Interactions Between the Augmentatively Released Predaceous Mite *Galendromus occidentalis* (Acari: Phytoseiidae) and Naturally Occurring Generalist Predators

R. G. COLFER, J. A. ROSENHEIM, L. D. GODFREY, AND C. L. HSU

Department of Entomology, University of California, One Shields Avenue, Davis, California, 95616

Environ. Entomol. 32(4): 840–852 (2003)

ABSTRACT Predatory mite releases can be an effective means of managing spider mites in many perennial cropping systems, yet little research has been performed in annual cropping systems. Herein we evaluate the compatibility of predaceous mite releases with the conservation of resident natural enemies in an annual agroecosystem. We quantify the impact of naturally occurring generalist predators, *Geocoris* spp. and *Orius tristicolor* White, and the omnivore *Frankliniella occidentalis* (Pergande), on the establishment of the western predatory mite *Galendromus occidentalis* (Nesbitt) and how these predator-predator interactions influence spider mite control. Field experiments showed that in the absence of generalist predators, released predatory mites can establish populations on cotton, increase in abundance through reproductive recruitment, and suppress spider mite populations. Hemipteran predators had a negative impact on predatory mite populations but generally improved spider mite suppression. The presence of *F. occidentalis* had no impact on predatory mite performance.

KEY WORDS augmentative biological control, generalist predator, intraguild predation, *Galendromus occidentalis*, *Gossypium hirsutum*

BIOLOGICAL CONTROL IS ONE of the most important alternatives to conventional pesticide use in pest management today. Biological control is free of many of the problems associated with pesticide use, such as pest resistance, environmental pollution, and worker health impacts. Recently, however, there has been a critical reevaluation of the compatibility of classical biological control (the introduction of exotic natural enemies) with the conservation of endemic arthropods, as a result of the potential impact of imported control agents on nontarget native fauna (Howarth 1991, Simberloff and Stiling 1996, Louda et al. 1998). These conservation concerns will likely place some limits on the future implementation of classical biological control. Therefore, there is a need to put greater emphasis on other areas of biological control, such as natural enemy conservation and augmentation (Parrella et al. 1992, Barbosa 1998, Pickett and Bugg 1998). In this study, we evaluate whether or not the conservation of naturally occurring generalist predators is compatible with augmentation of predatory phytoseiid mites.

Augmentative releases of predaceous phytoseiid mites have been shown experimentally to reduce spider mite densities in many perennial crops (McMurtry 1982, Hoy et al. 1982, Flaherty et al. 1985, Helle and Sabelis 1985, Croft and MacRae 1992b, Nyrop et al. 1998) and some annual row crops such as cotton (Osman and Zohdi 1976, Tijerina-Chavez 1991) and field corn (Pickett and Gilstrap 1986, Pickett et al. 1987). Attempts to improve augmentative biological control have focused primarily on factors such as selection of control agents, quality control, mass rearing techniques, release methods, and efficacy of target pest suppression (Van Driesche and Bellows 1996). Although all of these factors are critical to the successful use of augmentative biological control, there has been very little examination of how augmented natural enemies may interact with naturally occurring natural enemies. There is increasing recognition that complex multispecies interactions among natural enemies can be important in biological control (Rosenheim et al. 1995, Sunderland et al. 1997, Rosenheim 1998, see 'Invited Feature' Ecological Applications 9:363–429). In an annual crop such as cotton, generalist predators are often abundant (van den Bosch and Hagen 1966). As a result, predator-predator interactions may be common and could be a key factor influencing the establishment of augmentatively released natural enemies.

There is substantial evidence that generalist predators can have significant impacts on phytoseiid mites. Predation upon predatory phytoseiid mites has been studied (either directly or indirectly) in experiments conducted in the laboratory (Gillespie and Quiring 1992, Cloutier and Johnson 1993, Croft and Croft 1996,

0046-225X/03/0840–0852$04.00/0

Croft et al. 1996, MacRae and Croft 1996, Wittmann and Leather 1997, Schausberger and Croft 2000), greenhouse (Ramakers 1993, Brodsgaard and Enkegaard 1997, Schausberger and Walzer 2001) and field (Croft and MacRae, 1992a, 1992b, 1993; Croft 1994; Walde et al. 1997). Croft and MacRae (1992a) showed that predation by the generalist predatory mite *Zetzellia mali* usually displaced western predatory mite *Galendromus occidentalis* (Nesbitt) populations, which sometimes led to increases in phytophagous mite populations. Phytoseiid mites may be especially susceptible to predation by predatory insects because they are relatively small compared with insects (Polis et al. 1989), but there have been no field studies examining the impact of predatory insects on phytoseiid mites.

Our research was also motivated by earlier work in which releases of *G. occidentalis* into cotton were unsuccessful in establishing populations of this mite (R. G. Colfer, J. A. Rosenheim, L. D. Godfrey, C. L. Hsu, unpublished data). We were unable to establish *G. occidentalis* populations in the cotton agroecosystem even though the majority of the releases were made in fields that had abundant spider mite prey and were organically farmed (no pesticides were used).

In this study, we evaluate the importance of interactions between augmentatively released western predatory mites, *G. occidentalis*, and a group of important naturally occurring generalist predators. These predators include the minute pirate bug, *Orius tristicolor* (White) (Hemiptera: Anthocoridae), the bigeyed bugs, *Geocoris pallens* Stäl, *G. punctipes* (Say), and *G. atricolor* Montandon (Hemiptera: Lygaeidae), and the western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). These predators are commonly associated with the spider mite complex found in cotton grown in the San Joaquin Valley of California (Wilson et al. 1991a). Species in this spider mite complex include *Tetranychus pacificus* McGregor, *Tetranychus turkestani* Ugarov and Nikolski, and *Tetranychus urticae* Koch.

We address four questions in this study. First, can western predatory mites establish and build up populations through reproductive recruitment on cotton when spider mite availability is high and in the absence of generalist predators? Second, what impact do generalist predators have on western predatory mite population dynamics in cotton? Third, what impact do naturally occurring generalist predators have on spider mite population dynamics? Fourth, do the interactions between western predatory mites and generalist predators influence the overall level of spider mite suppression? We evaluated interactions between western predatory mites and generalist predators using two approaches: we examined short-term interactions under controlled conditions using small field cages in which we tested predators singly and in defined combinations; and, we examined longer-term interactions at a larger spatial scale using insecticide manipulations. In this later approach, we tested the impact of the whole generalist predator complex on western predatory mite and spider mite populations.

Materials and Methods

High Spider Mite Availability and High Predatory Mite Release Rate—Cage Experiment. This experiment was designed to quantify: (1) the ability of *G. occidentalis* to establish and build populations on cotton under conditions of high spider mite availability and low abundance of resident generalist predators; and (2) the impact of *G. occidentalis* releases on *T. urticae* abundance. The experiment was conducted from 31 May to 25 June 1997 in a 0.4-ha experimental planting of cotton, *Gossypium hirsutum* cultivar "Maxxa," at the UC Davis Plant Pathology Fieldhouse, Davis, CA (a field station with both field and greenhouse facilities). Plants were grown on rows separated by 76 cm following standard commercial practices, except that no acaricides or insecticides were used. Plants were small (≈8 mainstem nodes) and not yet flowering when the experiment was initiated.

The experimental unit was a single plant. On 31 May, plants were randomly selected and thoroughly sprayed with Safer Brand insecticidal soap (Woodstream Corp., Lititz, PA) at the labeled rate (20 ml soap/ L H_2O) to reduce resident populations of predators. Plants were then enclosed in cylindrical cages composed of a plastic polyvinyl chloride base (30 cm diameter) and No-Thrips mesh (Greentek Inc; pore size ≈150 μm; cage dimensions: height 45 cm, diameter 30 cm). Cage bases were imbedded in the ground to provide a tight seal at the base.

