THE POTENTIAL EFFECTS OF RED IMPORTED FIRE ANTS (*SOLENOPSIS INVICTA*) ON ARTHROPOD ABUNDANCE AND *CUCUMBER MOSAIC VIRUS*

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THE POTENTIAL EFFECTS OF RED IMPORTED FIRE ANTS (*SOLENOPSIS INVICTA*) ON ARTHROPOD ABUNDANCE AND *CUCUMBER MOSAIC VIRUS*

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Date of Graduation

THESIS ABSTRACT

THE POTENTIAL EFFECTS OF RED IMPORTED FIRE ANTS (*SOLENOPSIS INVICTA*) ON ARTHROPOD ABUNDANCE AND *CUCUMBER MOSAIC VIRUS*

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Mutualisms involving ants and honeydew-producing insects such as aphids, scales, and whiteflies may dramatically affect the population dynamics of these herbivorous insects. Furthermore, changes in the population size of honeydew-producing insects may have important consequences for other interacting organisms. We tested the hypothesis that ant-aphid mutualisms result in significant increases in aphid population size and aphid dispersal which, in turn, increases the spread of aphid-vectored plant viruses. We studied the invasive red imported fire ant (*Solenopsis invicta*), several common aphids that form facultative mutualisms with these ants, and a ubiquitous, aphid-vectored plant virus (*Cucumber mosaic virus* (CMV)). We found that aphids were significantly more abundant in small plots of tomato plants (*Lycopersicon esculentum)* with large fire ant populations than in small plots of tomato with suppressed fire ant populations. In a greenhouse experiment, we found that aphids dispersed to neighboring plants 59% more often in the presence of fire ants than in the absence of fire ants, suggesting that fire ants increase aphid movement. Most importantly, in a large-scale field study (≈ 2.4 hectare fields), we found that the abundance of alate aphids and the incidence of CMV (the proportion of plants infected with virus) were significantly higher in fields with high densities of fire ants than in fields with suppressed fire ant populations. This study suggests that ant-aphid mutualisms may have dramatic, previously undocumented effects on the dynamics of aphid-vectored plant viruses. This study also suggests that the continued range expansion of red imported fire ants could result in larger levels of virus infection in both agricultural crops and wild plants.

Understanding epidemiology of plant viruses requires knowledge of their ecology and hosts. Identifying reservoir hosts and inoculum sources of plant viruses is often imperative for understanding virus outbreaks in agricultural plants. We present here a 2-year analysis of the population dynamics of *Cucumber mosaic virus* (CMV) in herbaceous plants around fresh-market tomato fields in northern Alabama, a region where a persistent CMV epidemic has been ongoing for over ten years. Over the two year study, at least 50 herbaceous plant species belonging to 27 families were identified and tested for the presence of CMV. 18 plant species belonging to 12 plant families tested positive for CMV. In 2005, CMV incidence was positively correlated with planting date of the field for both tomato and herbaceous plants. There was no correlation between the overall CMV incidence in weed plots and CMV incidence in neighboring tomato fields, but there were strong, positive correlations between CMV incidence in tomato fields and the relative abundance of greenbriar (*Smilax* spp.), the relative abundance of ivy-leaf morningglory (*Ipomoea hederacea*), the abundance of aphids on ivy-leaf morningglory, and the number of aphids on blackberry (*Rubus* spp.). These results suggest that most herbaceous plants near Alabama tomato fields are relatively unimportant in the spread of CMV to neighboring tomato fields and that control efforts should be focused on only a handful of species.

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Fire Ants May Disrupt Biological Control in Tomato

1. Introduction:

Tomatoes (*Lycopersicon esculentum*) are the second most important vegetable crop in the United States, with over eight million tons produced annually in the U.S. (Brunke et al., 2003). The economic viability of tomatoes is threatened by numerous insect pests, some of which include Lepidopteran larvae, thrips (Thysanoptera: Thripidae), stinkbugs (Hemiptera: Pentatomidae), whiteflies (Hemiptera: Aleyrodidae) and aphids (Hemiptera; Aphididae) (Kemble et al., 2004; Nault and Speese, 2002). Pesticides are commonly used in tomato production to reduce damage from insect pests (Clark et al., 1998). Public concern regarding the use of pesticides in food production combined with governmental goals of reducing pesticide use is making it necessary for producers to develop alternative methods of insect pest control. Biological control of insect pests of tomato is one viable alternative (Clark et al., 1998). In the southern U.S., red imported fire ants, *Solenopsis invicta* (Buren), are the most abundant and potentially dominant predators in many agricultural systems (Reagan, 1986; Vinson, 1997; Eubanks, 2001), making them a potentially efficacious biological control agent in tomato. The goal of this study was to quantify the effects of red imported fire ants on beneficial and pest arthropods of tomato.

The red imported fire ant is an invasive species to the southern United States. Because they are aggressive, generalist predators, red imported fire ants may alter arthropod abundance resulting in a reduction of biodiversity and ecological simplification (Lofgren et al., 1975; Vinson, 1994; Eubanks, 2001; Eubanks et al., 2002; Harvey and Eubanks, 2004). Fire ants have been reported as predators of a wide variety of insect pests including the velvetbean caterpillar, *Anticarsia gemmatalis* Hübner (Lee et at., 1990), rednecked peanutworm, *Stegasta bosqueella* (Chambers) (Vogt et al., 2001), horn fly, *Haematobia irritans* (L.), boll weevil, *Anthonomus grandis* (Sterling, 1978; Jones and Sterling, 1979), cotton bollworm, *Helocoverpa zea* (Diaz et al., 2004); beet armyworm, *Spodoptera exigua* (Hubner) (Diaz et al., 2004), and the sugarcane borer, *Diatraea sacchari* (Zehntner) (Adams et al., 1981; Fuller and Reagan, 1988; Bessin & Reagan, 1993). Additionally, fire ants have been reported as predators of some beneficial insects. For example, Bugg and Dutcher (1989) reported significant levels of predation on natural enemies by *Solenopsis invicta* in pasture and pecan agroecosystems. In cotton, fire ants negatively affected predators of aphids, including ladybeetle larvae (Coleoptera: Coccinellidae) and green lacewing larvae (Neuroptera: Chrysopidae) (Eubanks et al., 2002; Kaplan and Eubanks, 2002). In Oklahoma peanuts, foraging fire ants collected minute pirate bugs (Hemiptera: Anthocoridae), spiders, parasitoids and lacewings (Vogt et al., 2001). Additionally, fire ants decrease the abundance of ticks, spiders, and predatory beetles (Summerlin et al., 1977; Lofgren, 1986; Long et al., 1987; Porter and Savignano, 1990). Thus, it is possible that fire ants may be beneficial insects in some agricultural crops, but disrupt biological control in other crops.

One factor that may influence the effect of red imported fire ants as predators is their propensity to engage in facultative mutualisms with honeydew-producing Hemipterans. Many ant species are known to develop mutualistic relationships with insects in the order Hemiptera (Way, 1963; Buckley, 1987). The basis of the mutualism is the production of honeydew, a byproduct of herbivory (Mittler, 1958; Douglas, 1993; Kaplan and Eubanks, 2002). In return for honeydew, ants may provide Hemipterans protection from natural enemies (Way, 1963; Buckley, 1987; Buckley, 1990; Jiggens et al., 1993; Stechmann et al., 1996; Queiroz and Oliveira, 2001; Kaplan and Eubanks, 2002). Because of the mutualistic relationship, red imported fire ants may have strong effects on aphid populations in tomatoes. Aphids are considered to be an important pest of tomatoes and many other fruit and vegetable crops because of their potential to vector numerous plant viruses (Harris and Maramorosch, 1977; Tomlinson, 1987).

The objective of this study was to quantify the effects of fire ants on both pest and beneficial arthropods of tomato. The overall goal of this work is to determine if red imported fire ants are beneficial insects in tomato or if they exacerbate insect pest problems in this crop. To address this objective, I conducted field experiments in which I manipulated fire ant abundance in experimental plots of tomatoes and tracked subsequent changes in arthropod abundance. Additionally, I conducted on-farm sampling in Blount Co., Alabama to quantify the relationship between red imported fire ants and other arthropods in intensively managed commercial tomato fields.

2. 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 one month or until they reached 20 cm in height, and were then placed outdoors for one week for acclimatization to natural conditions. In 2003, twelve, 3 m plots of tomato plants, separated by at least 10 m were established. Each plot consisted of 30 plants, spaced 45 cm apart and organized into three rows separated by 75 cm each. Plants were visually searched for aphids, fire ants, and other arthropods weekly for three weeks. 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 using the same plant and row spacing as in 2003. On August 18 and August 26 of the 2004 field season, all 30 plants per plot were searched. Nine plants per plot were visually searched on September 2, 2004.

Plots were randomly divided into two treatments: natural or high fire ant density (control) or suppressed fire ant density. Suppression treatments were established using Amdro® a commercially available, ant-specific bait. The active ingredient of Amdro® is hydramethylnon, which blocks the production of ATP, killing target ants by inhibiting energy production (Valles and Koehler, 1997). Amdro® is readily picked up by foraging fire ants and does not affect survival of non-target arthropods (Hu and Frank, 1996; Eubanks et al., 2002), and has been successfully used to suppress fire ants in similar sized and spaced plant plots in other studies (e.g., Harvey and Eubanks 2004, 2005). Amdro® was applied weekly to plots assigned to the fire ant suppression treatment, beginning one 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 using a “hotdog” trap. 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 ≈ 45 minutes, after which they were collected, sealed, and returned to the laboratory. Ants were counted within 48 hours.

In 2004, four fresh market tomato fields were sampled in Blount Co., Alabama for the presence of fire ants and other arthropods. Approximately 20 tomato plants per acre were visually searched for aphids, fire ants, and other arthropods weekly for seven weeks. Additionally "hotdog" traps were used to quantify the relative abundance of fire ants. Abundance data were averaged across all dates prior to analysis.

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 in tomato plots were compared between treatments with repeated measures ANOVA (SAS Proc Mixed with repeated statement; Khattree and Kaik, 1999). To avoid pseudo-replication, data for each plot were averaged to obtain mean plot values for analysis. Additionally, tests were performed for correlations between arthropod abundance and fire ant abundance in the experimental plots. Due to the intensely managed commercial tomato fields there were limited numbers of non-aphid arthropods. Therefore, aphid abundance and fire ant abundance in commercial tomato fields were tested for a correlation.

3. Results:

In 2003, the abundance of fire ants foraging on the ground in tomato plots was significantly reduced by the application of Amdro® ($F_{1,20} = 27.51$; $P = <0.0001$) (Figure 1A). The abundance of fire ants foraging on tomato plants, however, was not significantly different between treatments ($F_{1,24} = 1.07$; $P = 0.31$) (Figure 1B). In 2004, fire ant abundance on tomato plants was significantly reduced (by 37%) ($F_{1,29} = 4.63$; $P = 0.04$) in fire ant suppression plots (Figure 1C). In 2004, abundance of ground foraging fire ants, however, was not significantly different between control and suppression plots

($F_{1,30}$ = 2.54; P = 0.12), but fewer fire ants, on average, were present in treated plots than control plots (Figure 1D).

There were at least six different aphid species present on tomato plants, including *Myzus persicae, Aphis gossypii, A. fabae, Aulacorthium solani, Macrosiphum euphorbae, 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) (Figure 2A). Apterous aphids were 60% more abundant in control plots with relatively high densities of fire ants than in plots with suppressed densities of fire ants. Total aphid abundance was 48% greater in plots with high densities of fire ants than in plots with suppressed densities of fire ants. The abundance of alate aphids (F = 1.76; P = 0.19) was not statistically different between treatments, but the proportion of alate aphids in tomato plots with suppressed densities of fire ants was almost twice as great as aphids in plots with naturally occurring fire ants (41% versus 23%; X^2 = 212.4; $P < 0.05$). In 2004, 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 among the two treatments (Figure 2B). Alate aphids were 45% more abundant in control plots than in plots with relatively low densities of fire ants and total aphid abundance was 46% higher in control plots than fire ant suppression plots. In contrast to 2003, alate aphids made up over 95% of total aphids in both control and suppression plots in 2004.

In 2003, both date ($F_{1,30}$ = 8.57; P = 0.006) and treatment (F = 66.14; P = <0.001) had a significant effect on total aphid abundance, but the date by treatment interaction (F = 2.45; P = 0.1) was not significant (Table 3). In 2004, date (F =18.8; P = <0.001), treatment ($F = 27.1$; $P = <0.001$), and the date by treatment interaction ($F2_{,29} = 10.5$; $P = 0.0004$) all had significant effects on total aphid abundance.

In 2003 and 2004, several non-aphid herbivores were found feeding on tomato plants (Table 1); the most abundant were whiteflies (Aleyrodidae) followed by Lepidopteran larvae. In both 2003 ($F_{1,24} = 3.89$; $P = 0.06$) and 2004 ($F_{1,23} = 0.00$; $P=0.96$), non-aphid herbivore abundance was not significantly different between treatments, but their overall densities were quite low, especially in 2004 (Figure 3A, 3B).

A complex of natural enemies was present on tomato plants during weekly visual searches during 2003 and 2004 (Table 2). In 2003, natural enemies found on tomato plants included lady beetle larvae (Coccinellidae) and spiders (Table 2). Natural enemy abundance, however, was not significantly different between the two treatments ($F_{1,24} = 0.01$; $P = 0.93$) (Figure 4A). In 2004, the most abundant natural enemies were spiders followed by damsel bugs (Nabidae) and big-eyed bugs (Geocoridae). 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 (Figure 4B), with fewer natural enemies found in control plots. In 2003, date, treatment, and the date by treatment interaction did not affect herbivore abundance between high fire ant plots and suppressed fire ant plots. In 2004, date ($F = 5.61$; $P = 0.008$) and treatment ($F = 4.31$; $P = 0.05$) did have a significant affect of herbivore abundance.

In both 2003 and 2004, the abundance of fire ants foraging on tomato plants in experimental plots was not significantly correlated with aphids (2003: $r = 0.07$; $P = 0.08$; $N = 12$, 2004: $r = 0.48$; $P = 0.11$; $N = 12$) herbivores (2003: $r = -0.30$; $P = 0.33$; $N = 12$, 2004: $r = 0.33$; $P = 0.29$; $N = 12$) or natural enemies (2003: $r = -0.24$; $P = 0.45$; $N = 12$, 2004: r = 0.33; P = 0.28; N = 12). Additionally, the abundance of ground foraging fire ants was not significantly correlated with herbivores (2003: r = -0.14; P = 0.67; N = 12, 2004: r = -0.16; P = 0.61; N = 12) or natural enemies (2003: r = 0.07; P = 0.81; N = 12, 2004: r = 0.29; P = 0.35; N = 12). The abundance of ground foraging fire ants; however, was positively correlated with aphid abundance in 2003 (r = 0.56; P = 0.05; N = 12) but not in 2004 (r = 0.35; P = 0.25; N = 12). Similarly, I found that the abundance of fire ants and aphids were positively correlated in fresh market tomato fields (one-tailed test; r = 0.09; P = 0.04; N = 4) (Figure 5).

4. Discussion

I 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 and 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* (Hubner)) 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 taxa. One potential reason for the difference in my findings from other studies could be the composition of herbivores present. Most importantly, I found relatively few herbivore species in tomato and the overall abundance of non-aphid herbivores was quite low. The non-aphid herbivores in tomatoes were dominated by whiteflies and Lepidopteran larvae (Table 1), but they were present at relatively low densities. Like aphids, whiteflies produce honeydew and have been shown to be 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 (Table 1). The low densities of caterpillars coupled with their small size may have resulted in reduced predation by fire ants because 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 and Eubanks, 2004) and soybean (Styrsky et al., in press)).

