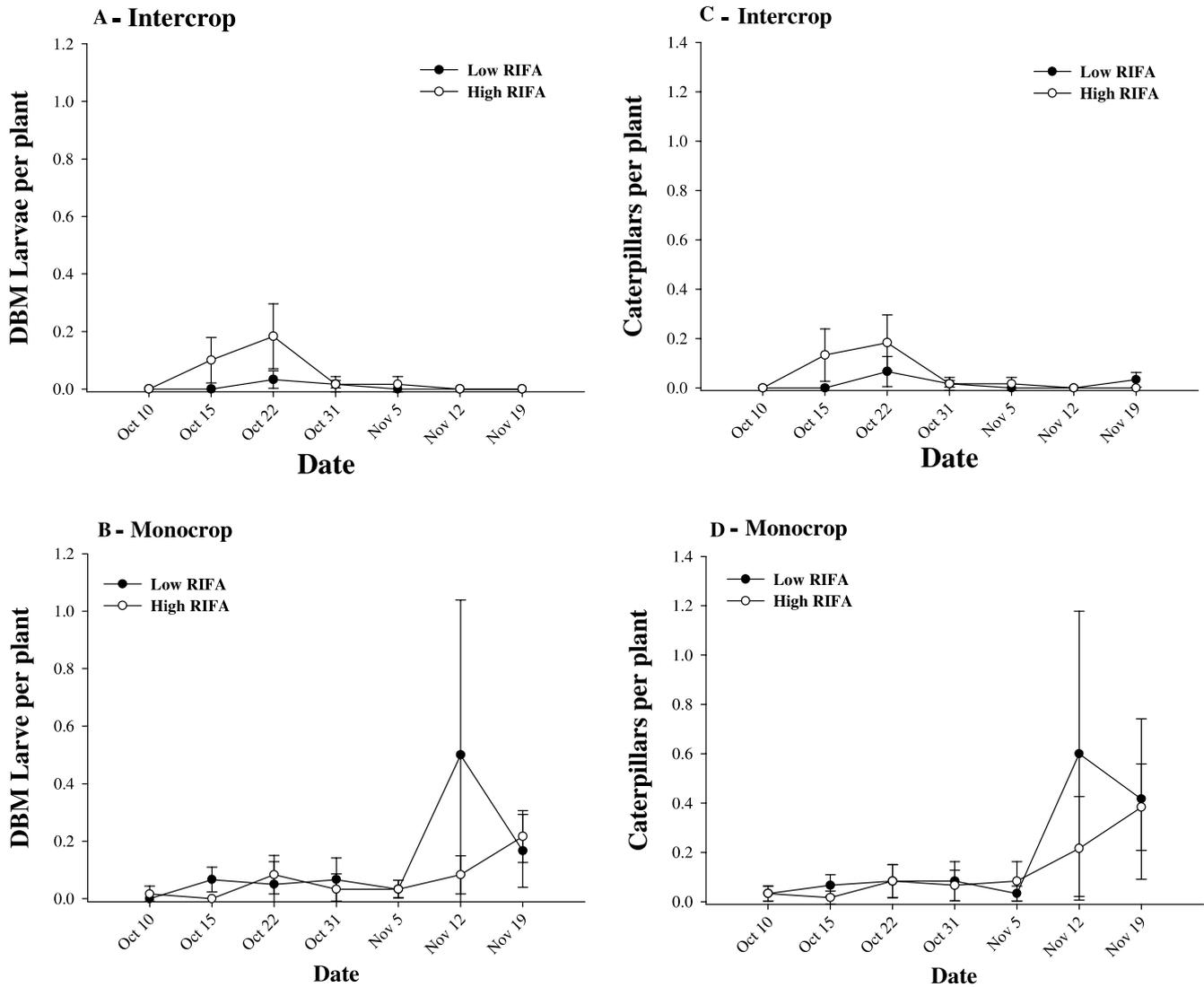


Fig. 4. Mean abundance of diamondback moth (DBM) and total lepidopteran larvae for fall 2001 in baited low red imported fire ant (low RIFA) and control (high RIFA) treatments in intercropped (A, C) and monocropped collards (B, D). Means were calculated from weekly, visual searches of collard plants (15 searches per plot). Data were $\log(n+1)$ transformed prior to analyses. Back-transformed data and 95% confidence limits are presented.

plots with low densities of fire ants. Our study joins a growing body of literature suggesting that, although fire ants are considered a serious health concern and nuisance pest of humans as well as occasional crop pests, they can play beneficial roles in agroecosystems (Vinson, 1997). It appears that fire ants are particularly effective predators of lepidopteran larvae in many systems, including collards (crucifers) (Ali and Reagan, 1985; Ali et al., 1984; Bessin and Reagan, 1989; Eubanks, 2001).