On 1 June, plants were randomly assigned to one of two treatments, each replicated twenty-eight times: (1) spider mites alone (*T. urticae*) or (2) spider mites plus western predatory mites (*G. occidentalis*). Spider mites were added to all replicates by placing two spider mite-infested cotton seedlings from a laboratory culture onto each plant; this delivered 471 ± 45 (mean ± 1 SE) mobile spider mites to each replicate. Western predatory mites were purchased from Biotactics Inc., Riverside, CA, and were released within 2 d of receiving the product. On 1 June, ≈10 adult predatory mites were added to each replicate of the predatory mite treatment. On 7 June, a second release of 68 ± 16 predatory mites in a corn-cob grit carrier was made to each replicate of the predatory mite treatment. The second predatory mite release was done to ensure that all replicates of the predatory mite release treatment contained predatory mite populations. A small number of spider mite eggs (<50 per release, *T. pacificus* McGregor) were included in the corn-cob grit carrier by Biotactics Inc. to feed predatory mites while in transit.

On 15 June, 18 out of the 28 replicates of each treatment were terminated (8 d after the second predatory mite release). The remaining 10 replicates of each treatment were collected on 25 June (18 d after the second predatory mite release). All leaves from these replicates were collected into plastic bags, preserved with 70% ethanol, and stored at 4°C. All arthropods were later removed from the leaf material using a leaf washing method developed by Leigh et al. (1984). Note that we did not use a repeated-measures

design, replicates were destructively sampled during the 8-d and 18-d sampling dates. To reduce the time necessary to quantify samples, we counted only the larger stages of mites and used a previously determined linear regression relationship to estimate the total number of motile mites. The linear regression relationship was determined by separating mites by size using two mesh sieves: one with 260-μm diameter pores to collect adults and larger immature mite stages (i.e., deutonymphs), and a second with 100-μm diameter pores to collect all other smaller stages (i.e., eggs, larvae, protonymphs). By quantifying all motile stages (eggs were not counted) in both sieves and using linear regression through the origin, we developed a relationship between the proportion of spider mites and phytoseiid mites found in the two sieves (spider mites: bottom sieve = top sieve $\times$ 0.937, $r^2 = 0.927$, $P < 0.0001$; phytoseiid mites: bottom sieve = top sieve $\times$ 0.358, $r^2 = 0.853$, $P < 0.0001$). The regression analysis allowed us to quantify only the larger stages of mites but obtain an estimate of the total number of motile mites. The relationship between large spider mites and total spider mites was similar for different treatments (R.G. Colfer, unpublished data).

Compatibility of Spider Mite Predators—Cage Experiment. This experiment was designed to quantify the impact of generalist predators *Geocoris* spp., *O. tristicolor*, and *F. occidentalis*, on spider mite and predatory mite abundance. The experiment was conducted from 14 to 30 August 1997 in a 0.2-ha experimental planting of *G. hirsutum* cultivar "Maxxa" at the UC Davis Agronomy Field Plots, Davis, CA. Plants were grown on rows separated by 76 cm, following standard commercial practices, except that no acaricides or insecticides were used. Plants were medium sized (≈20 mainstem nodes) and setting squares and bolls when the experiment began.

The experimental unit was a single mainstem leaf located at the fifth node from the plant terminal. From 14–15 August, plants were randomly selected and the fifth node mainstem leaf was thoroughly cleaned with a paint brush to reduce resident populations of western flower thrips and other insects. Leaves were then enclosed in square cages composed of No-Thrips mesh (Greentek Inc.; pore size ≈0.15 mm; cage dimensions: length and width 22.7 cm). Two seams were closed using plastic folder bindings to facilitate easy entry into cages; the petiole-side seam was closed using a combination of double-sided mounting tape, Duck tape, and rope caulk weather-stripping (Ace Hardware Corp., Oak Brook, IL).

Seven days later, between 21–22 August, cages were reopened and brushed a second time to remove newly emerged insects that have egg stages embedded in the leaf tissue (*F. occidentalis* and *O. tristicolor*). This was considered sufficient time for all eggs to hatch. This removal technique was effective for *O. tristicolor* but only partially effective for *F. occidentalis.* Once brushed, caged leaves were randomly allocated to one of five treatments, each replicated eighteen times: (1) spider mites alone (*T. urticae*, 147 ± 15 motile stages per leaf), (2) spider mites plus predaceous mites (*G. occidentalis*, 10.6 ± 0.7 motile stages per leaf), (3) spider mites, predaceous mites, and *O. tristicolor* (four first to third instar nymphs per leaf), (4) spider mites, predaceous mites, and *Geocoris* spp. (one first- to third-instar nymph per leaf), and (5) spider mites, predaceous mites, and *F. occidentalis* (≈12 adults per leaf). Densities were chosen to reflect natural densities of predators in cotton when spider mite densities are high (R.G. Colfer, unpublished data). *Tetranychus urticae* and *F. occidentalis* were collected from laboratory cultures, *G. occidentalis* was purchased from Biotactics Inc., and *Geocoris* and *O. tristicolor* were hand collected at or near the cotton field where this experiment was conducted. Spider mites were added to all replicates by placing one spider mite-infested cotton cotyledon from a laboratory culture onto each leaf; this delivered 147 ± 15 (mean ± 1 SE) mobile spider mites to each replicate. Predatory mites were delivered to cages within corn-cob grit carrier.

The duration of this experiment was 7 d (approximately the generation time for the spider mites, predaceous mites, and thrips). From 28–30 August, replicates were collected and all herbivorous and predatory arthropods were quantified in the laboratory with the aid of a dissecting stereomicroscope. Both the motile and egg stages of spider mites and predatory mites were quantified.

Compatibility of Spider Mite Predators—Open Plot Experiment. This experiment was designed to evaluate the compatibility of predaceous mites with the unmanipulated naturally occurring generalist predator community and to quantify the impact of the generalist predator community on spider mite populations. The experiment was conducted from 21 May to 15 July 1997 in a two ha planting of *G. hirsutum* cultivar "Maxxa" at the UC Cotton Research Station, Shafter, CA. Experimental units were cotton plots (28 m $\times$ 12 m) surrounded by 3.5 m of bare soil. Plots were randomly allocated to one of four treatments, each replicated seven times: (1) prerelease application of acephate (Orthene) and release of predatory mites, (2) prerelease application of acephate and no release, (3) release of predatory mites only, and (4) no manipulation control. Acephate was sprayed at 4.0 oz AI/ac on 21 May in an attempt to reduce naturally occurring populations of arthropod predators. On 30 May, a leaf-disk bioassay using leaves from sprayed and unsprayed plots showed that mortality of predatory mites on leaf disks from sprayed and unsprayed plots did not differ significantly ($P > 0.3$). Twelve hundred predatory mites were manually released per plot (release rate equivalent to 38,200 mites per ha) on 5 June. The manual released involved evenly distributing a mixture of predatory mites and corn-cob grit carrier onto each plant within the release plots. Releases were performed between 0600 and 0800 hours to minimize predatory mite mortality related to high midday temperatures. Plots were monitored every 2 wk using leaf and sweep (20 sweeps/plot) sampling techniques from 21 May to 15 July. Leaf sampling involved randomly collecting 25 mainstem leaves located five nodes below the apex of the plant. All leaf

samples were collected into plastic bags, preserved with 70% ethanol, and stored at 4°C. All arthropods were later removed from the leaf material using a leaf washing method developed by Leigh et al. (1984) and quantified using the methods described earlier (see first experiment). Mite populations were estimated using counts of the larger stages of mites and the previously described regression relationship. All adult phytoseiid mites recovered from the leaf samples were slide mounted and identified to species.