My results are consistent with studies indicating that the presence of fire ants results in increased aphid populations (Queiroz and Oliveira, 2001; Kaplan and Eubanks, 2002, 2005). I found that total aphid abundance in both 2003 and 2004 was significantly greater in tomato plots with high densities of fire ants (control) than in plots with suppressed fire ant densities, and in 2004 alate aphids were more than twice as abundant in high fire ant plots as in low fire ant plots. The size of the vector population is one of the most important factors influencing the spread of plant viruses (Irwin and Ruesink, 1986; Irwin et al., 2000). Because aphids are the primary vectors of many plant viruses, including many that dramatically affect tomato yield (e.g., Sikora et al. 1998), any factor that increases their abundance is likely to result in a subsequent increase in the spread of plant viruses (Madden et al., 2000; Jeger et al., 2004). Increases in alate aphids have been shown to be positively correlated with plant virus epidemics. For example, the abundance of alate aphids is positively correlated with *Barely yellow dwarf virus* in cereals (Power et al., 1991; Chapin et al., 2001; Fabre et al., 2003), with *Beet mosaic virus* in sugar beet (Dusi et al., 2000), and with *Potato virus Y* and *Potato leafroll virus* in potato (Baskey, 2002). The results from this study suggest that fire ants are affecting aphid population dynamics and could affect the movement of aphid-vectored plant viruses. I hope to directly test this hypothesis in the near future.

Natural enemies were not significantly different between treatments in 2003, suggesting that fire ants did not negatively affect natural enemies in tomato in that year. These results are inconsistent with results published by Bugg and Dutcher (1989), Eubanks et al. (2002), Kaplan and 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 two natural enemies, spiders and lady beetle larvae (Coccinellidae), were present at the time of visual searches, of which spiders were the most abundant (Table 2). It has been shown that spiders were able to 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 contrast to findings from 2003 natural enemies were more abundant in the suppressed fire ant treatment in 2004, suggesting that fire ants negatively affected natural enemies in the high fire ant treatment in that year. A greater diversity of natural enemies were found during visual searches in 2004 than in 2003 (Table 2), and this may explain the greater impact of fire ants on beneficial insects in this year. Other studies, for example, have shown that damsel bugs and big-eyed bugs, the second and third most abundant natural enemies in tomato plots in 2004, were much more susceptible to fire ants than are spiders (Eubanks, 2001; Eubanks et al., 2002; Eubanks et al., in preparation).

In previous studies fire ants have been shown to be potentially effective biological control agents of non-aphid herbivores. My results suggest that fire ants may only act as beneficial insects in agricultural crops that are either less susceptible to aphid-vectored plant viruses or that have relatively high densities of non-aphid herbivores. In tomatoes, fire ants had insignificant affects on non-aphid herbivores and fairly strong, positive effects on aphid populations. Taken together, the results of this study suggest that fire ants may not be useful biological control agents in this crop.

Table 1

Mean number of non-aphid herbivores found per tomato plant per season in high fire ant and suppressed fire ant plots in 2003 and 2004

	2003				2004			
Herbivore Taxa	**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
Lepidopteran 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
Membracidae	0	0	0	0	0	0	0.002	0.002
Curculionidae	0	0	0	0	0.028	0.014	0.034	0.01

Table 2

Average number of natural enemies found per tomato plant per season in high fire ant and suppressed fire ant treatments in 2003 and 2004

	2003				**2004**			
Natural Enemy Taxa	High fire ants	SE	Low fire ants	SE	High fire ants	SE	Low fire ants	SE
Spiders	0.09	0.004	0.09	0.03	0.09	0.028	0.09	0.01
Coccinellid Adults	0	0	0	0	0	0	0.005	0.005
Coccinellid Larvae	0.004	0.01	0	0	0	0	0	0
Reduviidae	0	0	0	0	0.014	0.009	0.01	0.005
Nabidae	0	0	0	0	0.56	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	0.019	0.007
Hymenoptera: Apocrita	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

Table 3

2003 & 2004 ANOVA results for the effects of fire ant suppression on the abundance of total aphids, alate aphids, apterous aphids, fire ants, herbivores and natural enemies

	2003						2004					
Arthropod	**date**		**treatment**		**date x treatment**		**date**		**treatment**		**date x treatment**	
	P	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**
Total aphid	0.006	8.57	<0.001	66.14	0.1	2.45	<0.001	18.8	<0.001	27.1	0.0004	10.5
Alate	0.003	9.82	<0.001	44.5	0.007	5.75	<0.001	18.3	<0.001	26.4	0.0002	11.4
Apterous	0.19	1.76	<0.001	49.77	0.73	0.32	0.005	6.44	0.198	1.73	0.48	0.74
Fire ants	0.34	1.12	0.11	2.66	0.34	1.12	0.18	1.79	0.04	4.63	0.61	0.5
Herbivore	0.06	3.89	0.24	1.52	0.16	1.96	0.008	10.2	0.96	0	0.82	0.2
Enemies	0.93	0.01	0.42	0.90	0.78	0.25	0.008	5.61	0.05	4.31	0.69	0.38

Data were log(n+1) transformed before analysis

Figure 1.

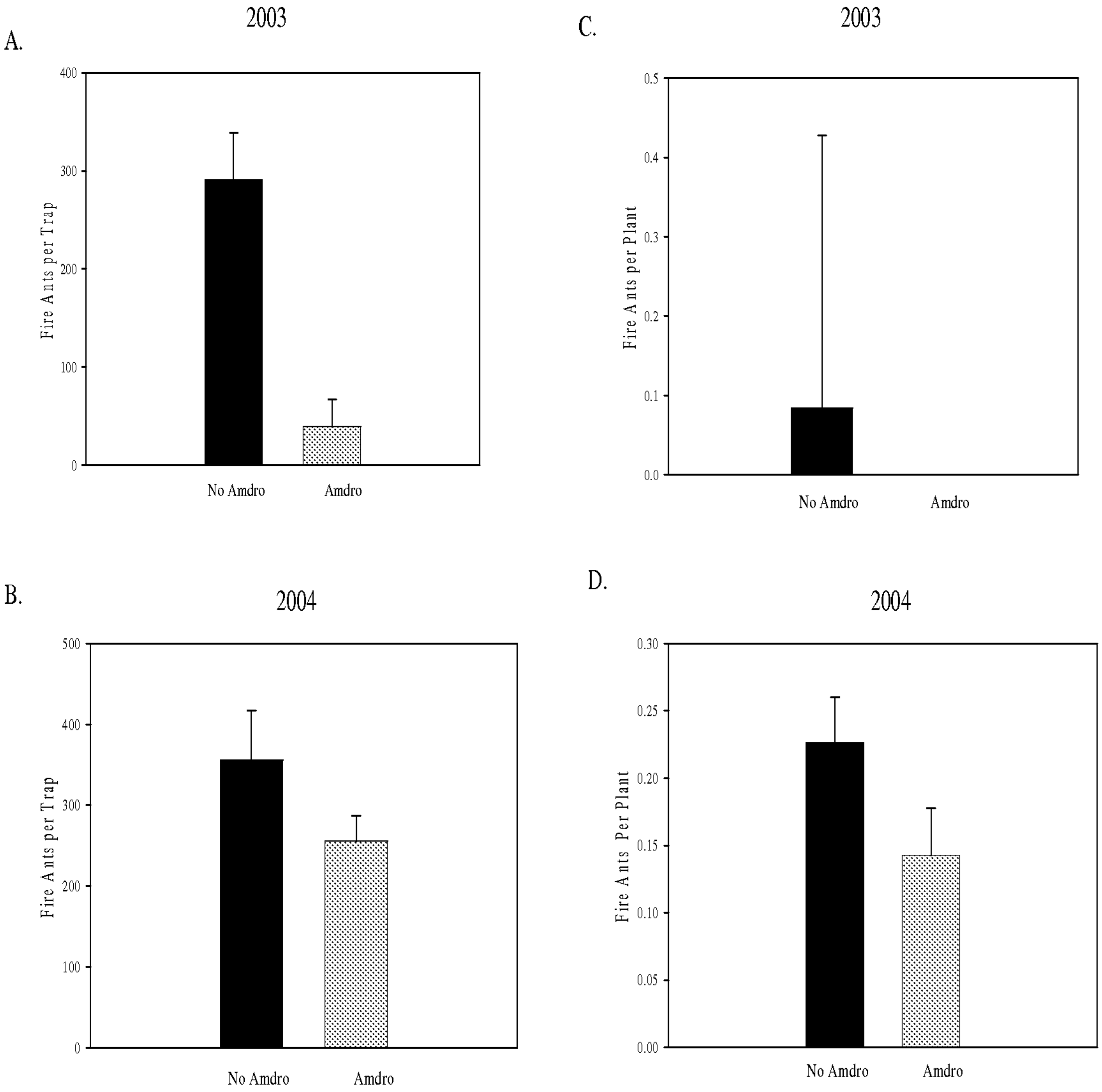

A.
2003
Fire Ants per Trap
0
100
200
300
400
No Amdro
Amdro
C.
2003
Fire Ants per Plant
0.0
0.1
0.2
0.3
0.4
0.5
No Amdro
Amdro
B.
2004
Fire Ants per Trap
0
100
200
300
400
500
No Amdro
Amdro
D.
2004
Fire Ants Per Plant
0.00
0.05
0.10
0.15
0.20
0.25
0.30
No Amdro
Amdro

Figure 2.

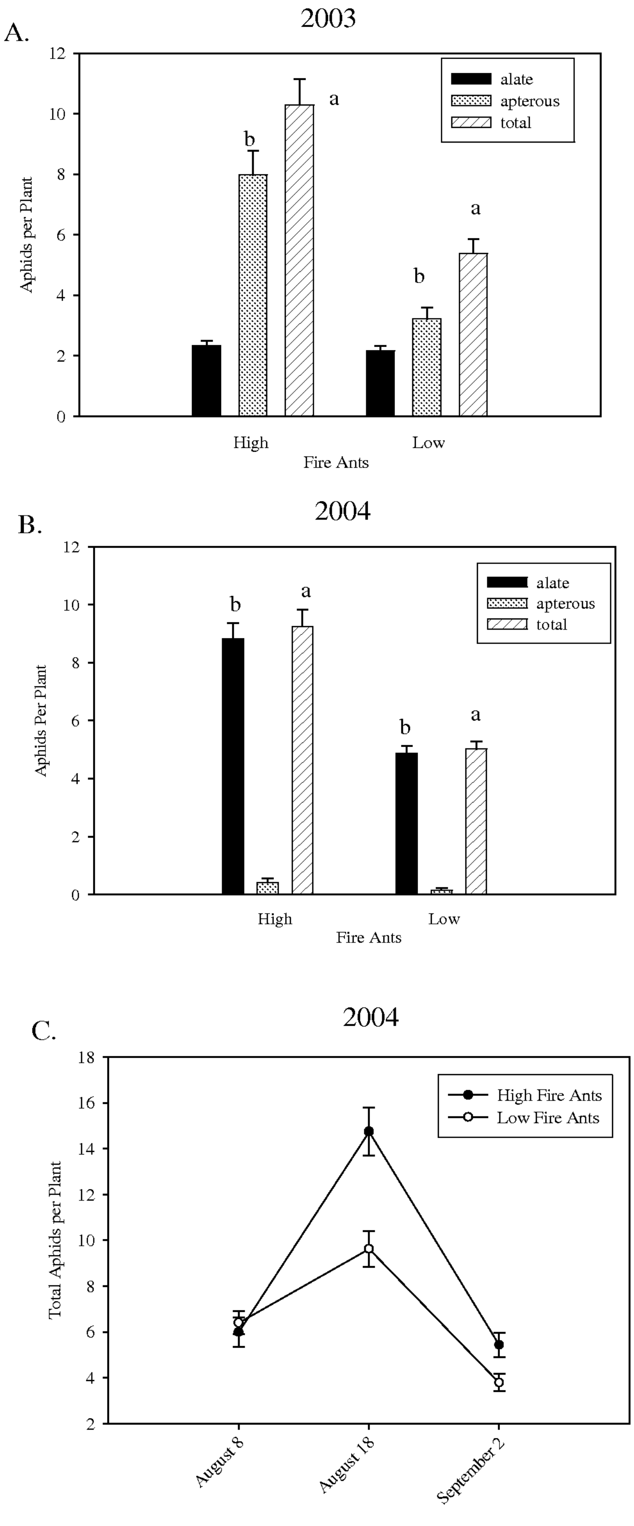

A.
2003
Aphids per Plant
0
2
4
6
8
10
12
alate
apterous
total
b
a
b
a
High
Low
Fire Ants
B.
2004
Aphids Per Plant
0
2
4
6
8
10
12
alate
apterous
total
b
a
b
a
High
Low
Fire Ants
C.
2004
Total Aphids per Plant
2
4
6
8
10
12
14
16
18
High Fire Ants
Low Fire Ants
August 8
August 18
September 2