The efficacy of fire ants as a biological control agent was greater in the more complex habitat. In field experiments, predation of DBM larvae by fire ants was more rapid and efficient in the collard-white clover intercrop than in the monocrop (Fig. 2), even though fire ants were 23% less abundant in the intercrop than the monocrop (Fig. 1). This may have occurred from fire

ants preferring the less shaded environment of the monocrop (Way and Khoo, 1992), but as a result, the per capita effect of fire ants on the survival of DBM larvae was greater in the intercrop than in the monocrop. Many studies have shown that mixed cropping increases the abundance of natural enemies (e.g., Root, 1973; Russell, 1989; Schellhorn and Sork, 1997), but very few studies have investigated the effect of mixed cropping on the per capita effect of a natural enemy (Symondson et al., 2002). The most likely explanation for this result is a decrease in collard plant architecture in the intercrop. Intercropped collards were smaller, had fewer leaves, fewer twisted or deformed leaves, and smoother leaf surfaces than monocropped collards (pers. obs.). Most studies that have investigated the effects of plant architecture on predator efficiency have

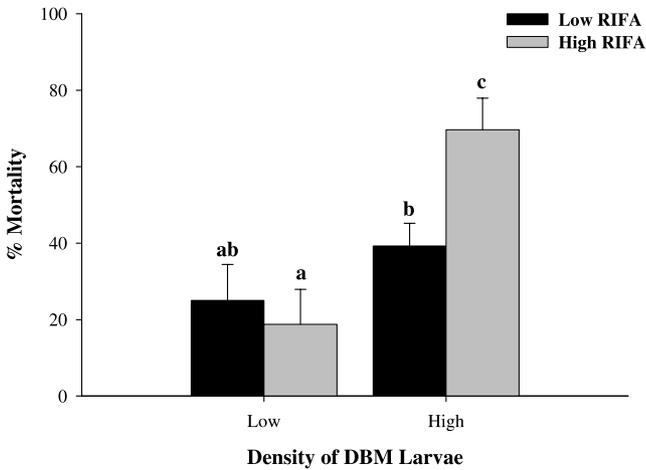


Fig. 5. Percentage of mortality for diamondback moth (DBM) larvae on collard plants infested with high (7) and low (2) densities of larvae in plots baited for red imported fire ants (low RIFA) and controls (high RIFA). Remaining larvae were counted after 24 h.

found that the per capita effect of predators (i.e., predator efficiency) is greater on architecturally simple plants than on architecturally complex plants (Clark and Messina, 1998; Freese, 1995; Gardner and Dixon, 1985; Kareiva and Sahakian, 1990). We hypothesize that fire ants were able to capture more prey per individual worker on the architecturally simple collards found in the collard-white clover intercrop than on the architecturally complex collards found in the monocrop.

Fire ants did not significantly affect caterpillar abundance in the second field experiment. This was surprising given the large effect of fire ants on DBM survival in the greenhouse mesocosm experiment and first field experiment. The inconsistency between the results of these experiments may be due to differences in caterpillar densities. In the greenhouse experiment and first field experiment, there were 7 DBM larvae/plant. This density regularly occurs on collards (Mitchell et al., 1997a), but in this study DBM field densities were much lower in both field seasons. During the second field experiment, caterpillar densities were never greater than 1.14 larva/plot (Fig. 3D) and caterpillar densities reached economic threshold on only one sampling date (May 30). These densities may have been too low to stimulate a strong numerical response of fire ants and the third field experiment provided evidence supporting this explanation. No significant effect of fire ants on DBM mortality was detected at densities of 2 DBM larvae/plant, but fire ant predation was intense when there were 7 DBM larvae/plant (Fig. 5). These results indicate that predation of DBM larvae by fire ants changes with larval density. A switch in predation intensity between prey at low densities and prey at high densities is a common behavior among generalist predators, including many ant species (Fowler, 1989; Murdoch, 1969; Risch and Carroll, 1982; Way and Khoo, 1992).