Statistical Analyses. For the first experiment, we analyzed the influence of predatory mite releases on final spider mite and predatory mite abundance using Kruskal-Wallis rank-sum tests for the 8-d and 18-d samples (Sokal and Rohlf 1995). For the second experiment, we analyzed the influence of different predators on spider mite and predatory mite abundance using Kruskal-Wallis rank-sum tests and planned paired comparisons using two-tailed Wilcoxon rank-sum tests (Sokal and Rohlf 1995). *P* values were adjusted for the number of pairwise comparisons to maintain an overall α value equal to 0.05. To determine whether competition and predation were important in the interactions between hemipteran predators and predatory mites, we used three-factor analysis of covariance (ANCOVA) where final predatory mite abundance was the response variable, final spider mite abundance was the covariate, and addition of *O. tristicolor*, *Geocoris*, and *F. occidentalis* were main factors (Neter et al. 1990). To meet the assumptions of ANCOVA, final spider mite and predatory mite abundance were log-transformed ($\ln[x+1]$). For the third experiment, we analyzed the influence of predatory mite releases and acephate applications on spider mite and predatory mite populations using a two-factor, repeated-measures analysis of variance (ANOVA) (Neter et al. 1990, von Ende 1993). The impact of the acephate on the abundance of immature predatory insects 2 wk after the application was analyzed with a one-factor ANOVA. Spider mite and predatory mite abundances were log-transformed to meet the requirements of the ANOVA tests. To determine whether competition and predation are important in the interactions between hemipteran predators and predatory mites in the large-scale, acephate experiment, we again used ANCOVA, where the acephate application was the main factor, spider mite abundance (summed over four weekly samples), and immature hemipteran abundance (from the sweep samples taken 2 wk after the acephate application) were covariates, and predatory mite abundance (summed over four weekly samples) was the response variable. Predatory mite and spider mite abundances were log-transformed to meet the assumptions of ANCOVA. All statistical analysis was performed using JMP statistical package (SAS Institute 1995).

Results

High Spider Mite Availability and High Predatory Mite Release Rate—Cage Experiment. The combination of insecticidal soap and the containment of plants within cages was fairly effective in keeping replicates free of naturally occurring predators of spider mites. Only 14% of cages contained naturally occurring predators, and within these replicates the densities of these predators were below densities seen on unmanipulated plants. On plants on which the generalist predator community was experimentally suppressed, the release of predatory mites greatly enhanced the number of predatory mites recovered at 8 d post release compared with the control ($\chi^2 = 27.6$, df = 1, $P < 0.001$; Table 1). However, the predaceous mite per capita population growth rate from initial release, when 78 mites were released, until the census on day 8 was slightly negative (per capita growth = [final density – release rate] / [release rate] = −0.33). In the replicates sampled at 18 d post release, the difference in predatory mite abundance between the release and control treatments remained very large ($\chi^2 = 13.6$, df = 1, $P < 0.001$), and the predaceous mite per capita growth rate from the time of the initial release rate was positive (per capita growth = 0.62), indicating the predatory mite population had established and grown by >60%. Regression analysis of the predaceous mite counts at both the 8- and 18-d censuses showed that predatory mite numbers were strongly correlated with spider mite densities (simple linear regression, $r^2 = 0.71$, $F = 64.7$, df = 1, $P < 0.001$; Fig. 1), suggesting that predatory mites had greater population recruitment under conditions of high spider mite densities.

Table 1. Density (mean ± SE) of motile spider mites and predatory mites per plant in the high spider mite availability/high predatory mite release rate experiment where generalist predators were suppressed

Arthropod abundance	Experimental treatment			
	Spider mites alone		Spider mites + *G. occidentalis*	
	Day 8	Day 18	Day 8	Day 18
Spider mites	782 ± 147	6931 ± 1354	296 ± 58**	2639 ± 1021*
Predatory mites	0.7 ± 0.3	1.7 ± 0.8	52.4 ± 6.2***	126.7 ± 33.2***

Statistical comparisons are made between treatments for the same sample date. Two-tailed Wilcoxon rank-sum tests: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, not significant.

Spider mite population abundance was significantly reduced by the predatory mite releases at both 8 d post release ($\chi^2 = 9.6$, df = 1, $P = 0.002$) and 18 d post release ($\chi^2 = 5.6$, df = 1, $P = 0.018$, Table 1). At both censuses, predatory mites reduced spider mite densities by ≈60% compared with the spider mites only treatment. Despite this suppressive effect, spider mite populations greatly increased in both treatments over the duration of the experiment. Spider mite populations were ≈9 times larger at day 18 than at day 8 in both treatments.

Compatibility of Spider Mite Predators—Cage Experiment. The manipulations of the generalist insect predators were successful, with much higher predator densities in treatments in which predators were added in comparison to the controls (Table 2). *Frankliniella*

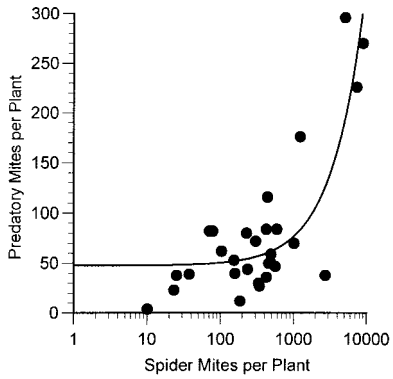

Fig. 1. Predatory mite and spider mite abundance per plant in the predatory mite release treatment in high spider mite availability/ high predatory mite release rate experiment. Numbers of spider and predatory mites were strongly correlated ($r^2 = 0.705$, $F = 64.7$, df = 1, $P < 0.0001$). The line represents the 'line-of-best-fit' from simple linear regression. Note that spider mite abundance is plotted on a $\log_{10}$ scale.

occidentalis was somewhat of an exception, because thrips were present in nearly all the treatments. Despite this problem, the thrips addition treatment had significantly higher thrips densities compared with the control ($\chi^2 = 6.7$, df = 1, $P = 0.01$).

Predatory mite releases enhanced the predaceous mite density (Table 2). Final densities of predatory mites were, however, lower than the release rate (release rate, 10.6 ± 0.7 mites per plant; final predator density; 3.7 ± 0.8), resulting in a negative per capita population growth rate (per capital growth = [(final abundance – initial abundance) / initial abundance] = −0.65). This result is similar to that observed at the 8-d census in experiment 1, in which there was also a period of negative per capita population growth after the initial release.

The addition of hemipteran predators had a strong negative impact on predatory mite abundance (Fig. 2A). Predatory mite abundance was reduced from 3.67 ± 0.78 in the predatory mite only treatment to 0.0 in the predatory mite + *O. tristicolor* treatment ($\chi^2 = 22.8$, df = 1, $P < 0.001$) and 0.83 ± 0.35 in the predatory mite + *Geocoris* treatment ($\chi^2 = 9.8$, df = 1, $P = 0.002$). In contrast, the addition of *F. occidentalis* did not have a significant effect on predatory mite abundance ($\chi^2 = 0.4$, df = 1, $P = 0.53$).

Table 2. Arthropod treatment manipulations in the predator compatibility cage experiment. Shown are the mean ± SE number of motile predators per cage at day 7. Means represent densities of predators in the four different predator addition treatments

Treatment	Control	Predator addition
Western predatory mite only	0	3.7 ± 0.8***
Thrips[a]	7.7 ± 1.7	13.0 ± 1.5*
Geocoris spp.	0	0.5 ± 0.1***
Orius tristicolor	0.05 ± 0.03	1.1 ± 0.3**

Two-tailed Wilcoxon rank-sum tests: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, not significant.