Figure 3

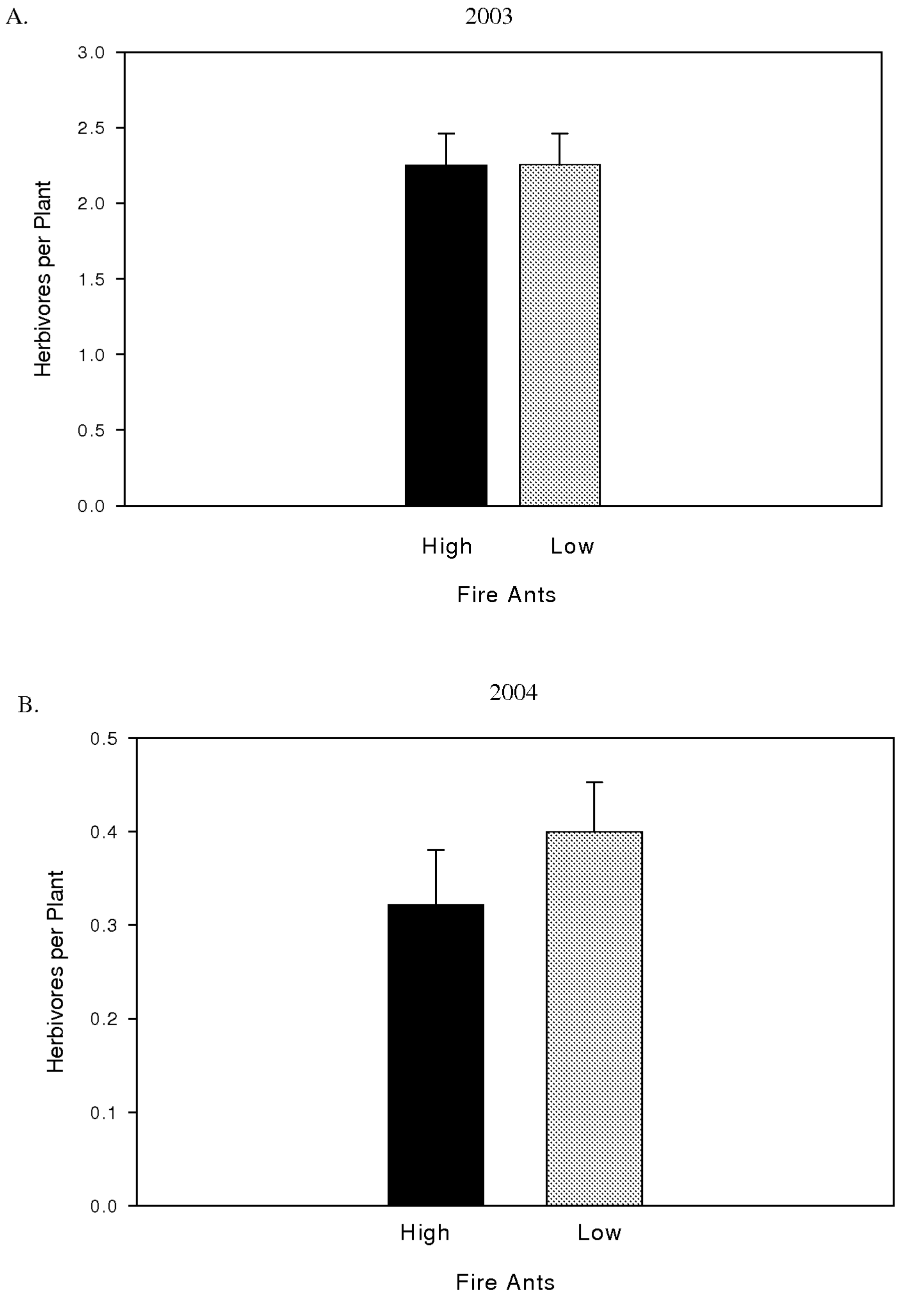
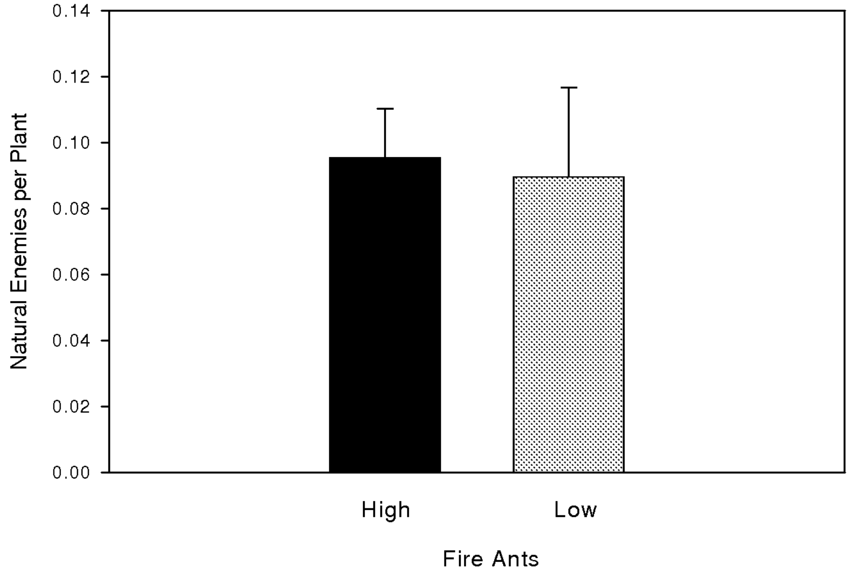

A.
2003
Herbivores per Plant
3.0
2.5
2.0
1.5
1.0
0.5
0.0
High
Low
Fire Ants
B.
2004
Herbivores per Plant
0.5
0.4
0.3
0.2
0.1
0.0
High
Low
Fire Ants

Figure 4

A. 2003



B. 2004

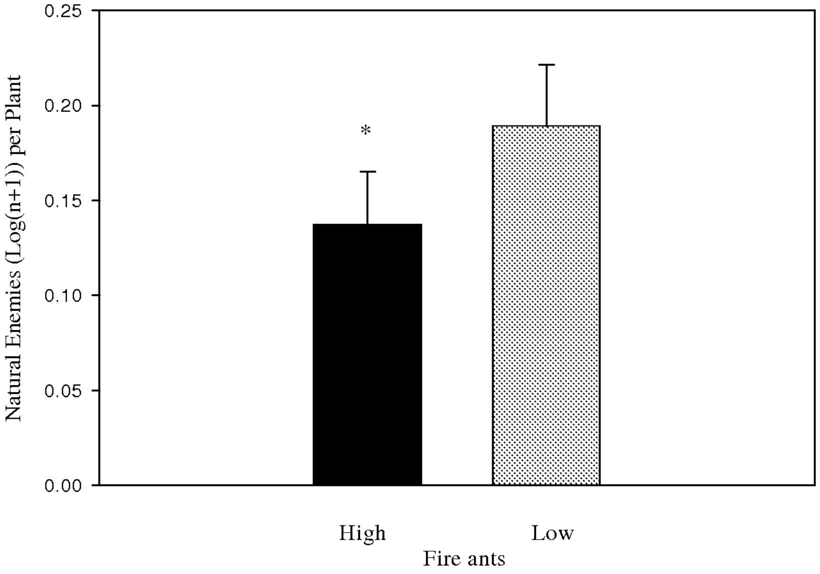


Figure 5

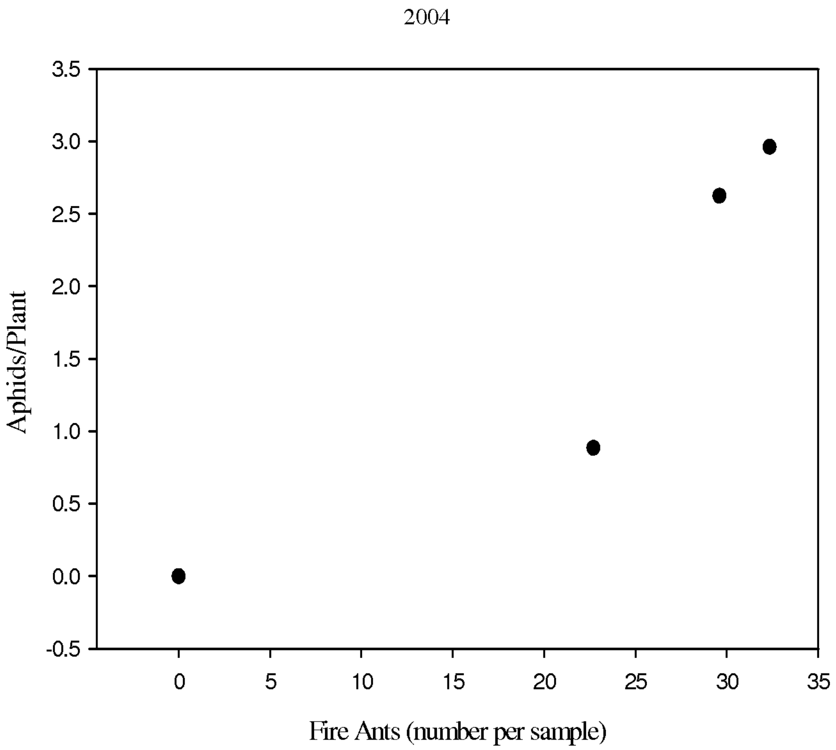

2004
Aphids/Plant
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
0
5
10
15
20
25
30
35
Fire Ants (number per sample)

Figure Legends

Figure 1: Mean seasonal number of fire ants present in no Amdro and Amdro fire ant treatments per trap (A) and per plant (B) in 2003 and per trap (C) and per plant (D) in 2004.

Figure 2: Mean seasonal abundance of aphids per tomato plant in high- fire ant and suppressed- fire ant plots in 2003 (A) and 2004 (B). (C) There was a significant total aphid by date by treatment effect (F = 10.51 P = .0004).

Figure 3: Mean seasonal number of non-aphid herbaceous arthropods found per tomato plant in high fire ant plots and suppressed fire ant plots in 2003 (A) and in 2003 (B). (A) Non-aphid herbivores were not significantly different between high fire ant plots (mean = 2.25; SE = 0.21) and suppressed fire ant plots (mean = 2.26; SE = 0.20). (B) Non-aphid herbivores were not significantly different between high fire ant plots (mean = 0.3217; SE = 0.058) and suppressed fire ant plots (mean = 0.4; SE = 0.05).

Figure 4: Mean seasonal number of natural enemies per tomato plant in high fire ant and suppressed low fire ant treatments in 2003 (A) and 2004 (B). (A) In 2003, the abundance of natural enemies between high fire ant plots (mean = 0.095; SE = 0.015) and suppressed fire ant plots (mean = 0.09; SE 0.027) were not significantly different. (B) In 2004, natural enemy abundance was significantly different between high fire ant plots (mean = 0.1373; SE = 0.0277) and suppressed fire ant plots (mean = 0.19; SE = 0.03).

Figure 5: The relationship between fire ant and aphid abundance in fresh market tomato fields.

EFFECTS OF FIRE ANT-APHID MUTUALISMS ON THE SPREAD OF AN APHID-VECTORED PLANT VIRUS

Introduction

Insect-vectored plant viruses are ubiquitous in both agricultural and wild plants populations and can severely reduce plant fitness/crop yield. For example, almost every agricultural crop is susceptible to at least one plant virus and most crop plants are susceptible to many viruses (Agrios 1997). Lettuce grown in California, for example, is routinely infected with over a dozen plant viruses, including *Lettuce mosaic virus*, *Beet curly top virus*, *Beet western yellows virus*, *Beet yellows virus*, *Beet necrotic yellow vein virus*, *Tomato bushy stunt virus*, *Tomato spotted wilt virus*, and *Tomato infectious chlorosis virus* (Wisler and Duffus 2000). Similarly, surveys of wild herbaceous plants routinely find high levels of virus infection involving agriculturally-important plant viruses. For example, Chatzivassiliou et al. (2001) intensively surveyed herbaceous plants near tobacco fields in Greece and found that 86 plant species representing 27 plant families (41% of those surveyed) were infected with *Tomato spotted wilt virus* and virus incidence (percentage of plants that were infected) was often high. A similar survey for *Cucumber mosaic virus* (CMV) in herbaceous plants near melon fields in Spain found that 40 species belonging to 17 plant families were infected and virus incidence reached

100% in some species (Sacristan et al. 2004). Virus infection typically leads to one or more types of symptoms in a plant and expression of these symptoms may change in type and intensity over time. Examples of commonly observed virus-induced symptoms include foliar chlorosis and mosaic, lesions on leaves and fruit, distortion of leaves, fruit, stems and roots, overall plant stunting and a shortened life span (Agrios 1997). These symptoms usually result in reduced plant fitness or crop yield and these effects can be extreme in many plants. For example, chronic epidemics of CMV lasting ten or more years in parts of North America and Europe have devastated tomato production in some areas. Yield losses have reached 80 – 100% in some years and acreage devoted to tomato production has decreased by as much as 80% in some areas (Galletelli et al. 1988, Jorda et al. 1992, Kaper et al. 1990, Sikora et al. 1998). These extreme effects of plant viruses are not uncommon. Insect-vectored viruses are responsible for 47% of emerging infectious plant diseases worldwide (Anderson et al. 2004) and their economic impact is estimated at several billion U.S. dollars per year (Rudolph 2003).

Because of their severe effects on plants, the epidemiology and control of plant viruses has received considerable attention. Insects, primarily aphids, are the predominant vectors of plant viruses (Tomlinson 1987). Some aphid-vectored plant viruses are transmitted in a persistent or circulative manner. These viruses are acquired from infected plants by insects but can not be immediately transmitted. The aphid vector must accumulate the virus internally and the virus can not be transmitted by the insect until the virus passes through insect tissues (Agrios 1997). Some other aphid-vectored plant viruses, however, are transmitted in a nonpersistent manner. These viruses are primarily vectored by aphids and have no latent period, acquisition and transmission occurs rapidly (in seconds). These viruses are highly concentrated in the epidermis of systemically infected host plants (Harris and Maramorosch 1977), bind to the stylets of aphids during brief probes of the plant epidermis, and can be immediately transmitted to new plants by the aphid (Pollard 1973, Fereres 2000). Management of nonpersistently transmitted viruses in agricultural crops is extremely difficult because acquisition and transmission occurs very rapidly. Applications of insecticides that target the vector (aphids) are commonly used and can be effective for persistently transmitted viruses, but typically fail to control nonpersistently transmitted viruses because aphids can acquire and transmit the viruses before they are intoxicated by insecticides. Furthermore, insecticides can cause increased probing in aphids resulting in increased plant-to-plant spread of viruses (Raccah et al. 1985, Perring et al. 1999). Thus the rate and extent of outbreaks of these viruses is largely dependent on aphid population dynamics and behavior (Spence 2001, Jeger 2004) and disrupting the population dynamics of aphids is critical for disease management (Irwin and Ruesink 1986, Irwin et al. 2000, Culbreath et al. 2003, Jones 2004, Jeger et al. 2004, Anderson et al. 2004). Therefore any factor that increases the abundance of aphids is likely to increase the spread of plant viruses and potentially lead to virus epidemics (Madden et al. 2000, Hull 2002, Jeger et al. 2004). For example, the abundance of aphids is positively correlated with the incidence of *Barely yellow dwarf virus* (Bencharki et al. 2000, Chapin et al. 2000, Fabre et al. 2003, Fabre et al. 2005), *Potato virus Y* (Basky 2000), *Potato leafroll virus* (Castle et al. 1998, Basky 2000), and *Beet mosaic virus* (Dusi et al. 2000).

Work in southeastern agricultural systems has identified an important ecological interaction that can dramatically alter the abundance of important virus vectors: fire ant –

aphid mutualisms. Red imported fire ants, *Solenopsis invicta* 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 1900's, now range across the southern United States from North Carolina to Arizona, and have recently invaded California (MacKay and Fagerlund 1997, Vinson 1997, Anonymous 1999, Mobley and Redding 2005). Fire ants reach extremely high densities and consume large numbers of other arthropods (Porter and Savignano 1990, Williams 1994, Vinson 1997). Fire ants, like almost all ant species, readily form facultative mutualisms with honeydew-producing insects such as aphids, scales, and whiteflies (Reilly and Sterling 1983a, 1983b, Vinson and Scarborough 1989, Vinson 1997, Helms and Vinson 2002).

Studies on the ecological consequences of fire ant – aphid mutualisms in Alabama have been ongoing for several years. These studies have shown that fire ants are very attracted to plants infested with aphids. Fire ants, for example, preferentially foraged on aphid-infested cotton plants compared to aphid-free cotton plants in greenhouse experiments and fire ant and cotton aphid abundances are positively correlated in the field (Kaplan and Eubanks 2002, 2005). Fire ants are very effective at protecting aphids from predators. Fire ant predation of lady beetle larvae was twice as high on aphid-infested plants as on aphid-free plants (Kaplan and Eubanks 2002). Furthermore, predator larvae were more than twice as abundant in cotton fields with suppressed densities of fire ants than in control fields with large fire ant populations. Consequently, cotton aphids were three to five times more abundant in cotton fields with large fire ant populations than in fields with suppressed fire ant populations (Kaplan and Eubanks 2002, 2005).

Diaz et al. (2004) found similar, positive effects of fire ants on cotton aphids in Texas. It is likely that aphid-tending by fire ants results in large populations of most aphids and other honeydew-producing insects (Vinson 1997, Helms and Vinson 2002).

The positive effect of ants on aphid population density is likely to 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 three to five fold increase in aphid population density (i.e., Kaplan and Eubanks 2002, 2005), then it is likely that fire ant protection will result in a three to five 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 primary goal of this project is to test this hypothesis.