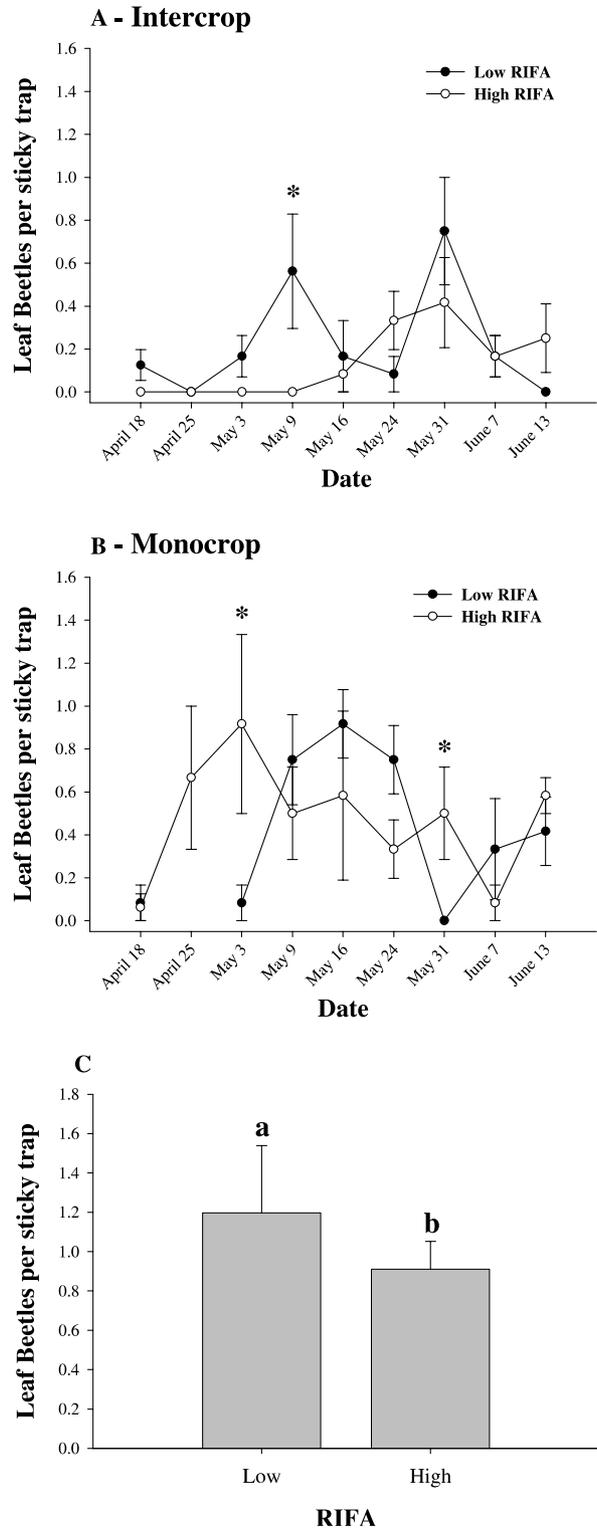


Fig. 6. Mean abundance of leaf beetles for 2001 in plots baited for red imported fire ants (low RIFA) and controls (high RIFA) in spring intercropped (A) and monocropped collards (B) and overall in fall (C). Means were calculated from three sticky traps per plot. Data were $\log(n + 1)$ transformed prior to analyses. Untransformed data (\pm SE) are presented.