[a] Dominant species was *Frankliniella occidentalis;* minor species included *Caliothrips fasciatus* and *Scolothrips sexmaculatus.*

The negative impact that *O. tristicolor* and *Geocoris* had on the predatory mites was caused by either predation, competition, or both. In an attempt to distinguish between these effects, we performed an ANCOVA with final spider mite abundance as the covariate and main effects for *Orius* and *Geocoris* presence. This analysis showed that final spider mite abundance did not affect final predatory mite abundance ($F = 1.5$, df = 1, $P = 0.22$) but that the addition of both *Geocoris* and *O. tristicolor* significantly depressed final predatory mite abundance ($F = 11.4$, df = 1, $P = 0.001$; $F = 9.2$, df = 1, $P = 0.003$, respectively). A preliminary ANCOVA test verified that there was no significant interaction between the covariate and the main factors. Therefore, this analysis suggests that predation on predatory mites by *Geocoris* and *O. tristicolor* played a more important role than did competition for spider mite prey.

The addition of predatory mites reduced spider mite densities to 47% of the density reached in the control ($\chi^2 = 7.6$, df = 1, $P = 0.006$; Fig. 2B). The simultaneous addition of predatory mites + thrips, or predatory mites + *Geocoris* produced levels of spider mite suppression that were significant in comparison to the control ($\chi^2 = 12.9$, df = 1, $P < 0.001$; $\chi^2 = 15.4$, df = 1, $P < 0.001$, respectively), but not significantly different from the predatory mites alone treatment ($\chi^2 = 0.4$, df = 1, $P = 0.53$; $\chi^2 = 2.5$, df = 1, $P = 0.12$, respectively). However, the addition of predatory mites + *O. tristicolor* lowered spider mite abundance below both the control and the predatory mite alone treatment levels ($\chi^2 = 26.9$, df = 1, $P < 0.001$; $\chi^2 = 21.7$, df = 1, $P < 0.001$, respectively).

Although we attempted to exclude thrips from all the treatments except one, we observed thrips in all treatments; however, the densities of these naturally present thrips were substantially reduced in the hemipteran predator treatments (Fig. 2C). Final densities of thrips were significantly lower in treatments containing *Orius* and *Geocoris* compared with the spider mite alone treatment ($\chi^2 = 23.5$, df = 1, $P < 0.001$; $\chi^2 = 9.8$, df = 1, $P = 0.002$, respectively). However, the presence of western predatory mites alone did not affect thrips abundance ($\chi^2 = 0.3$, df = 1, $P = 0.57$).

Compatibility of Spider Mite Predators—Open Plot Experiment. In this experiment, acephate was applied to plots to reduce the densities of naturally occurring generalist predators while minimizing the pesticide-induced mortality of spider mites. The application of acephate was effective at reducing predators; 2 wk after the acephate application immature predator abundance (excluding western flower thrips) was reduced by 80% ($\chi^2 = 13.6$, df = 1, $P < 0.001$, Fig. 3A) and western flower thrips abundance was reduced by 48% ($\chi^2 = 4.8$, df = 1, $P = 0.026$, Table 3). Some generalist predators, such as *Geocoris* spp., remained at suppressed densities in the acephate-treated plots throughout the 8-wk experiment ($F = 35.8$, df = 1, $P < 0.001$, Table 3). Other predators, such as *O. tristicolor* and *F. occidentalis*, actually became more abundant in

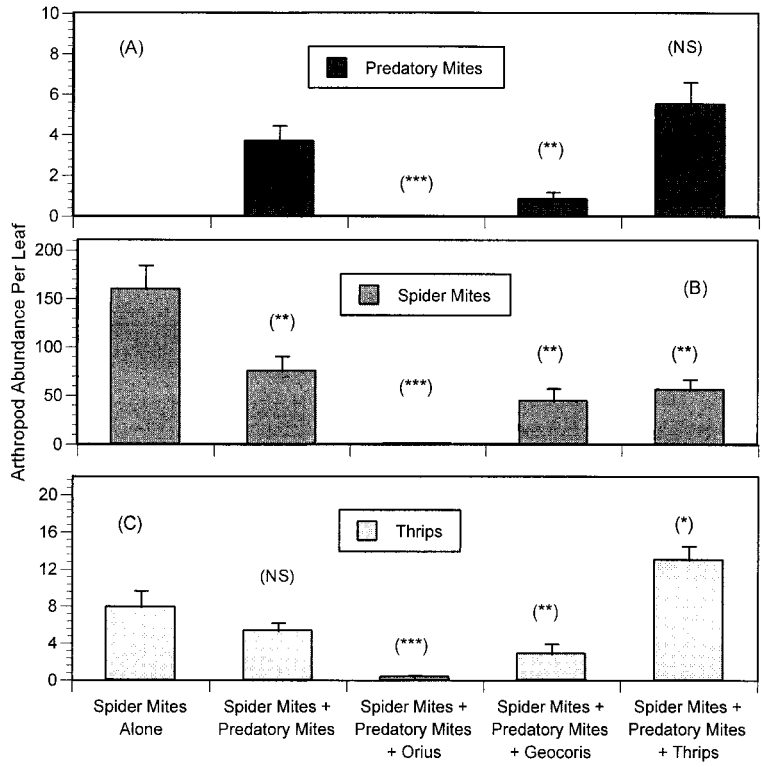

Fig. 2. Mean (+SE) arthropod abundance per leaf in predator compatibility cage experiment. (A) Predatory mite abundance in treatments with predatory mites alone and in treatments where predatory mites were combined with the generalist predators: minute pirate bug (*Orius tristicolor*), big-eyed bug (*Geocoris* spp.), and western flower thrips (*Frankliniella occidentalis*). (B) Spider mite abundance in treatments with spider mites alone and spider mites combined with different combinations of predatory mites and generalist predators. (C) Thrips abundance in all treatments. Symbols above bars display results of statistical tests comparing arthropod species abundance in each predator treatment with the species alone treatments.

the acephate plots than in the control plots 6 wk after the acephate applications (*O. tristicolor:* $\chi^2 = 16.5$, df = 1, $P < 0.001$; *F. occidentalis:* $\chi^2 = 7.9$, df = 1, $P = 0.005$; Table 3).

Predatory mite numbers increased significantly in plots sprayed with acephate over the duration of the experiment ($F = 10.6$, df = 1, $P = 0.003$, Fig. 4). This increase was especially conspicuous when viewed as cumulative predatory mite abundance across the four sampling dates after the acephate application ($\chi^2 = 11.4$, df = 1, $P < 0.001$, Fig. 3B). Predatory mite releases, however, did not have any detectable effect on total predatory mite densities over the duration of the experiment follow the releases ($F = 0.0$, df = 1, $P = 0.91$, Fig. 4). Predatory mites recovered from the field included *G. occidentalis* (94/114, 82%), *Neoseiulus aurescens* Athias-Henriot (15%), and *Neoseiulus fallacis* (Garman) (3%). On 2 June, before the release of *G. occidentalis*, the most abundant species was *N. aurescens* (14/25, 56%) followed by *G. occidentalis* (44%). On 15 and 29 June, 2 and 4 wk after the predatory mite release, the predatory mite community was dominated by *G. occidentalis* (Table 4). *Galendromus occidentalis* was, however, equally common in both the release and control plots in the postrelease samples (release: 96% *G. occidentalis*, no release: 92% *G. occidentalis*).

With the decline in predatory insect abundance, we observed higher spider mite densities in acephate treated plots compared with untreated plots over the duration of the experiment ($F = 29.0$, df = 1, $P < 0.001$, Fig. 5). Spider mite densities in treated plots were 4.2 times greater and 9.8 times greater than the untreated plots 2 and 4 weeks after the acephate application, respectively. Spider mites declined in both sprayed and unsprayed plots after 2 June, and sprayed and unsprayed plots had similarly low densities of spider mites by 15 July ($F = 2.2$, df = 1, $P = 0.14$); the decrease in spider mite populations was correlated with an increase in insect predator abundance across sampling dates (Spearmans $\rho = -0.3$, $P < 0.001$). Given that the releases of predatory mites had no effect on overall predatory mite densities (Fig. 4), it was not surprising that these releases also had no detectable effect on spider mite densities ($F = 0.3$, df = 1, $P = 0.60$; Fig. 5).