Because mutualisms involving ants and aphids are extremely ubiquitous in nature and these mutualisms can dramatically affect aphid population dynamics (Way 1963, Hölldobler and Wilson 1990), it is very possible that ants play a major and to date undiscovered role in the dispersal of aphids and the subsequent spread of aphid-vectored viruses. For example, even cursory searches of the literature show that key vectors of many viruses are often strongly affected by mutualisms with ants. Cotton aphids (*Aphis gossypii*), for example, are one of the most important worldwide vectors of CMV (Palukaitis et al. 1992) and many other viruses including *Zucchini yellow mosaic virus* (Mahgoub et al. 1997), *Citrus tristeza virus* (Cambra et al. 2000), *Cucurbit aphid-borne* *yellows virus* (Reinbold 2003), *Sugarcane mosaic virus* (Gambley et al. 2004), and *Lettuce mosaic virus* (Nebreda et al. 2004). This aphid species routinely forms important facultative mutualisms with fire ants in the U.S. (e.g., Kaplan and Eubanks 2002) and the ants *Lasius niger* and *Pristomyrex pungens* in Japan (Kaneko 2003). Likewise, *Aphis fabae* is an important vector of *Beet yellows virus* and *Beet mosaic virus* (Fernandez-Quintanilla 2002) as well as *Potato virus Y* (Basky and Almasi 2005) and *Plum pox virus* (Gildow et al. 2004). This aphid is tended by *Lasius niger* in Europe (Offenberg et al. 2001, Woodring et al. 2004) and *Formica neoclara* (Capinera and Roltsch 1981) and *Lasius neoniger* (J.P. Harmon unpublished data) in the U.S. *Rhopalosiphum padi*, a widely distributed and extremely important vector of *Barley* and *Cereal yellow dwarf viruses* (Gillet et al. 1990, Plumb et al. 1990), forms facultative mutualisms with the ant *Lasius niger* in Europe (Glinwood et al. 2003), fire ants in the U.S. (Vinson and Scarborough 1991), and Argentine ants in South America (Córdova-Yamauchi et al. 1998). Similarly, *Toxoptera citricida* is an important vector of *Citrus tristeza virus* (Halbert et al. 2004, Powell and Lin 2005) and is tended by the ant *Tapinoma simrothi* in Europe (Dartiguies 1992) and fire ants in the U.S. and Puerto Rico (Michaud 1999). Although often undocumented and sometimes even unnoticed, ant – aphid mutualisms are everywhere, alter the population dynamics of aphids, and, as a result probably alter the dispersal of aphids (Way 1963, Buckley 1987, Holway et al. 2002).

The objective of this study was to quantify the indirect effects of fire ants on a nonpersistently transmitted plant virus. To address this objective, I conducted a series of small plot experiments, greenhouse experiments, and large-scale field experiments. Plot experiments were conducted at E.V. Smith Research Center in Macon County, Alabama, during 2003 and 2004 to investigate the effects of fire ants on aphid abundance. A greenhouse experiment was conducted at Auburn University, Auburn, Alabama, to test the effects of fire ants on aphid dispersal. On-farm sampling was conducted during 2004 in Blount Co., Alabama, to quantify the relationship between red imported fire ants, aphids, and the incidence of CMV. In 2005, red imported fire ant abundance was manipulated in large tomato fields and subsequent changes in aphid abundance and virus incidence were documented. This is the first study to suggest that an important and ubiquitous ecological interaction, ant – aphid mutualisms, can influence the spread of plant viruses.

Materials and Methods

Small Plot Experiment

Small plot experiments were conducted at the E.V. Smith Research Center in Macon County, Alabama during 2003 and 2004. For both field seasons, tomatoes (*Solanum lycopersicum* variety: Floralina) were grown from seeds in the greenhouse for one month or until they reached 20 cm in height, and were then placed outdoors for one week for acclimatization to natural conditions. In 2003, twelve, 3 m plots of tomato plants, separated by at least 10 m were established. Each plot consisted of 30 plants, spaced 45 cm apart and organized into three rows separated by 75 cm each. Plants were visually searched for aphids and fire ants. 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 using the same plant and row spacing as in 2003. On August 18 and August 26 of the 2004 field season, all 30 plants per plot were searched. Nine plants per plot were visually searched on September 2, 2004.

Plots were randomly divided into two treatments: natural/high fire ant density (control) or suppressed fire ant density (treatment). Suppression treatments were established using Amdro®, a commercially available, ant-specific bait. The active ingredient of Amdro® is hydramethylnon, which blocks the production of ATP, killing target ants by inhibiting energy production (Valles and Koehler 1997). Amdro® is readily picked up by foraging fire ants and does not affect survival of non-target arthropods (Hu and Frank 1996, Eubanks et al. 2002), and has been successfully used to suppress fire ants in similar sized and spaced plant plots in other studies (e.g., Harvey and Eubanks 2004, 2005). Amdro® was applied weekly to plots assigned to the fire ant suppression treatment, beginning one week prior to sampling, and fire ants were allowed to naturally colonize control (natural/high fire ant) plots. Fire ant abundance was quantified weekly within each plot using a tube trap. 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 ≈ 45 minutes, after which they were collected, sealed, and returned to the laboratory. Ants were counted within 48 hours.

Greenhouse Experiment

In 2003, a greenhouse experiment was conducted to test the effect of fire ants on aphid movement. Wading pools (1.5 m diameter) were caged and four tomato plants were planted equal distance from an aphid infested central cotton plant in each pool. All plants were separated by approximately 1 m. At the beginning of the experiment aphid densities were not significantly different between pools with and without red imported fire ants. A red imported fire ant colony, with approximately 500 workers, was placed in the center of caged pools, at the base of the aphid-infested cotton plant. Each tomato plant was visually searched for the presence of aphids and fire ants after 72 hours. This experiment was repeated 9 times.

Whole Field Survey and Experiment

The tomato fields used in the 2004 and 2005 study were managed by two growers (Farm one and Farm two) and each field was approximately 2.4 hectares. It was important to use fields managed by different growers because of differences in pesticide use, soil type and nutrients, irrigation and the species composition of surrounding herbaceous vegetation. Both of these tomato growers follow a cultivation practice of planting tomato transplants every three weeks from April through August, resulting in fields of tomatoes ranging in age. In both 2004 and 2005, all of the tomato fields managed by farm one were located on the top of a small ridge within 5 km of each other. Fields managed by farm two in 2004 were 5 to 35 km from fields managed by farm one.

In 2004, I surveyed four fields in Blount County, Alabama, for fire ants and aphids weekly for 8 weeks. Surveying consisted of visually searching approximately 20 randomly selected tomato plants per 0.4 hectare of tomato for the presence of fire ants and aphids. All aphids present on a tomato plant were collected for identification. To quantify the relative abundance of fire ants within a tomato field, eight tube traps were randomly distributed throughout the field. Traps consisted of a 12 cm long plastic tube baited with a 5 cm long piece of hotdog. Ants were able to recruit for at least one hour before being collected. All traps were stored in a freezer at 0°C before ants were counted.

In addition to tomato plants, we visually searched herbaceous plants around tomato fields for the presence of aphids and fire ants. Herbaceous plants found to be hosting aphids were identified and aphids were collected for later identification. In addition to visually searching plants we placed two tube traps within herbaceous areas around each tomato field to quantify the relative abundance of fire ants. Ants were able to recruit to traps for at least one hour before being collected.

To test for CMV infection, leaf tissue from tomato and herbaceous plants was collected, samples were wrapped in a moist paper towel, and placed on ice and transported to Auburn University and stored at 20° C until assayed. Approximately 20 tomato plants and 20 herbaceous plants per 0.4 hectare were sampled four times throughout the season. Each sample to be tested for CMV infection by enzyme-linked immunosorbent assay (ELISA) consisted of a terminal leaflet for tomato or upper leaves for herbaceous plant samples. Samples were ground using a motorized leaf press with the sap extracts tested for CMV by ELISA. An Agdia, Inc. commercial ELISA kit was used according to the manufacturer's instructions (Agdia, Inc., Elkhart, IN). Each sample was processed in 2 ml of extraction buffer (according to kit directions) and added to a microtiter plate at a final dilution of 1:4 (sap extract to buffer). All subsequent steps were as described by the manufacturer. Reactions were read at 405 nm using a Sunrise microtiter plate reader (Phenix Research Products, Hayward, CA). A sample was considered positive for the presence of CMV when the ELISA absorbance value was greater than the threshold (mean plus three standard deviations) determined from uninfected samples.

In 2005, I surveyed 12 fresh market tomato fields in Blount County, Alabama, for 14 weeks, following the same protocol as in 2004. Due to logistical constraints, two of these fields were not surveyed for fire ants and aphids. Six fields were treated with fire ant suppressing baits (Extinguish® was used within the tomato field and in surrounding vegetation, Extinguish Plus® and Amdro Pro® were used only within surrounding vegetation) and six fields were left untreated, resulting in naturally occurring, high densities of fire ants. Fire ant suppressing baits were applied to each treatment field at rate of ≈1.5 lbs per 0.4 hectare. In an ideal situation, each replicate of this experiment would contain both a treatment and control field of the same age (similar planting date) on the same farm. Unfortunately, the ideal situation is not possible because of the cultural practices of growers only planting one field at a time, thus one replicate of the experiment consisted of a pair of fields of the same age on different farms: one at farm one and one at farm two. Fields were randomly selected as control or fire ant suppression treatments.

In order to quantify the relative abundance of fire ants, I placed two pitfall traps per 0.4 hectare within the tomato fields. Pitfall traps were replaced every seven days.

Additionally, two tube traps per 0.4 hectares were placed at the edges of the tomato field. Tube traps were left for at least one hour before they were collected. Due to initial low counts of fire ants in both pitfall traps and tube traps, a visual search for fire ants within tomato fields was conducted. During each sample approximately 6 m of bare ground in between tomato rows was visually searched and at least four visual searches were conducted for each sampling date at each field.

In order to examine the role of herbaceous plants in the dynamics of CMV, I established 1 x 3 m herbaceous plots (~ one per 0.4 hectare) around each tomato field. Each week every plant in the plot was visually searched for the presence of aphids and fire ants. Representative aphids were collected to be identified at a later date. Each plot had one pitfall trap and one tube trap to quantify the relative abundance of fire ants. I identified all of the plants in each plot and their relative abundance.

To test for CMV infection, leaf tissue from tomato and herbaceous plants were collected, samples were wrapped in a moist paper towel, placed on ice, and transported to Auburn University and stored at 20° C until assayed. In 2005, plants were sampled once per field when the tomato plants within the field were approximately nine weeks old. Approximately 20 tomato samples per 0.4 hectare were collected within each tomato field and approximately 20 herbaceous plant samples were collected from each herbaceous plot. At least one plant sample of every herbaceous plant species in a plot was collected and additional plant samples were collected according to their relative abundance in the plot. Each sample was tested for CMV by ELISA following the same protocol as in 2004.

Results

Field Plot Experiment

The Amdro® applications resulted in reduced fire ant densities in the small plot experiments. For example, in 2003, the abundance of fire ants foraging on the ground in tomato plots was significantly reduced by the application of Amdro® (No Amdro® mean = 290.66 ± 48.13, Amdro® mean = 39.17 ± 27.88, $F_{1,20} = 27.51$, $P = <0.0001$). Similarly, in 2004 fire ant abundance on tomato plants was significantly lower in treated plots than in control plots (No Amdro® mean = 0.23 ± 0.03, Amdro® mean = 0.14 ± 0.03, $F_{1,29} = 4.63$, $P = 0.04$).

Changes in fire ant abundance resulted in changes in aphid abundance. For example, in 2003 aphid abundance was 48% greater in plots with high densities of fire ants than in plots with suppressed densities of fire ants ($F_{1,30} = 8.57$, $P = 0.01$) (Figure 1A). Similarly, in 2004 the abundance of aphids was 46% greater in high fire ant plots than in suppressed fire ant plots ($F_{1,29} = 27.2$, $P < 0.0001$) (Figure 1B). These results suggest that fire ants can rapidly affect the abundance of aphids at relatively small scales.

Greenhouse Experiment

In the greenhouse experiment, significantly more aphids were found on tomato plants adjacent to aphid-infested cotton plants that were exposed to fire ants (mean = 19.4

± 6.2) than on plants adjacent to aphid-infested cotton plants without fire ants (mean = 12.2 ± 5.8) ($F_{1,}$ = 5.34 P= 0.02) (Figure 2). These results indicate that aphids were 59% more likely to move among plants in the presence of fire ants than in the absence of fire ants.

Whole Field Experiment

In 2004, the abundance of fire ants and aphids were positively correlated in fresh market tomato fields (one-tailed test, r = 0.09, P = 0.04, N = 4) (Figure 3A) and aphid abundance was positively correlated with CMV incidence (r = 0.09, P = 0.05, N = 4) (Figure 3B). Most importantly, fire ant abundance was positively correlated with CMV incidence (r = 0.09, P = 0.01, N = 4) (Figure 3C).

The large-scale manipulation of fire ant abundance was successful as indicated by differences in fire ant abundance as estimated by several sampling methods. For example, in 2005 the number of fire ants observed during visual searches was significantly higher in tomato fields with naturally occurring, high fire ant densities (control fields) than in fields with suppressed fire ant densities (baited fields) ($F_{1,9}$ = 10.8, P = 0.01) (Figure 4A). Likewise, the number of fire ants captured in tube traps also differed between farms ($F_{1,9}$ = 13.2, P = 0.01) (Figure 4B) and between tomato fields with naturally occurring (control fields) and suppressed fire ant densities (baited fields) ($F_{1,9}$ = 4.77, P = 0.07) (Figure 4C). Additionally, the number of fire ants collected in pitfall traps was significantly different between treatments, with fire ants approximately 2.5 times more abundant in control fields than treated fields ($F_{1,9}$ = 4.83, P = 0.07) (Figure 4D).

Alate aphids were significantly more abundant in tomato fields with high densities of fire ants than in fields with suppressed fire ant densities ($F_{1,9} = 5.97$, $P = 0.05$). Additionally, total aphid abundance (alate and apterous aphids combined) was significantly higher in control tomato fields than in baited tomato fields ($F_{1,9} = 6.26$, $P = 0.04$) (Figure 5).

There was a significant farm by treatment interaction on CMV incidence, (the proportion of plants that tested positive for CMV), during the field experiment ($F_{2,11} = 15.95$, $P = 0.0016$) (Figure 6A). On farm two, the number of aphids per tomato plant (mean = 5.08 ± 1.7) was higher than on farm one (mean = 4.3 ± 4.3). Additionally, fire ants were detected in tomatoes at higher densities on farm one (mean = 50 ± 14) than farm two (mean = 8 ± 3.8). There was also a significant positive correlation between planting date and CMV incidence (one tailed test: $r = 0.57$, $P = 0.03$, $N = 12$) (Figure 6B). Additionally, there was a positive correlation between alate aphids and CMV incidence (one tailed test: $r = 0.48$, $P = .08$, $N = 10$).