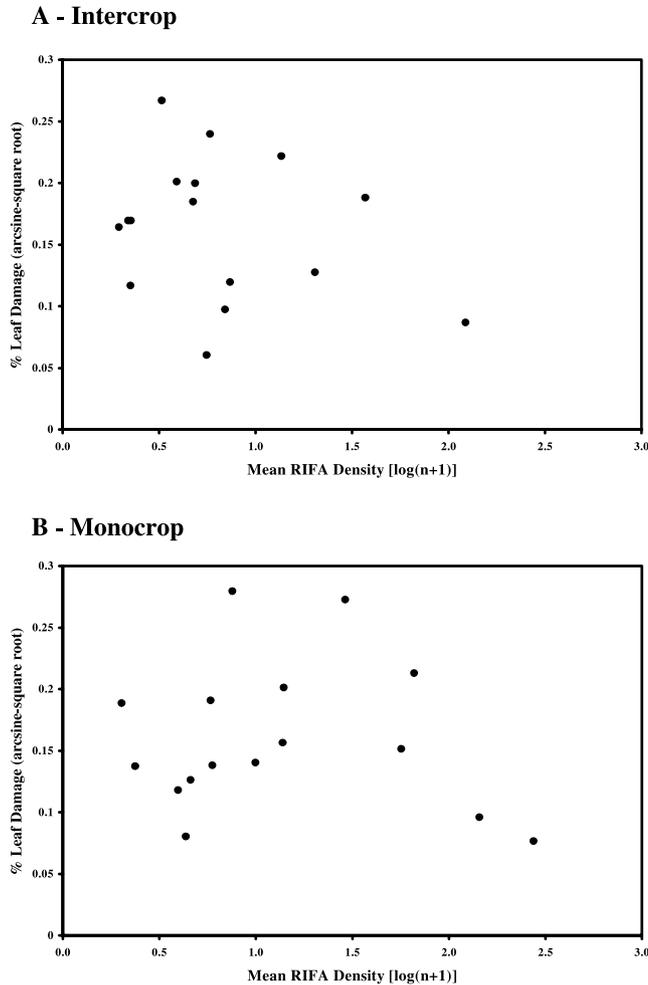


Fig. 7. Relationship between crop damage (% leaf damage) and red imported fire ant (RIFA) density in intercropped (A; $R = 0.75$) and monocropped collards (B; $R = 0.34$) in 2001.

Ultimately, to be an effective biological control agent, the action of a natural enemy must result in decreased crop damage and increased yield (Symondson et al., 2002). In our study, fire ant density was inversely associated with crop damage and fire ants were more effective at reducing damage in the intercrop (Fig. 7). In spring 2001, damage to collard leaves was 33% greater in plots with suppressed fire ant densities than in control plots. In fall 2001, overall crop damage was still 26% greater in collard plots with suppressed fire ant densities, even though the highest leaf damage occurred in monocropped plots with high fire ant densities.

Crop yields were lower in the intercrop than the monocrop in both field seasons. This effect was most likely due to competition among the collards and clover and, given the increased efficacy of fire ants in the intercrop, not associated with their biological control potential. Furthermore, in spring 2001, crop yield was 28% greater in collard plots with high densities of fire ants. This result is analogous to a trophic cascade in

natural ecosystems where the effect of a natural enemy on an herbivore population cascades down the food web and indirectly increases plant growth and fitness (Paine, 1980; Schmitz et al., 2000). Therefore, fire ants are effective contributors to biological control that reduce damage and increase yield in collards.

The apparent beneficial effects of fire ants on damage and yield are somewhat surprising since fire ants did not significantly affect the abundance of caterpillars in the second field experiment (Figs. 3 and 4). Red imported fire ants did, however, reduce the densities of leaf beetles by 45% in 2001 (Fig. 6). These herbivores are economically important particularly when the plants are small and most vulnerable to defoliators (Adams, 1991; Latheef and Ortiz, 1984). This result suggests that lepidopteran larvae may not have been the most damaging collard pests in central Alabama during 2001.

Our study supports that fire ants can be important and effective biological control agents. In addition, this study found that increasing habitat complexity can enhance the efficacy of fire ants as biological control agents. Consequently, intercropping may be more economically favorable in areas that have been invaded by fire ants, although yields in the intercrop were not overall as high as in the monocrop in this experiment. Fire ants are one of the most abundant, but not the only important natural enemies in southern agroecosystems. Future work should not only focus on the impact of fire ants in other complex and simple systems, but also determine if potential interactions among fire ants and other natural enemies are affected by habitat complexity.

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