Acephate sprays led to decreases in the populations of generalist insect predators and increases in the

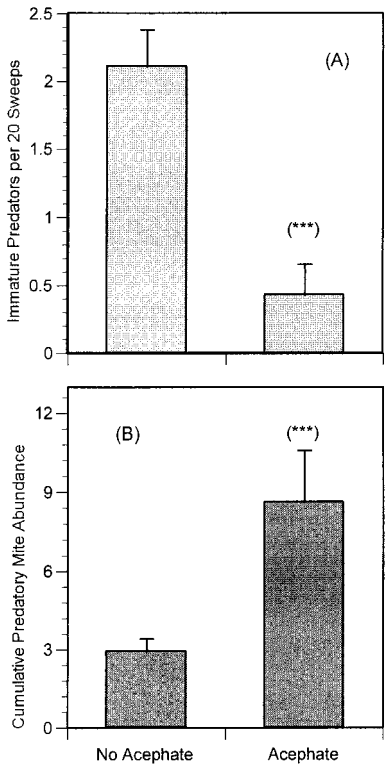

Fig. 3. Generalist predator and predatory mite abundance in the predator compatibility, acephate, open-plot experiment. (A) Mean (+SE) immature predator abundance in plots that were sprayed with acephate and in unsprayed plots. Predators included big-eyed bugs (*Geocoris* spp.), minute pirate bugs (*Orius tristicolor*), damsel bugs (*Nabis* spp.), lacewings (chrysopid spp.), and coccinellid spp. (listed in order of abundance). Samples consisted of 20 sweeps of the plant canopy using a sweep net. Samples were collected 2 wk follow the acephate spray. (B) Mean (+ SE) cumulative predatory mite abundance in acephate sprayed and unsprayed plots. Mite abundance was summed from the four sampling dates (25 leaves per sample) after the acephate application.

populations of predatory mites and spider mites. The most likely reason that spider mite populations increased after the acephate spray is that they experienced less predation pressure from generalist predators. Predatory mite populations might have increased after sprays either because they experienced less predation pressure or because they experienced less competition for spider mite prey. To determine which of these factors was more important for the variation in predatory mite abundance between the sprayed and unsprayed plots, we used ANCOVA on the census data after the acephate spray. In this analysis, predatory mite abundance (population abundance summed across four sampling dates) was the response variable, generalist predator abundance (from sweep samples 2 wk after the acephate application) and spider mite abundance (population abundance summed across four sampling dates) were the covariates, and the acephate spray was the main effect. A preliminary ANCOVA test verified that there was no significant interaction between the covariates and the main factor. Spider mite abundance had a significant effect on predatory mite abundance ($F = 4.4$, df = 1, $P = 0.043$); generalist predator abundance and the acephate spray did not affect predatory mite abundance ($F = 1.0$, df = 1, $P = 0.3$; $F = 2.3$, df = 1, $P = 0.14$, respectively). This analysis indicates that competition with generalist predators for spider mite prey may have had a greater influence on predatory mite populations than did direct predation. This result was in contrast to the small cage experiment where generalist predator additions had an impact on predatory mite abundance but spider mite abundance did not.

Discussion

In this study, our first objective was to determine if commercially reared western predatory mites could establish and increase their population size on cotton if generalist predators were removed. We found in our first experiment that *G. occidentalis* could establish and increase its population size by 60% over 18 d on cotton under conditions of high spider mite availability and low generalist predator abundance. This result is of interest because earlier field releases of *G. occidentalis* at low release rates were not successful in establishing predatory mite populations (R. G. Colfer, J. A. Rosenheim, L. D. Godfrey, C. L. Hsu, unpublished data). For our second objective, we evaluated the impact that naturally occurring generalist predators, including *Geocoris* spp., *O. tristicolor*, and *F. occidentalis*, have on western predatory mite establishment and on spider mite control. We examined the impact of these generalist predators at two scales: in a well-controlled small-scale manipulative experiment em-

Table 3. Density (mean ± SE) of generalist predators associated with spider mites over the duration of the acephate open-plot experiment

Treatments	2 wk after spray		4 wk after spray		6 wk after spray	
	Insecticide	Control	Insecticide	Control	Insecticide	Control
Geocoris spp.[a]	1.8 ± 0.3	5.0 ± 0.5***	–	–	5.1 ± 1.0	10.9 ± 0.7***
Orius tristicolor[a]	1.2 ± 0.3	0.7 ± 0.2 NS	–	–	14.0 ± 1.6	6.2 ± 0.7***
F. occidentalis[b]	20.4 ± 2.2	38.9 ± 7.1*	135.2 ± 16.0	73.9 ± 7.6***	65.1 ± 7.7	45.5 ± 2.6**

Two-tailed Wilcoxon rank-sum tests: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, not significant.
[a] *Geocoris* and *Orius* abundances are from sweep samples (reported as number of predators per 20 sweeps).
[b] *F. occidentalis* abundance is from leaf samples (reported as thrips per 25 leaves).

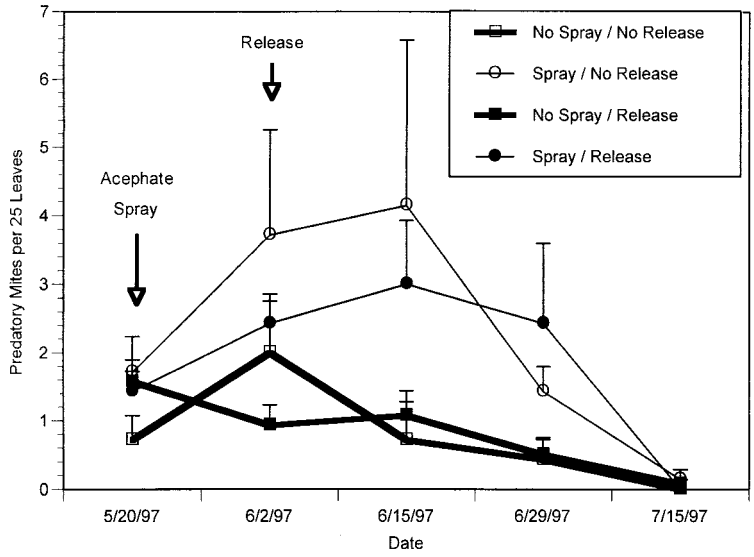

Fig. 4. Population dynamics of predatory mites (mean + SE) in plots in which generalist predators were suppressed with an acephate application and in which western predatory mites were released in the acephate, open-plot experiment. Arrows indicate when plots received an acephate application and/or a predatory mite release.

ploying cages, and in a less-controlled larger-scale manipulative experiment done with open plots. We found that when western predatory mites were combined with the hemipteran predators *Geocoris* spp. or *O. tristicolor*, their densities were greatly reduced. The outcome was similar in the insecticide manipulation experiment; western predatory mites nearly tripled their abundance when generalist predators were chemically suppressed. In the cage experiments, in which insect predator exclusion was nearly complete, predatory mites could suppress spider mites when release rates were high (Table 1, Fig. 2B). However, in the open-plot experiment, in which predatory insect exclusion was only partial, predatory mite releases had no impact on spider mite densities (Fig. 5). The strong negative effect that generalist predators had on western predatory mites did not, however, disrupt spider mite biological control; the hemipteran predators compensated for their impact on *G. occidentalis* by consuming spider mites themselves (Fig. 2B). Generalist predators effectively suppressed spider mites compared with treatments where they were excluded.