Discussion

The results of this study strongly suggest that aphid-tending by the invasive red imported fire ant increases aphid populations and subsequently increases the spread of aphid-vectored plant viruses. Mutualisms involving ants and aphids are extremely ubiquitous in nature and these mutualisms can dramatically affect aphid population dynamics (Way 1963, Hölldobler and Wilson 1990). Since aphids are the primary vector of many plant viruses, any factor that increases their abundance is likely to increase the spread of virus and the potential for a virus epidemic (Madden et al. 2000, Hull 2002, Jeger et al. 2004). Changes in the abundance of pathogen vectors as a result of human activity are thought to be a primary cause of new disease epidemics. Work on the indirect effect of an invasive ant on the spread of an aphid-vectored plant virus suggests that species introductions by humans may have profound effects on the ecology of plant diseases. These results have important implications for both future management of aphid-vectored plant viruses and the potential impact of red imported fire ants as they increase their range into California and other areas.

The effects of plant viruses on plants include stunting, reduction in fitness/yield, and plant death. The worldwide impact of these viruses can be economically devastating, costing several billion U.S. dollars per year. For example, in southern Illinois bell pepper production, CMV has resulted in significant losses since 1992 (Hobbs et al. 2000). These losses are due to fruit spotting, fruit malformation, and reduction in size and number of fruit (Hobbs et al. 2000). In the Mediterranean basin CMV incidences in tomatoes, melons, and peppers range from 30-100%, resulting in severe economic losses (Gallitelli et al. 1995, Gallitelli 2000, Alonso-Prados et al. 1997, Luis-Arteaga et al. 1998, Varveri and Boutsika 1999). Additionally, CMV has resulted in up to 100% yield losses in the main tomato production areas in Italy and Spain (Gallitelli et al. 1988, Gallitelli 2000, Jorda et al.1992).

Due to the economically devastating effects of aphid-vectored plant viruses, agricultural management schemes utilize pesticides that target aphid vectors as a primary method of plant virus control. Targeting aphid vectors may prove effective if one is attempting to control persistently transmitted viruses, but not for viruses transmitted in a non-persistent manner. Viruses transmitted in a non-persistent manner are difficult to control because acquisition and transmission can occur within seconds. Application of chemical pesticides is usually ineffective because aphids can acquire and transmit viruses before they are disabled and some chemicals can actually enhance the spread of plant viruses by increasing aphid activity (Maelzer 1986, Lowery and Boiteau 1988, Roberts et al. 1993, Perring et al. 1999). For an insecticide to be useful in controlling plant viruses transmitted in a non-persistent manner, it must kill the vector rapidly, repel the vector or modify vector behavior to prevent probing (Broadbent 1957, Heinrichs 1979, Perring et al. 1999). That said, growers in fire ant infested areas may be targeting the wrong pest in their attempts to manage aphid-vectored plant viruses. Our results indicate that by targeting red imported fire ants, growers may be able to reduce the spread of aphid-vectored plant viruses by as much as 95%, resulting in an increase in yield. This increase in yield via a reduction in plant virus could result in the potential savings of thousands of dollars per field. Fire ants can be controlled by using ant-specific baits, which act to block the production of ATP, resulting in death via inhibition of energy production (Valles and Koehler 1997). These ant-suppressing baits are only picked up by foraging fire ant workers and do not affect the survival of non-target arthropods (Hu and Frank 1996). Therefore by targeting fire ants, growers can reduce the economic cost of controlling for aphid-vectored plant viruses and reduce the damage to the environment and not-target organisms via the reduction of harmful pesticide applications.

As the red imported fire ant expands its territory our results indicate that this invasive species may dramatically affect the spread of aphid-vectored plant viruses. Currently in the U.S. the red imported fire ant is found in all or part of 13 southern states ranging from North Carolina to Southern California (Mobley and Redding 2005).

Additionally, the red imported fire ant has been found in Australia, Antigua and Barbuda, Bahamas, Hong Kong, Malaysia, Puerto Rico, Taiwan, Trinidad and Tobago, Turks and Caicos Islands, and the British Virgin Islands (ISSG Global Invasive Species Database). Other invasive ants such as the Argentine ant (*Linepithema humile*) vigorously tend aphids (Holway et al. 2002) and may have similar effects on the spread of aphid-vectored plant viruses.

The effects of fire ant suppression on CMV incidence did, however, differ among the two farms. In the 2005 field experiment, CMV incidence was significantly greater in fields on farm two with high densities of fire ants than fields with suppressed fire ant densities. In contrast, CMV incidence was not statistically different among control and baited fields on farm one (Figure 6A). Variation in the effects of fire ant suppression on CMV incidence among the two farms may have occurred for several reasons. First, the effects of fire ants on aphid abundance may have differed among the farms resulting in little effect of fire ant suppression on aphid population dynamics on farm one. This, however, was not the case: fire ant suppression translated into reductions in the number of aphids in tomato on both farms (Table 1). Second, the amount of the virus available for aphids to acquire and move into tomato fields may have differed among the farms. If the infection rate (percent of herbaceous plants that are infected with virus) is high, then it takes relatively few aphids to spread nonpersistently transmitted viruses and cause epidemics (Tomlinson 1987, Irwin et al. 2000, Jeger et al. 2004). Under this condition, changes in the abundance of aphids are unlikely to alter the dynamics of CMV. If infection rates were higher on farm one than farm two, then this may explain why changes in aphid abundance due to fire ant suppression on farm one had little effect on

CMV incidence in tomato. Infection rates, however, did not differ among the two farms and were relatively low around all the fields on both farms (Table 2). The percent of herbaceous plants infected with CMV was 10 % or less at every field and there was no relationship between this value and CMV incidence in tomato. Thus, it appears unlikely that differences in infection rates affected the results of this study. Third, it is possible that the composition of aphid species differed among the two farms. Variation in aphid species can be important because some aphid species are more efficient vectors of CMV than other aphid species (Tomlinson 1987). A preliminary analysis of the aphids sampled on each farm, however, indicates that the aphid community was composed of the same aphid species (primarily *Myzus persicae, Aphis fabae, A. gossypii, Microsiphum rosae, M. euphorbiae, Uroleucon ambrosiae,* and *Aulacorthum solani*), so variation in the abundance of different aphid species is unlikely to explain variation in CMV incidence among farms. A fourth possibility is that random variation in the timing of the arrival of virus into tomato fields produced the differences among farms. It has been documented that extensive CMV outbreaks in the southern U.S. tend to occur in mid July, but that the outbreak of CMV and other plant viruses can vary by a few weeks on neighboring farms (Sikora et al. 1998, Garcia-Ruiz and Murphy 2001). When looking at CMV incidence in pairs of control and bait-treated fields planted at different times of the season (Figure 6B), one can see that CMV incidence was higher in the control fields than in the fire ant suppressed fields in four out of the six pairs. The pair of fields with the earliest planting date had no virus and so did not differ in CMV incidence. The third pair of fields did differ in CMV incidence, but opposite of my prediction: the bait-treated field had higher CMV incidence (0.51) than the control field (0.01). In this pair of fields the bait-treated field was at farm one and the control field was at farm two. I believe that the CMV outbreak started approximately two to three weeks earlier on farm one than farm two. This means that the tomato plants in the third field at farm two were not exposed to CMV during their most vulnerable stage of plant development resulting in a lower than expected incidence of CMV (0.01).

In conclusion, fire ants directly affect aphid populations and therefore indirectly affect the incidence of aphid-vectored plant viruses. Therefore, the invasive red imported fire ant may have considerable importance in the epidemiology of aphid-vectored plant viruses. These results indicate a need to explore the effects of invasive ants and native ants on the spread of aphid-vectored plant viruses. Additionally, a more definitive test with greater replication needs to be conducted in order to fully understand the role of fire ants in plant virus epidemics. A model which included the infection rate, inoculum sources, change in aphid population size and aphid composition would be of great benefit in mediating the effect of ant-aphid mutualisms on the spread of aphid-vectored plant viruses.

Tables

Table 1

2005: CMV Incidence, Mean Aphid and Fire Ant Abundance in Tomato

Field	Treatment	Farm	CMV incidence[a]	Aphids[b]	Aphids Combo[c]	Fire ants[d]
1	H	farm one	0	4.5	9.5	38.3
1	L	farm two	0.01	2.08	4.4	1.23
2	H	farm one	0.06	2.02	4.25	66.7
2	L	farm two	0.009	0.9	1.94	2.36
3	H	farm one	0.01	1.2	2.48	94.8
3	L	farm two	0.51	0.83	1.82	1.29
4	H	farm two	0.98	NA	NA	NA
4	L	farm one	0.81	NA	NA	NA
5	H	farm two	1	5.56	11.2	18.3
5	L	farm one	0.22	1.54	3.06	16.4
6	H	farm two	1	3	6.03	15.96
6	L	farm one	0.05	1.14	2.32	32.1

[a] The proportion of tomato plants that tested positive for CMV.

[b] The average aphids per tomato plant .

[c] The total average total aphids present per plant and per pitfall trap in tomato fields.

[d] The average total fire ants present per plant, per pitfall trap and per tube trap in tomato fields

Table 2

2005: CMV Incidence, Mean Aphid and Fire Ant Abundance in Herbaceous Plants

Field	Treatment	Farm	CMV incidence[a]	Aphids[b]	Aphids Combo[c]	Fire ants[d]
1	H	farm one	0.09	5.4	11.4	35.4
1	L	farm two	0.10	1.68	3.5	4.99
2	H	farm one	0.01	6.2	12.4	68.6
2	L	farm two	0.07	5.7	11.8	11.8
3	H	farm one	0.08	0.08	0.25	121.7
3	L	farm two	0.08	5.7	11.8	11.8
5	H	farm two	0.07	1.3	2.67	44.5
5	L	farm one	0.01	8.7	17.4	0.7
6	H	farm two	0	1.6	8	86.33
6	L	farm one	0.04	2.57	5.14	13.75

[a] The proportion of tomato plants that tested positive for CMV.

[b] The average aphids per tomato plant .

[c] The total average total aphids present per plant and per pitfall trap in tomato fields.

[d] The average total fire ants present per plant, per pitfall trap and per tube trap in tomato fields

Figure Legends

Figure 1

Mean seasonal abundance of aphids per tomato plant in high- fire ant and suppressed- fire ant plots in 2003 (A) and 2004 (B)

Figure 2

Mean aphid abundance per tomato plant in high-fire ant and low-fire ant greenhouse pools in 2003.

Figure 3

The relationship between fire ants and aphids (A), aphids and the incidence of CMV and (B) fire ants and the incidence of CMV (C) in fresh market tomato fields for the 2004 season

Figure 4

(A) Mean fire ant abundance per 20 row feet for high and suppressed fire ant tomato fields. (B) Mean fire ant density per trap on farm one and farm two and (C) for high and suppressed fire ant tomato fields. (D) Mean abundance of fire ants per pitfall trap in high and suppressed fire ant tomato fields.

Figure 5

Mean total aphids per tomato plant and for high and suppressed fire ant tomato fields.

Figure 6

2005 (A) CMV incidence by farm and treatment (B) CMV incidence by setting and treatment