Impact of Hemipteran Predation on Western Predatory Mite Populations. In this study, we demonstrated that generalist hemipteran predators, such as *Geocoris* spp. and *O. tristicolor*, can have negative impacts on *G. occidentalis* populations. In our cage experiment, the addition of *Geocoris* spp. and *O. tristicolor* reduced predatory mite densities to 23% and 0%, respectively, compared with the density observed in the predatory mite alone treatment. In our insecticide manipulation experiment, predatory mite abundance was nearly three times greater in plots in which generalist predators were chemically suppressed compared with control plots. The negative effects that *Orius* spp. can have on predaceous phytoseiid mites has been studied in the laboratory (Gillespie and Quiring 1992, Cloutier and Johnson 1993, Wittmann and Leather 1997), and in greenhouse nurseries (Ramakers 1993, Brodsgaard and Enkegaard 1997) where both groups are used as biological control agents. However, we know of no studies that have documented predatory interactions between *Orius* and phytoseiid mites under field conditions or predatory interactions between *Geocoris* and phytoseiids under any conditions. Both of these hemipteran predators are very common in cotton and other row crops and are important naturally occurring spider mite predators (Wilson et al. 1991a).

In contrast to the hemipteran predators, western flower thrips (*F. occidentalis*) did not appear to have negative effects on western predatory mites. This result is in contrast to the impact that *F. occidentalis* has on spider mite population via egg predation (Trichilo and Leigh 1986, Agrawal et al. 1999, Agrawal and Klein 2000, R. G. Colfer and A. A. Agrawal, unpublished data). Western flower thrips have been shown to consume predatory phytoseiid mite eggs under laboratory conditions (Colfer et al. 1998, Roda et al. 2000). Perhaps predatory mites were able to avoid egg predation by thrips by laying their eggs in close proximity to

Table 4. Predatory phytoseiid mite species composition over the duration of the acephate open-plot experiment for all treatments

	Galendromus occidentalis	*Neoseiulus aurescens*	*Neoseiulus fallacis*	Sample size
2 wk after spray	44%	56%	0%	$n = 25$
4 wk after spray	95%	3%	2%	$n = 61$
6 wk after spray	89%	4%	7%	$n = 28$
Total	82%	15%	3%	$n = 114$

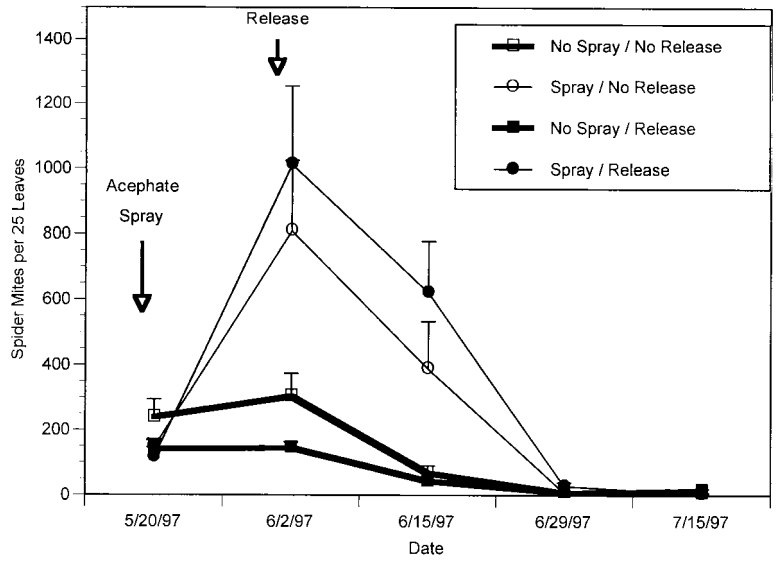

Fig. 5. Population dynamics of spider mites (mean + SE) in plots in which generalist predators were suppressed with an acephate application and in which western predatory mites were released in the acephate, open-plot experiment. Arrows indicate when plots received an acephate application and/or a predatory mite release.

spider mite webbing and cotton leaf trichomes that are common on Acala cotton (the type of cotton most grown in the San Joaquin Valley). Roda et al. (2000) found that predatory mite egg predation as a result of western flower thrips was significantly reduced when eggs were located on leaves with artificial trichromes or spider mite webbing versus on trichome-free leaves. Another explanation is that predatory mite eggs may be a suboptimal food item for western flower thrips that they chose not to feed on when other food sources are available such as spider mite eggs and pollen. Also, our experimental approaches did not completely exclude thrips from experimental units (cages, open-plots). Thrips contamination limits our ability to evaluate the impact of thrips on western predatory mites.

Each of the experimental approaches that we used to evaluate the compatibility of predators has limitations. The cage experiments contained fairly small populations of arthropods that were confined within the enclosures. In the open-plot experiment, in addition to our desired effect of reducing generalist predator populations, the acephate application could have influenced the arthropod communities in other ways. Because we observed similar outcomes using these very different experimental approaches, we believe the negative impact of hemipteran predators on the western predatory mite populations is real. Generalist hemipteran predators are common in many annual cropping systems, and our findings suggest that the augmentation of predatory mites or other biological control agents could be generally limited in annual agroecosystems by these predators.

When one predator has a negative impact on another predator, there are two major mechanisms that may be operating. First, one predator can consume the second species, known as intraguild predation (Polis et al. 1989, Rosenheim et al. 1995). Second, one predator species can have a detrimental effect on a second predator species by depleting a resource that the second predator requires. This type of interaction is known as exploitative competition (Schoener 1983). Hemipteran predators could have negatively influenced predatory mite populations by means of intraguild predation, exploitative competition, or both of these mechanisms. In the cage experiment, our analysis indicated that intraguild predation was the more important mechanism by which western predatory mite populations were suppressed. However, in the large-scale insecticide experiment, our analysis suggested that exploitative competition for spider mites may have been the more important mechanism causing the reduction in western predatory mite populations. As a caveat, the use of ANCOVA to determine whether predation or competition was more important to predatory mite populations has limitations. In systems with intraguild predation, it is difficult to tease apart statistically the effects of predation and competition, because the intensity of both of these forces may be mediated by the availability of the shared resource (Schoener 1983, Polis et al. 1989).

There are four major differences between the cage experiment and large-scale insecticide experiment that may explain why intraguild predation played the more important role in the cage experiment and exploitative competition played a more important role in the large-scale acephate experiment. First, the difference in predator communities in the cage experiment was discrete; hemipteran predators were either present or absent from cages, depending on the treatment. In contrast, the exclusion of hemipteran predators in the large-scale acephate experiment was par-

tial and occurred during a single event (one acephate application). Bare soil surrounding the experimental plots was the only barrier against generalist predators reestablishing in sprayed plots. Thus, the difference in potential predation pressure on western predatory mites between treatments where hemipteran predators were present or absent was more distinct in the cage experiment than the acephate experiment. The cage experiment was, therefore, more appropriately designed for evaluating predation as a factor limiting western predatory mite populations. Second, densities of spider mites used in the cage experiment were representative of high density field conditions (R.G. Colfer and J.A. Rosenheim, unpublished data). In the large-scale acephate experiment, initial spider mite densities were low, compared with their densities in the cage experiment (acephate experiment: 6.4 per leaf; cage experiment: 147 mites per leaf). The lower densities of spider mites in the acephate experiment likely increased the importance of exploitative competition (Schoener 1983). Predatory mite abundance may have been more limited by spider mite prey availability than by predation. Third, the duration of the large-scale acephate experiment was much longer than the cage experiment (56 d versus 7 d). Theory predicts that effects from indirect interactions such as exploitative competition should take a longer time to observe than direct effects (Bender et al. 1984, Yodzis 1988). The longer duration of the acephate experiment may have made this experiment more conducive for detecting exploitative competition compared with the cage experiment. It should be noted, however, that reviews of experimental manipulations of communities have indicated that indirect effects tend to take equal or only slightly more time to detect than do direct effects (Schoener 1993; Menge 1995, 1997). Fourth, the confinement of the cages could potentially have increased the likelihood that organisms would interact with each other. However, more recent experiments that allowed predator movement and increased cage size produced very similar results as the predator compatibility cage experiment described above (R. G. Colfer and J. A. Rosenheim, unpublished data), indicating that this factor is less important than the others.

Influence of Predator-Predator Interactions on Spider Mite Control. Although the simultaneous addition of predatory mites and hemipteran predators had negative effects on predatory mite establishment, it did not interfere with spider mite suppression. Indeed, the best spider mite suppression in the small-scale cage experiment was in the *O. tristicolor* + predatory mite treatment. Results from this study as well as from larger-scale, longer-term exclusion cage experiments (R. G. Colfer and J. A. Rosenheim, unpublished data), indicate that although intraguild predation by hemipteran predators on western predatory mites prevented predatory mite populations from reaching high abundance, it does not appear to disrupt spider mite biological control.

These results are in contrast to some other arthropod systems where the occurrence of predator-predator interactions cause reductions in the efficacy of biological control (Croft and MacRae 1993, Rosenheim et al. 1993, Cisneros and Rosenheim 1997, Rosenheim 2001, Snyder and Wise 2001, Snyder and Ives 2001). Indeed, in the apple agroecosystem, predation by *Zetzellia mali* on *G. occidentalis* can disrupt control of *Panonychus ulmi* (Croft and MacRae 1992a). However our results are in agreement with other systems with high levels of intraguild predation. In both early-season cotton and alfalfa, aphid suppression was improved by combining predators with aphid parasitoids compared with systems with aphid parasitoids alone, even though predators readily fed on immature parasitoids (Colfer and Rosenheim 2001, Snyder and Ives 2002). Thus, in systems with multiple predators, intraguild predation may have a variety of impacts on herbivore biological control: herbivore suppression may be disrupted, unchanged, or improved by combining predator species. In the case of augmentative biological control, releases may not be economically feasible if the released natural enemies do not establish populations for the duration of the growing season, even if they improve herbivore suppression over the short term.

In our open-plot experiment, we found that acephate substantially reduced generalist predator densities and caused spider mite densities to increase 4.2–9.8 times above mite densities in unsprayed plots. There are several potential causes of such a secondary outbreak of spider mites. One of the best supported explanations for this observation is that insecticides decimate naturally occurring generalist predators, yet cause little mortality to spider mites (Gonzalez et al. 1982, Trichilo and Leigh 1986, Wilson et al. 1991a, Sclar et al. 1998, this study). When spider mite populations are no longer limited by predation they can expand and cause severe foliar damage to cotton plants (Wilson et al. 1991b). Another potential reason for secondary outbreaks of mites is that broad spectrum insecticides may cause spider mite population growth rates to increase either directly or indirectly by modifying plant quality (Leigh and Wynholds 1980). Although both of these factors may contribute to spider mite outbreaks, simulation analysis of this system has shown that the reduction in predator abundance is more important (Trichilo and Wilson 1993). In this study we employed several techniques to evaluate natural enemy impacts on spider mites. Because the magnitude of the impact of generalist predators on spider mite populations was similar whether predators were excluded with cages or with insecticides, we conclude that the accelerated spider mite population growth after the acephate treatment was primarily a result of the suppression of generalist predators.

Factors Influencing Western Predatory Mite Establishment in the Cotton Agroecosystem. The outcome of the experiment evaluating predatory mite establishment under conditions of high spider mite availability and low generalist predator abundance differed in important ways from the results of an earlier study of predatory mite releases in grower fields, in which we failed to obtain establishment of the released mites

(R. G. Colfer, J. A. Rosenheim, L. D. Godfrey, C. L. Hsu, unpublished data). First, in this study, using high release rates, we were able to greatly increase the predatory mite population compared with the naturally-occurring background population. This effect was probably caused by our experimental preparation of replicates (spraying of insecticidal soap and brushing of plant material), which may have reduced the background level of predatory mites in these replicates. Second, the released predatory mite populations increased at least 60% in size over 18 d when afforded high spider mite availability and low predation risk (this calculation excludes predatory mite eggs, so the actual population increase was likely to be well above 60%). This result is important in that it demonstrates that *G. occidentalis* can build up populations in cotton. Predatory mite densities were highly correlated with spider mite densities, suggesting that predatory mites showed the greatest recruitment on plants that had greater availability of prey. Whether *G. occidentalis* mites need these high spider mite densities to reproduce in cotton remains unknown at this time.

It is unclear why releases of predatory mites in the open-plot, acephate experiment did not boost predatory mite abundance in the sprayed plots, in which generalist predator abundance had been reduced. There are three potential bases for this result. First, release rates in the open-plot experiment were relatively modest (37,500 mites per ha or ≈0.5 per plant) compared with the cage experiment (78 mites per plant). The combination of post release mortality of predatory mites and release rates that were slightly less than the resident population of predator mites could help explain why the releases did not increase predatory mite populations (resident predatory mite density at the time of the release: 0.74 mites per plant). Second, whereas the exclusion of predators from the cage experiment was nearly complete, the acephate treatment produced only a partial and temporary suppression of hemipteran predators. Thus, hemipteran predators may have continued to impose predation risks on *G. occidentalis.* We released western predatory mites 2 wk after the acephate application, after our leaf assay showed that the acephate was no longer toxic to western predatory mites. At the time of the release, it is likely that the acephate was no longer toxic to hemipteran predators and their populations were reestablishing in these plots. Third, our field site may have had greater densities of *G. occidentalis* than generally observed in cotton, because it was downwind from an almond orchard that could have been a source of *G. occidentalis.* Western predatory mites are known to develop high densities and to disperse aerially over large distances in almond orchards (Hoy 1982, Grafton-Cardwell et al. 1991). Indeed, predatory mite abundance declined with increasing distance from the almond orchard (cumulative predatory mites for June sample dates: $r^2 = 0.16$, $F = 7.4$, df = 1, $P = 0.01$).

In summary, we found that the naturally occurring generalist predators *Geocoris* spp. and *O. tristicolor* substantially reduced the abundance of an augmentatively released predator—the western predatory mite. Despite the negative effect of these hemipteran predators on *G. occidentialis,* the presence of these predators improved spider mite control. No effect of *F. occidentalis* was observed on western predatory mite populations. Under conditions of high spider mite availability, low generalist predator abundance, and high release rates, western predatory mite releases increased predatory mite populations; these populations subsequently increased their abundance through reproductive recruitment and suppressed spider mite populations. However, a lower release rate in an open-plot experiment did not increase predatory mite abundance. This study indicates that augmentative releases of *G. occidentalis* may be limited by naturally occurring generalist predators in the cotton agroecosystem. Also, our results suggest that there can be intraguild predation between natural enemies without disrupting biological control.

Acknowledgments

We thank Tobias Glik, Paola Santillán, Gail Siu, SusieteVillanueva, and Elmer Yee for research assistance. We thank John Peterson and the staff at the UC Shafter Research Extension Center, the staff at the UCD Plant Pathology Fieldhouse, and the staff at the UCD Agronomy Field Shop. This research was partially funded by grants from the California State Support Board of Cotton Incorporated, the Department of Pesticide Regulation (Cal EPA), the California Cotton Pest Control Board, and the U.S. Environmental Protection Agency (STAR Fellowship Program).

References Cited

Agrawal, A. A., and C. N. Klein. 2000. What omnivores eat: direct effects of induced plant resistance on herbivores and indirect consequences for diet selection by omnivores. J. Anim. Ecol. 69: 525–535.

Agrawal, A. A., C. Kobayashi, and J. S. Thaler. 1999. Influence of prey availability and induced host-plant resistance on omnivory by western flower thrips. Ecology 80: 518–523.

Barbosa, P. 1998. Conservation biological control. Academic, San Diego, CA.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: Theory and practice. Ecology 65: 1–13.