Figures

Figure 1

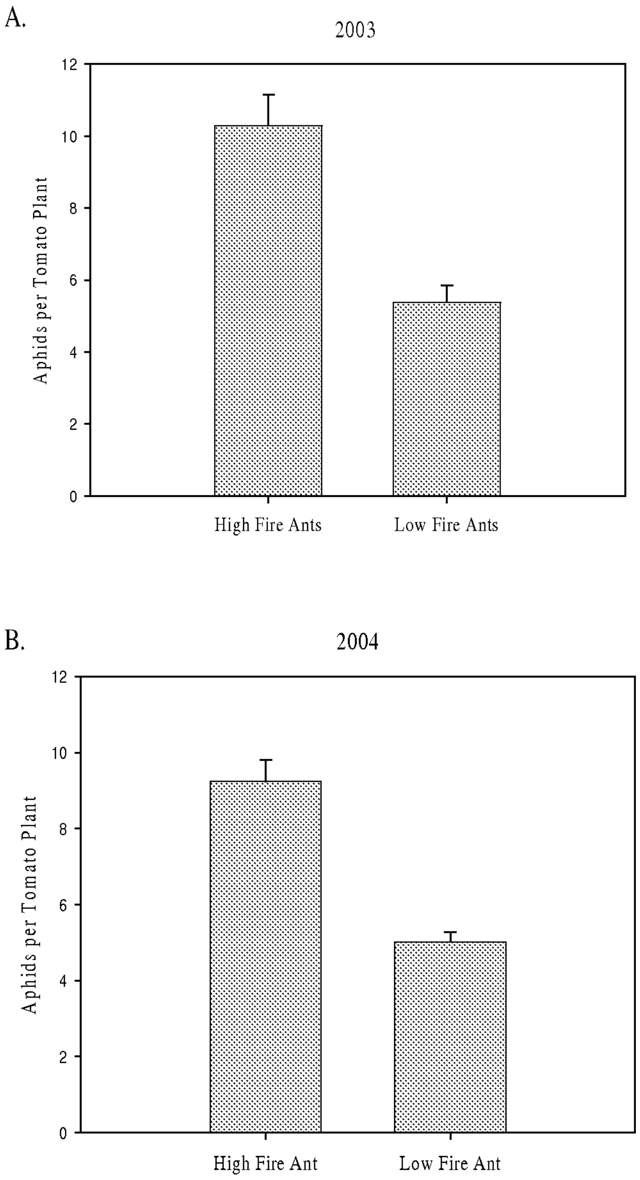


Figure 2

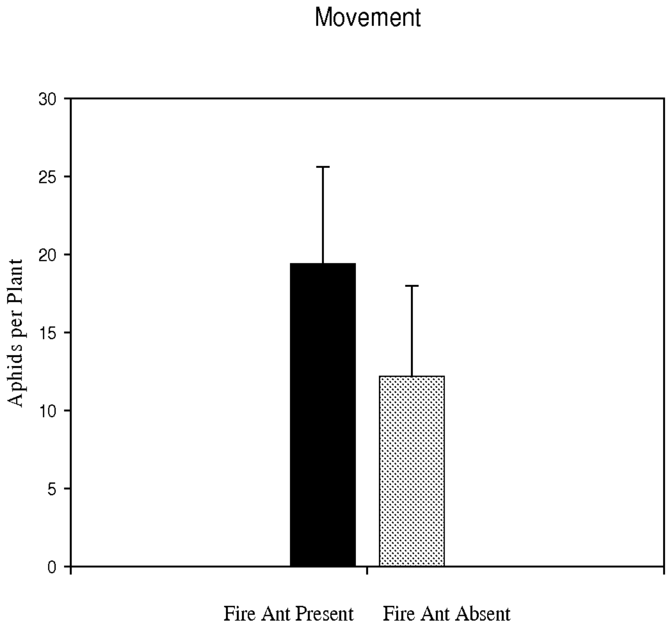

Movement
30
25
20
15
10
5
0
Aphids per Plant
Fire Ant Present
Fire Ant Absent

Figure 3

2004

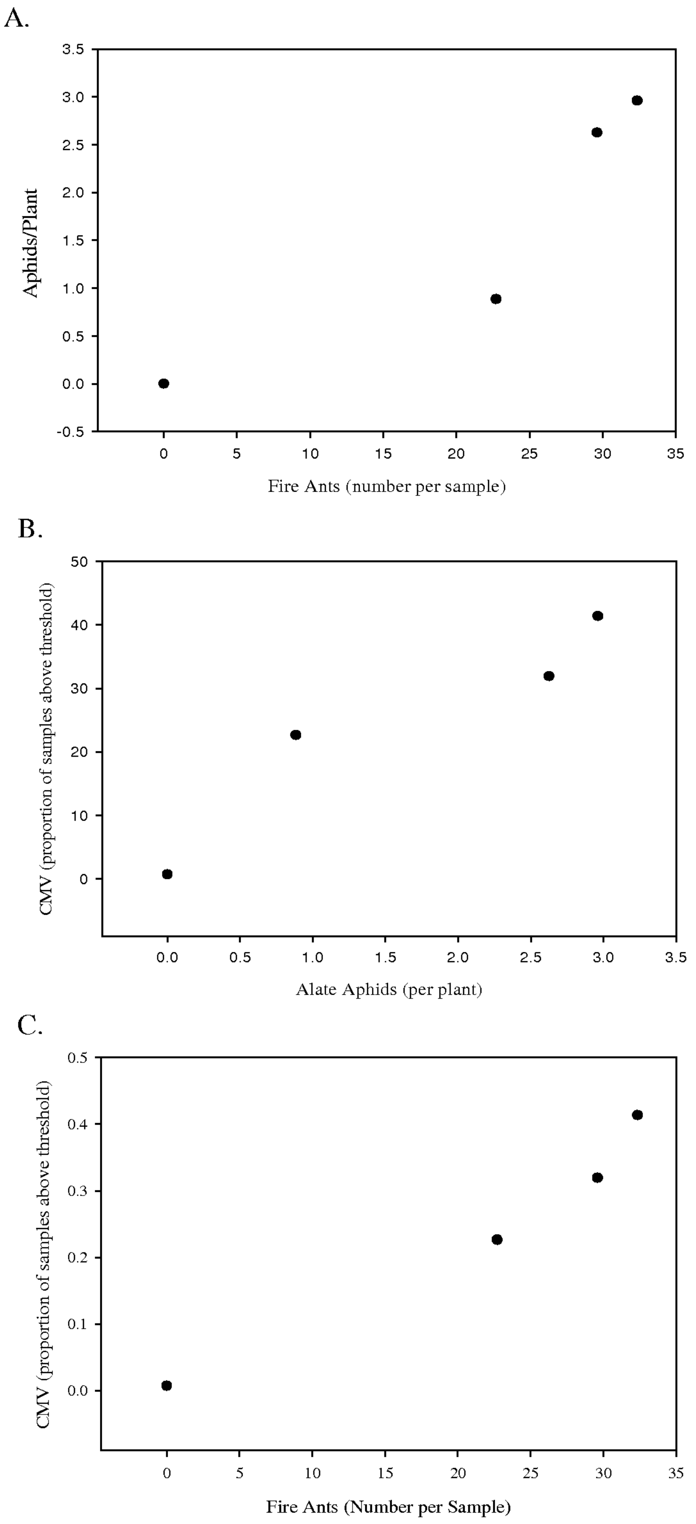


Figure 4

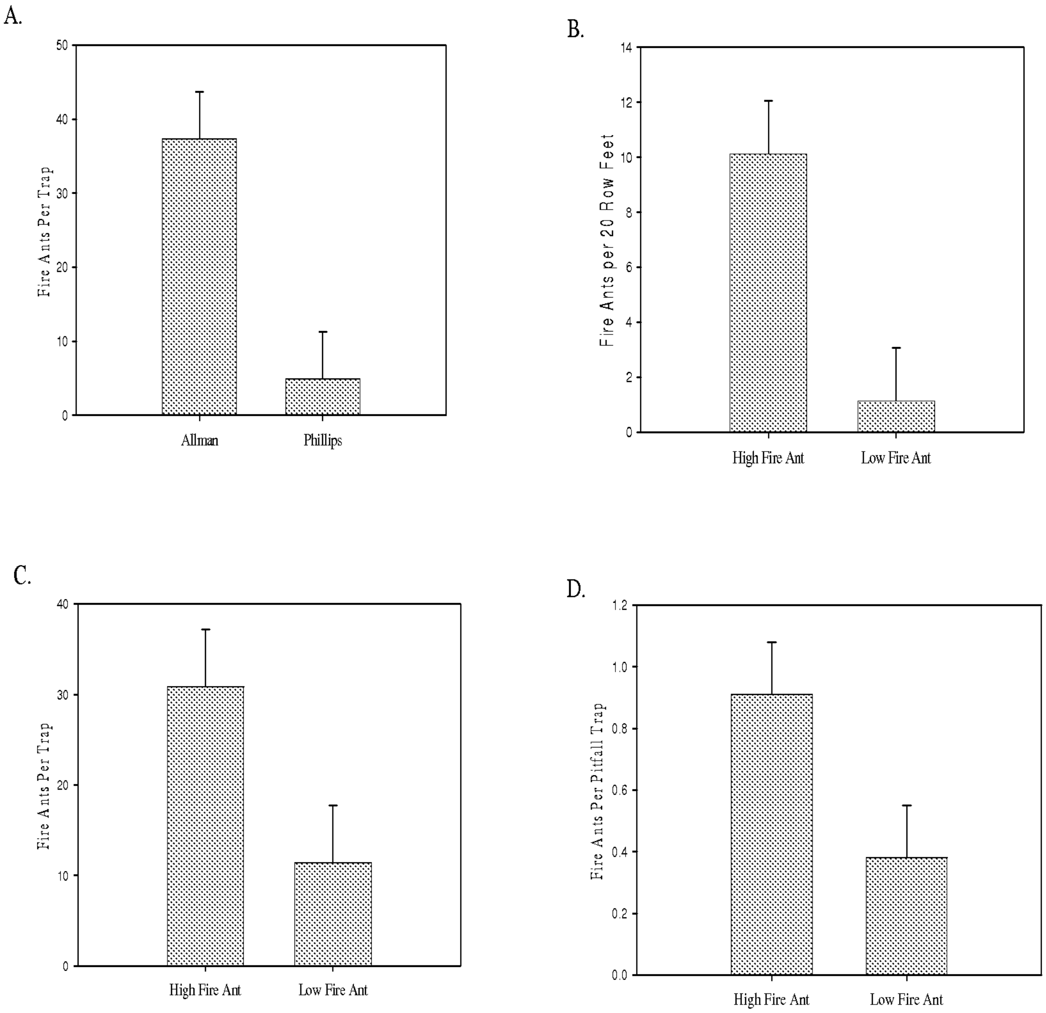

A.
Fire Ants Per Trap
0
10
20
30
40
50
Allman
Phillips
B.
Fire Ants per 20 Row Feet
0
2
4
6
8
10
12
14
High Fire Ant
Low Fire Ant
C.
Fire Ants Per Trap
0
10
20
30
40
High Fire Ant
Low Fire Ant
D.
Fire Ants Per Pitfall Trap
0.0
0.2
0.4
0.6
0.8
1.0
1.2
High Fire Ant
Low Fire Ant

Figure 5

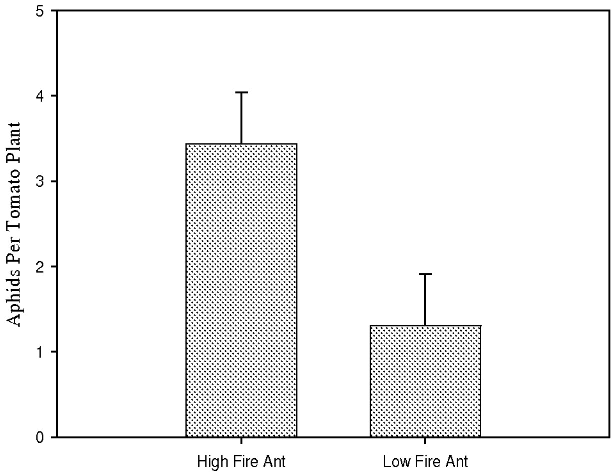
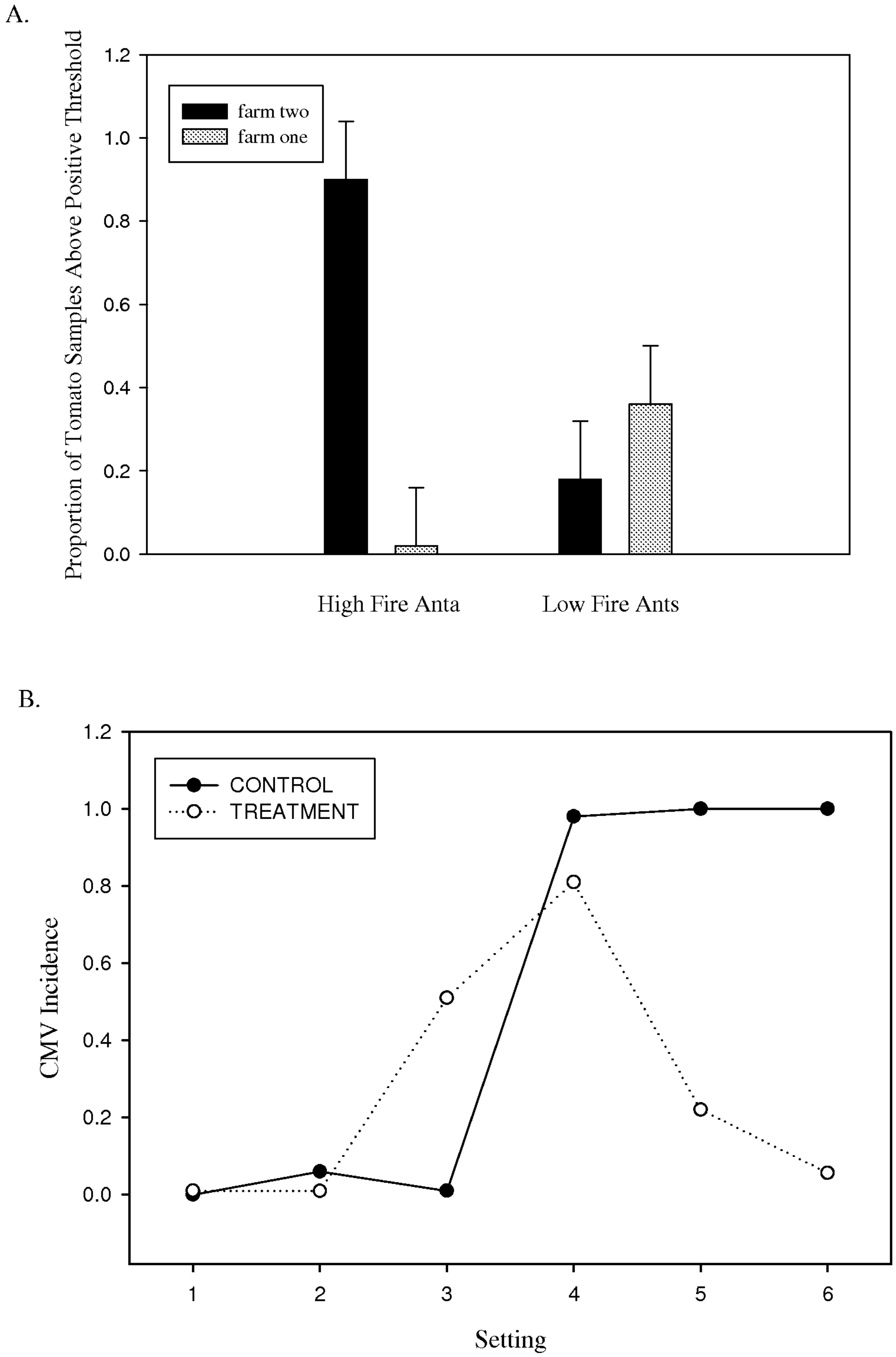


Figure 6


A.
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of Tomato Samples Above Positive Threshold
farm two
farm one
High Fire Anta
Low Fire Ants
B.
1.2
1.0
0.8
0.6
0.4
0.2
0.0
CMV Incidence
CONTROL
TREATMENT
1
2
3
4
5
6
Setting

HERBACEOUS PLANTS ASSOCIATED WITH A *CUCUMBER MOSAIC VIRUS* (CMV) EPIDEMIC IN ALABAMA FRESH MARKET TOMATO

Introduction

Due to the economic importance of plant viruses, their management is of paramount importance. The control of these devastating plant viruses is dependant on knowledge of plant virus ecology, especially sources of inoculum. Once inoculum sources have been identified, then the control of plant viruses can begin. Previous studies have indicated that herbaceous plants are considered to be reservoirs or inoculum sources (Tomlinson et al. 1970, Dinoor 1974, Tomlinson 1987, Agrios 1997, Gilbert 2002), therefore management of plant viruses should be focused on control of weed plants that function as inoculum sources

Host plants of viruses are common components of agricultural landscapes both as cultivated crops and as volunteer, spontaneous species in non-cultivated areas. Herbaceous plants contribute to epidemics of plant disease by hosting plant viruses between seasons, crops, and locations (Dinoor, 1974). Bridging hosts may either perpetuate foci of infection for the production of additional inoculum or harbor dormant stages of the pathogen, both of which can be accomplished through alternative annual or perennial hosts (Dinoor, 1974). Herbaceous hosts are likely to be important in virus "survival" through periods when crops are absent. Due to the importance of herbaceous plants in viral ecology, many studies have surveyed herbaceous plants near agricultural fields for plant viruses to identify "weed" targets for control (e.g., Brunt et al., 1996; Chatzivassiliou et al., 2001; Sacristán et al., 2004).

This study focuses on a very common aphid-vectored plant virus, *Cucumber mosaic virus* (CMV), which is transmitted in a nonpersistent manner by over 80 aphid species (Edwardson, 1986; Hobbs et al., 2000). Plant viruses transmitted in a nonpersistent manner are considered to be the most abundant and widespread of all plant viruses (Fereres 2000). Many growers try to control insect vectors to suppress the spread of plant viruses, but this is impractical when dealing with viruses transmitted in a nonpersistent manner, such as CMV. The application of chemical pesticides is usually ineffective because aphids can acquire and transmit viruses before they are disabled and some chemicals can actually enhance the spread of plant viruses by increasing aphid activity (Maelzer 1986, Lowery and Boiteau 1988, Roberts et al. 1993, Perring et al. 1999). For an insecticide to be useful in controlling plant viruses transmitted in a non-persistent manner, it must kill the vector rapidly, repel the vector or modify vector behavior to prevent probing (Broadbent 1957, Heinrichs 1979, Perring et al. 1999). The ineffectiveness of vector management indicates that a better management tactic would be to control inoculum sources in weedy areas. CMV has the largest known host range of plant viruses, infecting over 1,000 plant species in 100 plant families (Edwardson and Chrsitie, 1991; Palukaitis et al., 1992; Hobbs et al., 2000). Tomlinson (1987) listed CMV as the virus of greatest economic importance in celery, cowpea, cucurbits, lettuce, pepper, and tomato. Additionally CMV is of great economic importance in banana (Palukaitis et al. 1992; Gafney et al., 1996), pasture legumes (Latham et al., 1999), and ornamentals

(Flasiniski et al., 1995). With the extensive host range of CMV, herbaceous plants almost certainly play an important role in this virus' ecology, attributing to its great economic importance.

The objective of this study was to provide information on the distribution of CMV in field-grown tomato crops and associated herbaceous plants in the major tomato production region of Alabama. To address these objectives, a field study was conducted in Blount County, Alabama in 2004 and 2005. In 2004, I surveyed herbaceous plants around tomato fields for CMV haphazardly, focusing on abundant plant species that I found hosting aphids. In 2005, I conducted a quantitative and systematic survey of the plant community for CMV around Alabama fresh-market tomato fields.

Materials and Methods:

In 2004, we surveyed six fresh market tomato fields in Blount County, Alabama for 8 eight weeks. Surveying consisted of visually searching approximately 20 randomly selected tomato plants per 0.4 hectare of tomato for the presence of aphids. All aphids present on a tomato plant were collected and stored in 75% alcohol for later identification. Herbaceous plants around tomato fields were visually searched for the presence of aphids. Herbaceous plants found to be hosting aphids were identified and, aphids on such plants were collected and stored in 75% alcohol for later identification. In 2005, we surveyed 12 fresh market tomato fields in Blount County, Alabama, for 14 weeks. Tomato plants were visually searched following the same protocol as in 2004. Plots of herbaceous plants were marked in locations surrounding 10 of these fresh market tomato fields. Approximately one, 1 x 3 m plot was established per 0.4 hectare of tomato.

Each week every plant in the plot was visually searched for the presence of aphids. Representative aphids were collected and stored in 75% alcohol to be identified at a later date. All herbaceous plants in each plot were identified and their relative abundances were recorded.

To test for CMV infection, leaf tissue from tomato and herbaceous plants were collected, samples were wrapped in a moist paper towel, and placed on ice for transport to Auburn University. All samples were stored at 20° C until assayed. In 2004, approximately 20 herbaceous plants per 0.4 hectare of tomatoes, which were known to host aphids, were sampled four times (26 July, 17 August, 15 September, and 24 September) throughout the season, with each field being sampled once. In 2005, plants were sampled once per field (6 June, 14 July and 6 September). Approximately 20 tomato plants per 0.04 hectare were sampled with all tomato plants being at least 7 weeks old. Approximately 20 herbaceous plant samples were collected from each plot. At least one of every herbaceous plant species represented was collected and subsequent samples were collected according to their relative abundance in the plot.

Each sample tested for CMV infection by enzyme-linked immunosorbent assay (ELISA) consisted of a terminal leaflet of each tomato and herbaceous plant sample. Samples were ground using a motorized leaf press with the sap extracts tested for CMV by ELISA. An Agdia, Inc. commercial ELISA kit was used according to the manufacturer's instructions (Agdia, Inc., Elkhart, IN). Each sample was processed in 2 ml of extraction buffer (according to kit directions) and added to a microtiter plate at a final dilution of 1:4 (sap extract to buffer). All subsequent steps were as described by the manufacturer. Reactions were read at 405 nm using a Sunrise microtiter plate reader

(Phenix Research Products, Hayward, CA). A sample was considered positive for the presence of CMV when the ELISA absorbance value was greater than the threshold (mean plus three standard deviations) determined from uninfected samples.

In order to better understand the relationship between CMV in "weed" plants and CMV in tomato plants, we correlated CMV incidence in weeds and tomato plants. Additionally, I investigated the seasonal dynamics of CMV infection in tomato and herbaceous plants. CMV incidence (proportion of plants infected with CMV) was arcsine-square root transformed prior to analysis to meet the parameters of the analysis.

Results

A total of 2274 tomato and 811 herbaceous plants were analyzed. A total of 539 (24%) of tomato samples and 82 (10%) of herbaceous plants tested positive for CMV. The proportion of plants infected with CMV varied among fields (Figure 1) and date for tomato (Figure 2) as well as in herbaceous plants (Figure 3). In 2004, CMV incidence in tomato plants was not significantly correlated with date (r = -0.54, P = 0.26, N = 6) (Figure 2A). In 2005, however, CMV incidence was positively correlated with planting date of the tomato field for both tomato (r = 0.57 P = 0.052, N = 12) and herbaceous plants (r = -0.65, P = 0.039, N = 10) (Figures 2B and 3B).

Over the two year study, at least 50 herbaceous plant species belonging to 27 families were identified and tested for the presence of CMV. Of these 50 plants species, 18 species belonging to 12 families tested positive for CMV (Table 1). Additionally, aphids were present on 14 plant species belonging to 10 families (Table 1). The herbaceous plants that tested positive for CMV included: *Erechtites hieracifolia, Rubus* *spp. Solanum carolinense, Stellaria media, Trifolium spp., Rumex crispus, Poaceae spp., Smilax spp., Solidago spp., Lonicera japonica, Lactuca canadensis, Conyza canadensis, Ipomoea hederacea, I. purpurea, Vitus rotundifolia, Amaranthus spp., Ligustrum vulgare, Ambrosia artemisiifolia,* and *Geranium carolinianum* (Table 1). Aphids were found on: *Rubus spp. Solanum carolinense, Trifolium spp, Senna obtusifolia, Rumex crispus, Poaceae spp., Solidago spp., Lactuca canadensis, Conyza canadensis, Pycnanthemum spp., Ipomoea hederacea, I. purpurea, Amaranthus spp.,* and *Geranium carolinianum.* With the exception of *Senna obtusifolia* and *Pycnanthemum spp* all plants with aphids tested positive for CMV.

CMV incidence in weed plots was significantly lower (mean = 0.05 ± 0.03) than CMV incidence in tomato fields (mean = 0.39 ± 0.44) ($F_{1,20}$ = 5.71 P = 0.03) and there was no correlation between the overall incidence of CMV in weed plots and CMV incidence in neighboring tomato fields. There were, however, strong, positive correlations between CMV incidence in tomato fields and the relative abundance of greenbriar (*Smilax* spp.) (r = 0.48, P = 0.0013, N = 42) and ivy-leaf morningglory (*Ipomoea hederacea*) (r = 0.37, P = 0.01, N = 42), the abundance of aphids on ivy-leaf morningglory (r = 0.33, P = 0.03, N = 42), and the number of aphids on blackberry (*Rubus* spp.) (r = 0.44, P = 0.0038, N = 42) surrounding tomato fields.

Discussion

The ecology of plant viruses in alternative hosts other than crops has been recognized as relevant to predicting and controlling virus epidemics (Duffus, 1971, Sacristán et al., 2004). By identifying herbaceous plants as inoculum sources around agricultural fields, one can begin to develop management strategies targeting those inoculum sources. I analyzed the dynamics of CMV infection in herbaceous plants growing around tomato fields in Blount County, Alabama. These results are consistent with other studies and show that CMV incidence in herbaceous plants around agricultural fields is distributed among several plant families, but the overall infection rate of herbaceous plants in this study were relatively low. This study, however, identified three herbaceous plant species that likely play an important role in the spread of CMV from "weedy" areas to tomato fields in northern Alabama.

Of the plant species tested for the presence of CMV, 34.5% of plant species around tomato fields hosted CMV. Similar studies by Chatzivassiliou et al., (2004) and Hobbs et al. (2000) found 82.6% and 7.2%, respectively, of plant species tested were positive for CMV. My work in Blount County, Alabama tomato fields is consistent with Chatzivassilious et al. (2004). During this study we tested 50 plant species belonging to 27 families. Eighteen plant species tested positive for CMV, ranging in incidence from 2.6-100% infection. Chatzivassilious et al. (2004) tested 23 plant species belonging to 14 families around tobacco fields in Greece and found 19 plant species hosting CMV, infection ranged from 0.6 to 100%. Additionally, my results indicate higher infection rates than reported by Hobbs et al. (2000) around pepper fields in southern Illinois, reporting infection rates from 0.4-15%.

During the 2005 survey, results indicate that crop planting date was significantly correlated with the incidence of CMV in both tomato and herbaceous plants. Tomatoes planted in early June to mid July had the greatest CMV incidence in 2005. CMV incidence did not exceed 10% in herbaceous plants among the 10 fields surveyed and the

CMV incidence among herbaceous plants declined throughout the season. Thus, overall CMV incidence in “weeds” and tomato was not correlated and actually showed opposite seasonal trends. This seasonal decline in CMV incidence in herbaceous plants may be due to several factors. First, severely and systemically infected weed plants may have high mortality rates, resulting in a decrease in virus inoculum throughout the field season. This is difficult to determine, since weed composition surveys were only completed once before plants were sampled for CMV. Additionally, I did not take multiple CMV samples of the same plots over time to estimate inoculation levels of herbaceous plants in a given plot throughout the growing season. Second, plant species that serve as overwintering or early inoculum sources may be at the end of their lifecycle for that growing season. In a preliminary study (March 3) in 2005, curly dock, golden rod, and marestail were infected with CMV (proportion of plants that tested positive: curly dock 0.096; golden rod 0.4; marestail 0.2), indicating that these plants probably serve as overwintering hosts of CMV at our field sites. These plant species, and more, were also found to be hosting CMV throughout the field survey. During this survey, I found that curlydock, goldenrod and marestail all had infection rates greater than 12%. Third, early inoculum sources may have been out-competed by newly emerging vegetation throughout the year.

Herbaceous plant communities varied between fields and this variation in plant composition may have resulted in detecting overall low infection rates in the herbaceous plants (Figures 4). Some herbaceous plant species tested positive, with relatively high infection rates, while other plant species had little or no virus detected. There were strong, positive correlations between CMV incidence in tomato fields and the relative abundance of greenbriar (*Smilax* spp.), the relative abundance of ivy-leaf morningglory

(*Ipomoea hederacea*), the abundance of aphids on ivy-leaf morningglory, and the number of aphids on blackberry (*Rubus* spp.) surrounding tomato fields. These results suggest that most herbaceous plants near Alabama tomato fields, in Blount County are relatively unimportant in the spread of CMV to neighboring tomato fields and that control efforts focused on only three plant species may dramatically reduce the spread of CMV from "weedy" areas into tomato fields. Many plants such as flattop goldenrod, rabbitfoot clover, grasses, and clover species had low infection rates (3% or lower incidence). Intense management of these plants may be frivolous.

The importance of herbaceous plants as sources of inoculum has been stressed for CMV (Rist and Lorbeer, 1991). The potential of managing CMV by the removal of herbaceous hosts near tomato fields has been suggested (Cho et al., 1989; Rist and Lorbeer, 1991), and with a better understanding of the inoculum sources better management decisions can be implemented.

Table 1

Incidence of CMV in herbaceous plants around tomato fields during a two year field survey (2004-2005) in Alabama.

Plant family/ species	**Common name**	**number of plants tested** [a]	**% infected****
Amaranthaceae			
*Amaranthus spp.**	Pigweed	11(4)	36.3
Asteraceae			
Ambrosia aremisiifolia	Ragweed	10(1)	10
Chrysanthemum spp.		1	0
*Conyza Canadensis**	Marestail	37(7)	18.9
Erichitites hieraciifolia	American Burnweed	3	0
Erigeron annuus	Daisy Fleebane	3	0
Eupatorium capillifolium	Dogfennel	4	0
Euthamia spp.	Flat-topped Goldenrod	48	0
Gnaphalium	Cudweed	4	0
Helenium amarum	Bitter Sneezeweed	1	0
*Lactuca Canadensis**	Tall Lettuce	39(5)	12.8
*Solidago altissima**	Goldenrod	112(14)	12.5
Bignoniaceae			
Campis radicans	Trumpet Creeper	3	0
Campanulaceae			

Tridanis perfoliata	Common Venuslookingglass	1	0
Caprifoliaceae			
Lonicera japonica	Honeysuckle	34(2)	5.8
Caryophyllaceae			
Stellaria media	Common Chickweed	6(1)	16.6
Convolvulaceae			
*Ipomoea Hederacea**	Ivy-leaved Morningglory	13(8)	61.5
*Ipomoea purpurea**	Common Moringglory	30(11)	36.6
Ipomoea spp.		2	0
Cruciferae			
Lepidium virginicum	Virginia Pepperweed	4	0
Cyoressaceae			
Juniperus spp.	Juniper	3	0
Fabaceae			
Desmodium spp.		1	0
*Senna obtusifolia**	Coffee-weed	5	0
Trifolium arvense	Rabbit foot Clover	14	0
*Trifolium spp.**	Clover	32(1)	3
Vicia sativa	Narrow Leaf Vetch	6	0
Fagaceae			
Betula nigra	River Birch	1	0
Betula spp.	Birch	2	0
Geraniaceae			

*Geranium carolinianum**	Carolina Geranium	8(4)	50
Lamiaceae*			
*Pycnanthemum spp.**	Mountain Mint	1	0
Liliaceae			
Allium canadense	Wild Onion	1	0
Oleaceae			
Ligustrum vulgare	Common Privet	12(6)	50
Passifloraceae			
Passiflora incarnate	Passion-flower	2	0
Phytolaccaceae			
Phytolacca americana	Pokeweed	2	0
Pinaceae			
Pinus spp.	Pine	2	0
Plantaginaceae			
Plantago aristata	Plantain	1	0
Plantago spp.	Plantain	1	0
Poaceae spp.*[b]	Grass	189(5)	2.6
Polygonaceae			
Polygonum pensylvanicum	Lady's-thumb	6	0
*Rumex crispus**	Curly Dock	12(2)	16.6
Salicaceae			
Salix spp.	Willow	1	0
Smilacaceae			

Smilax spp.	Greenbrier	2(1)	50
Rosaceae			
Fragaria spp.	Wild Strawberry	1	0
*Rubus spp.**	Blackberry	38(2)	5.2
Rubiaceae			
Diodia teres	Poorjoe	10	0
Galium aparine	Catchweed Bedstraw	1	0
Solanacaeae			
*Solanum carolinense**	Carolina Horsenettle	10(6)	60
Valerianaceae			
Valerianella radiate	Cornsalad	1	0
Vitaceae			
Parthenocissus quinquefolia	Viginia Creeper	15	0
Vitis rotundifolia	Muscadine	1(1)	100

* Aphids present

** determined by ELISA

[a] the number in parenthesis indicates the number of samples that tested positive

[b] Grasses were not identified to species during this study

Figure Legend

Figure 1

(A) The proportion of CMV infected tomato plants for each field surveyed in 2004 and (B) 2005. Figure 2

(A) The relationship between CMV incidence in tomato and the planting date of tomato fields 2004 and (B) 2005.

Figure 3

(A) The proportion of CMV infected herbaceous plants for each field surveyed in 2005.

(B) The incidence of CMV in herbaceous plants by planting date in 2005.

Figure 4

The composition of the herbaceous plant community surrounding ten tomato fields in 2005.

Key: C = Clover F = Flattop goldenrod, GR = Goldenrod, H = Honeysuckle, M = Marestail, MG = Morningglory, O = Other, P = Privet, R = Rubus, RF = Rabbitfoot clover, VC = Virginia creeper, WG = Wild geranium.

Figure 1

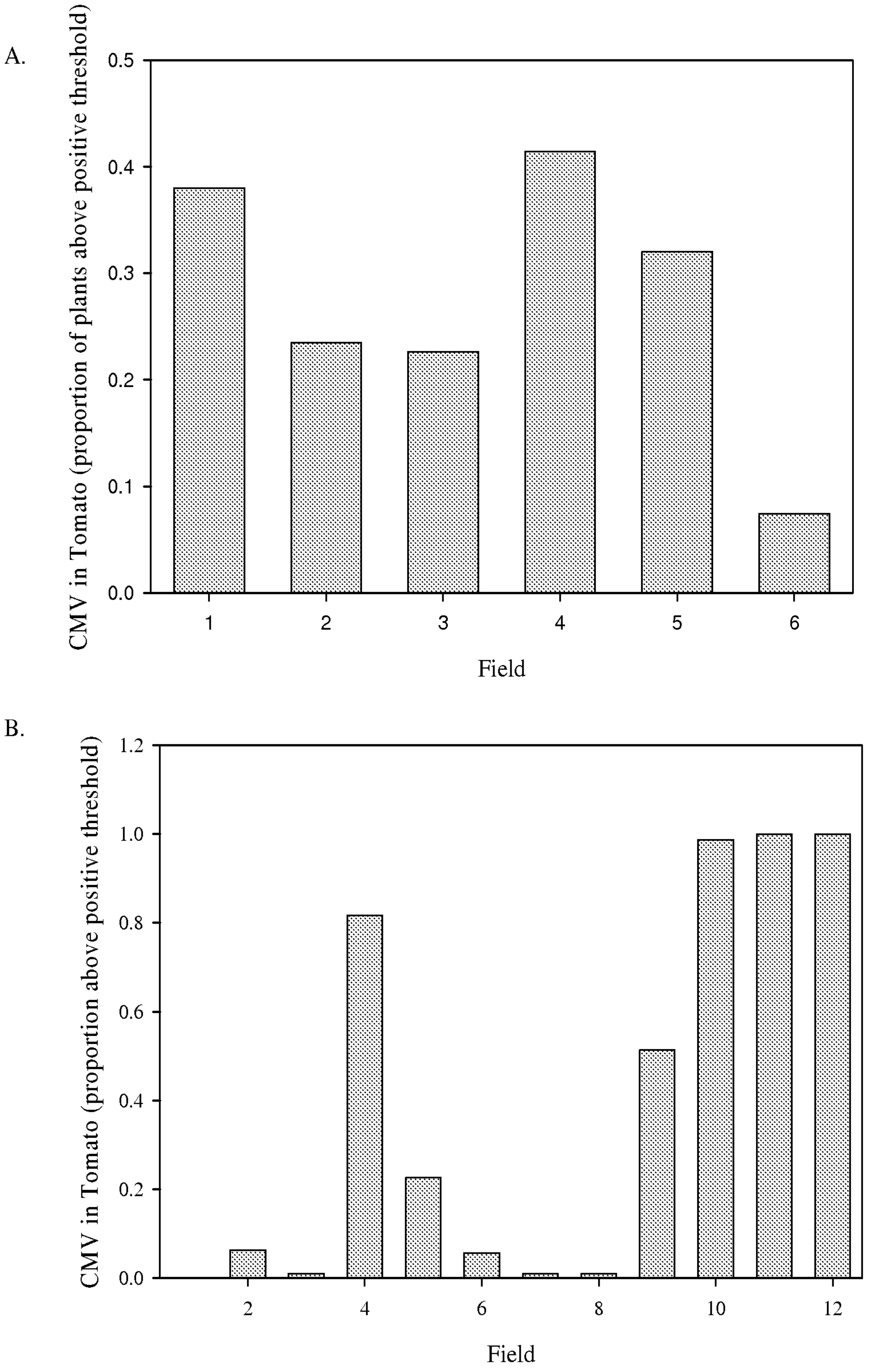

A.
CMV in Tomato (proportion of plants above positive threshold)
0.0
0.1
0.2
0.3
0.4
0.5
1
2
3
4
5
6
Field
B.
CMV in Tomato (proportion above positive threshold)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
2
4
6
8
10
12
Field

Figure 2

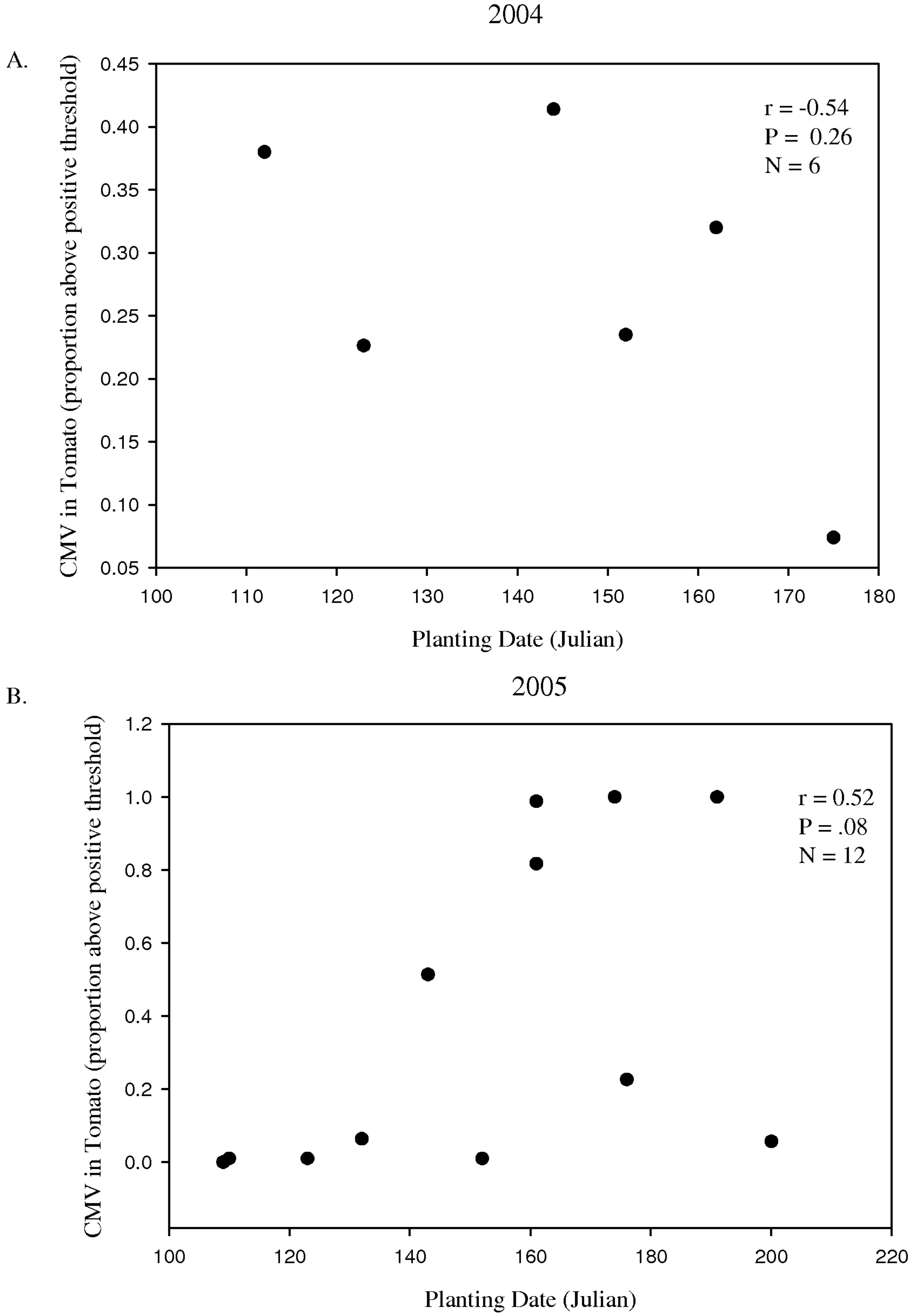

2004
A.
CMV in Tomato (proportion above positive threshold)
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
100
110
120
130
140
150
160
170
180
Planting Date (Julian)
r = -0.54
P = 0.26
N = 6
B.
2005
CMV in Tomato (proportion above positive threshold)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
100
120
140
160
180
200
220
Planting Date (Julian)
r = 0.52
P = .08
N = 12

Figure 3

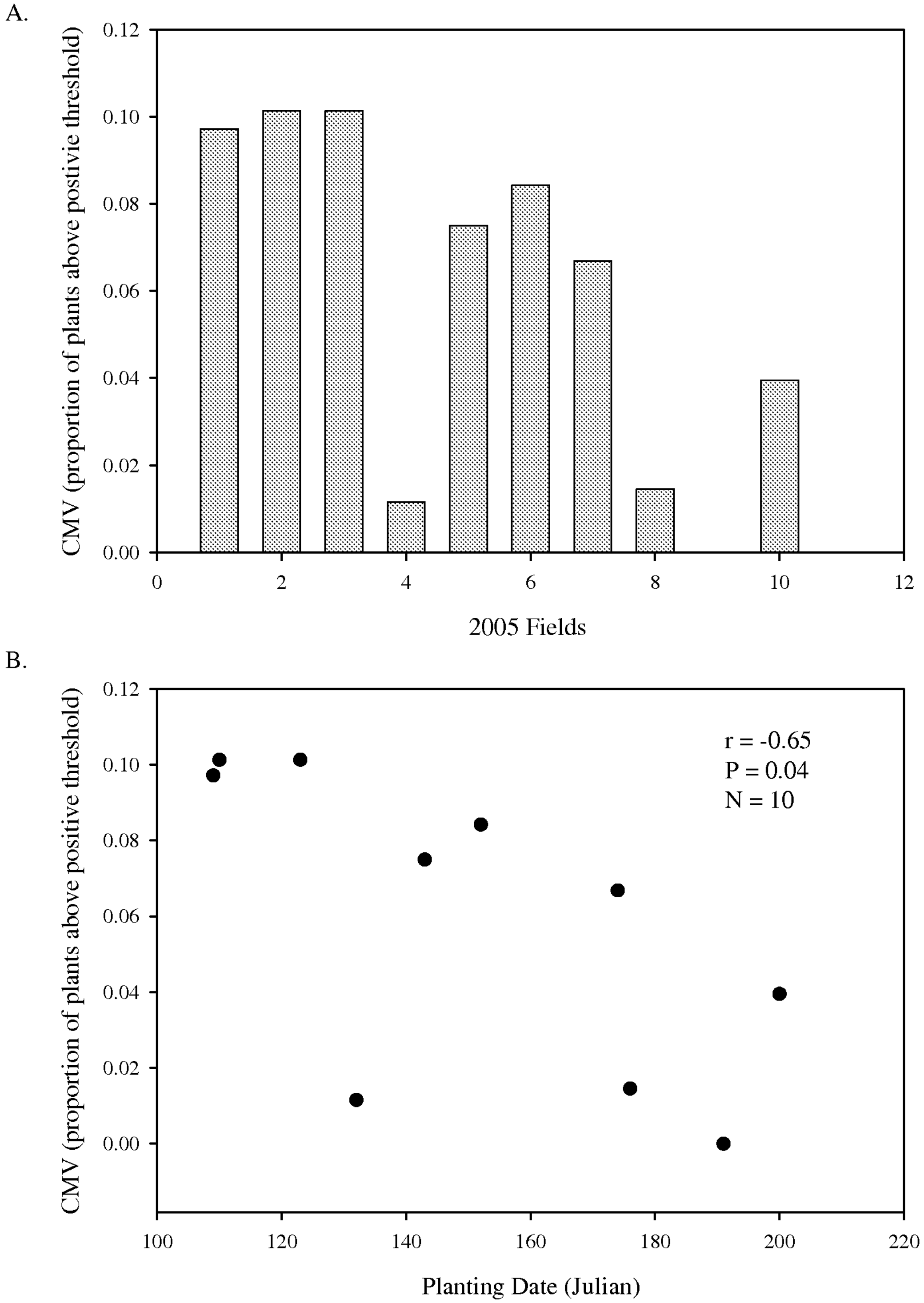
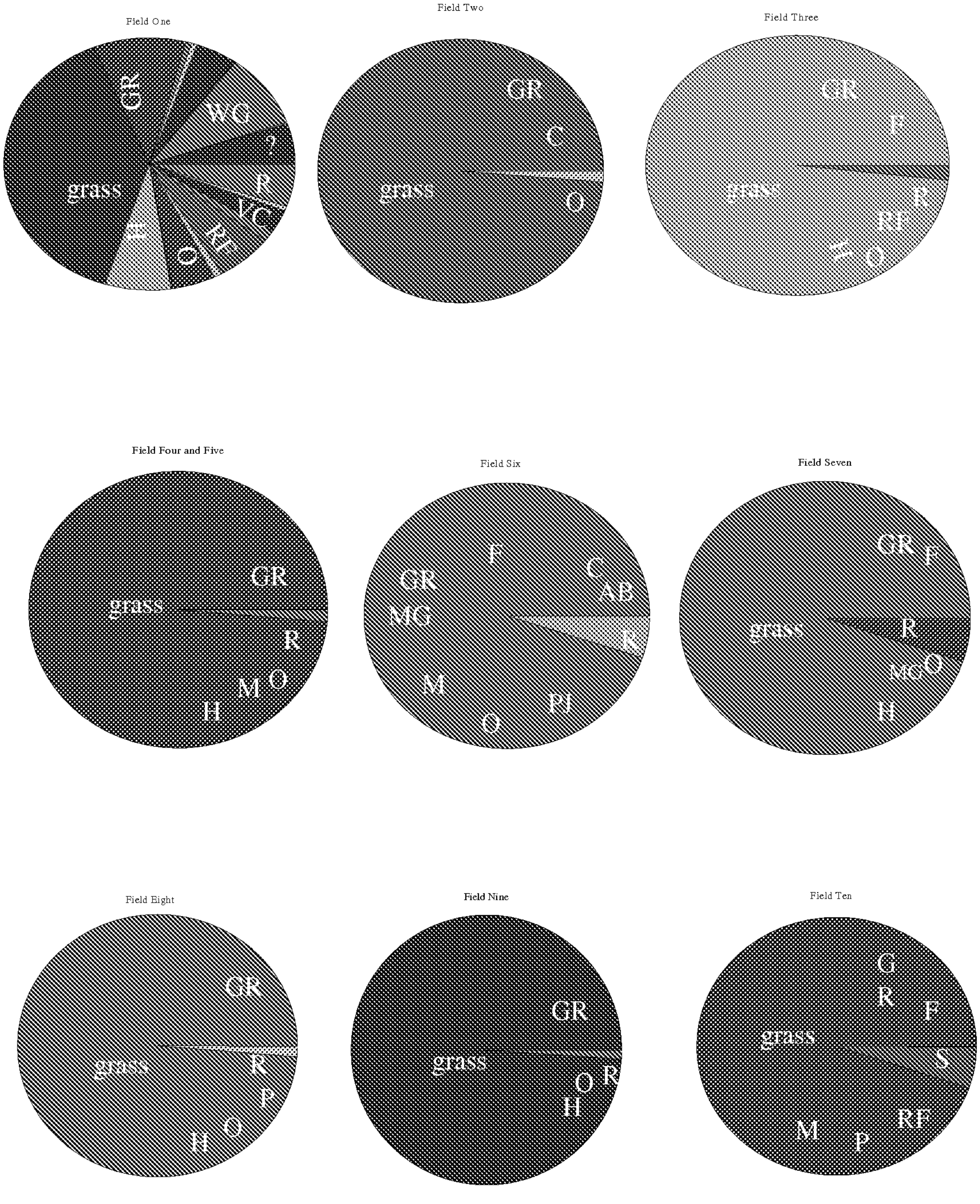

A.
CMV (proportion of plants above postivie threshold)
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0
2
4
6
8
10
12
2005 Fields
B.
CMV (proportion of plants above positive threshold)
0.00
0.02
0.04
0.06
0.08
0.10
0.12
r = -0.65
P = 0.04
N = 10
100
120
140
160
180
200
220
Planting Date (Julian)

Figure 4


Field One
GR
WG
?
grass
R
VC
RF
O
H
Field Two
GR
C
grass
O
Field Three
GR
F
grass
R
RF
H
O
Field Four and Five
GR
grass
R
M
O
H
Field Six
F
C
GR
AB
MG
R
M
PJ
O
Field Seven
GR
F
grass
R
MG
O
H
Field Eight
GR
grass
R
P
O
H
Field Nine
GR
grass
O
R
H
Field Ten
G
R
F
grass
S
RF
M
P

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