Brodsgaard, H. F., and A. Enkegaard. 1997. Interactions among polyphagous anthocorid bugs used for thrips control and other beneficials in multi-species biological pest management systems. Rec. Res. Devel. Entomol. 1: 153–160.

Cisneros, J. J., and J. A. Rosenheim. 1997. Ontogenetic change of prey preference in a generalist predator, *Zelus renardii,* and its influence on the intensity of predator-predator interactions. Ecol. Entomol. 22: 399–407.

Cloutier, C., and S. G. Johnson. 1993. Predation by *Orius tristicolor* (Hemipteran: Anthocoridae) on *Phytoseiulus persimilis* (Acarina: Phytoseiidae): testing for compatibility between biocontrol agents. Environ. Entomol. 22: 477–482.

Colfer, R. G., J. A. Rosenheim, L. D. Godfrey, and C. L. Hsu. 1998. Evaluation of predaceous mite releases for spider

mite management. Proc. Beltwide Cotton Conf. 2: 976–982.

Colfer, R. G., and J. A. Rosenheim. 2001. Predation on immature parasitoids and its impact on aphid suppression. Oecologia (Berl.). 126: 292–304.

Croft, B. A. 1994. Biological control of apple mites by a phytoseiid mite complex and *Zetzellia mali* (Acari: Stigmaeidae): long term effects and impact of azinphosmethyl on colonization by *Amblyseius andersoni* (Acari: Phytoseiidae). Environ. Entomol. 23: 1317–1325.

Croft, B. A., and M. B. Croft. 1996. Intra- and interspecific predation among adult female phytoseiid mites (Acari: Phytoseiidae): effects on survival and reproduction. Environ. Entomol. 25: 853–858.

Croft, B. A., S. S. Kim, and D. I. Kim. 1996. Intra- and interspecific predation on four life stage groups by the adult females of *Metaseiulus occidentalis, Typhlodromus pyri, Neoseiulus fallacis* and *Amblyseius andersoni.* Exp. Appl. Acarol. 20: 435–444.

Croft, B. A., and I. V. MacRae. 1992a. Persistence of *Typhlodromus pyri* and *Metaseiulus occidentalis* (Acari: Phytoseiidae) on apple after inoculative release and competition with *Zetzellia mali* (Acari: Stigmaeidae). Environ. Entomol. 21: 1168–1177.

Croft, B. A., and I. V. MacRae. 1992b. Biological control of apple mites by mixed populations of *Metaseiulus occidentalis* (Nesbitt) and *Typholodromus pyri* Scheuten (Acari: Phtyoseiidae). Environ. Entomol. 21: 202–209.

Croft, B. A., and I. V. MacRae. 1993. Biological control of apple mites: impact of *Zetzellia mali* (Acari: Stigmaeidae) on *Typhlodromus pyri* and *Metaseiulus occidentalis* (Acari: Phytoseiidae). Environ. Entomol. 22: 865–873.

Flaherty, D. L., L. T. Wilson, V. M. Stern, and H. Kido. 1985. Biological control in San Joaquin Valley vineyards, pp. 501–520. *In* M. A. Hoy and D. C. Herzog [eds.], Biological control in agricultural IPM systems. Academic, Orlando, FL.

Gillespie, D. R., and D.J.M. Quiring. 1992. Competition between *Orius tristicolor* (White) (Hemipteran:Anthocoridae) and *Amblyseius cucumeris* (Oudemans) (Acari: Phytoseiidae) feeding on *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). Can. Entomol. 124: 1123–1128.

Gonzalez, D., B. R. Patterson, T. F. Leigh, and L. T. Wilson. 1982. Mites: a primary food source for two predators in San Joaquin cotton. Calif. Agric. 36: 18–20.

Grafton-Cardwell, E., J. Granett, and S. M. Normington. 1991. Influence of dispersal from almonds on the population dynamics and acaricide resistance frequencies of spider mites infesting neighboring cotton. Exp. Appl. Acarol.

Helle, W., and M. W. Sabelis. 1985. World crop pests: spider mites their biology, natural enemies and control, vol. 2b. Elsevier Publishers B. V., Amsterdam, The Netherlands.

Howarth, F. G. 1991. Environmental impacts of classical biological control. Annu. Rev. Entomol. 36: 485–509.

Hoy, M. A. 1982. Aerial dispersal and field efficacy of a genetically improved strain of the spider mite predator *Metaseiulus occidentalis.* Entomol. Exp. Appl. 32: 205–212.

Hoy, M. A., W. Barnett, and W. D. Reil. 1982. Large scale releases of pesticide resistant spider mite predators. Calif. Agric. 35: 8–10.

Leigh, T. F., V. L Maggi, and L. T Wilson. 1984. Development and use of a machine for recovery of arthropods from plant leaves. Environ. Entomol. 77: 271–276.

Leigh, T. F., and P. F. Wynholds. 1980. Do insecticides trigger spider mite reproduction? Calif. Ariz. Cotton 15: 19–21.

Louda, S. M., D. Kendall, J. Connor, and D. Simberloff. 1998. Ecological effects of an insect introduced for the biological control of weeds. Science 277: 1088–1090.

MacRae, I. V., and B. A. Croft. 1996. Differential impact of egg predation by *Zetzellia mali* (Acari: Stigmaeidae) on *Metaseiulus occidentalis* and *Typhlodromus pyri* (Acari: Phytoseiidae). Exp. Appl. Acarol. 20: 143–154.

McMurtry, J. A. 1982. The use of phytoseiids for biological control: progress and future prospects, pp. 23–48. *In* M. A. Hoy [ed.], Recent advances in knowledge of the phytoseiidae. University of California Press, Berkeley, CA.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecol. Monogr. 65: 21–74.

Menge, B. A. 1997. Detection of direct versus indirect effects: were experiments long enough? Am. Nat. 149: 801–823.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models, 3rd ed. Richard D. Irwin, Inc., Homewood, IL

Nyrop, J., G. English-Loeb, and A. Roda. 1998. Conservation biological control of spider mites in perennial cropping systems, pp. 307–333. *In* P. Barbosa [ed.], Conservation of natural enemies of pest species. Academic, San Diego, CA.

Osman, A. A., and G. Zohdi. 1976. Suppression of the spider mites on cotton with mass releases of *Amblyseius gossipi* (El Badry). Z. Ang. Entomol. 81: 245–8.

Parrella, M. P., K. M. Heinz, and L. Nunney. 1992. Biological control through augmentative releases of natural enemies: a strategy whose time has come. Am. Entomol. 38: 172–179.

Pickett, C. H. and R. L. Bugg [eds.]. 1998. Enhancing biological control: habitat management to promote natural enemies of agricultural pests. University of California Press, Berkeley, CA.

Pickett, C. H., and F. E. Gilstrap. 1986. Inoculative releases of phytoseiids (Acari) for the biological control of spider mites (Acari: Tetranychidae) in corn. Environ. Entomol. 15: 790–794.

Pickett, C. H., F. E. Gilstrap, R. K. Morrison, and L. F. Bouse. 1987. Release of predatory mites (Acari: Phytoseiidae) by aircraft for the biological control of spider mites (Acari: Tetranychidae) infesting corn. J. Econ. Entomol. 80: 906–910.

Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu. Rev. Ecol. Syst. 20: 297–330.

Ramakers, P.M.J. 1993. Coexistence of two thrips predators, the anthocorid *Orius insidiosus* and the phytoseiid *Amblyseius cucumeris* on sweet pepper. Bulletin OILB/SROP 16: 133–136.

Roda, A., J. Nyrop, M. Dicke, and G. English-Loeb. 2000. Trichomes and spider-mite webbing protect predatory mite eggs from intraguild predation. Oecologia (Berl.) 125: 428–435.

Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect herbivore populations. Annu. Rev. Entomol. 43: 421–447.

Rosenheim, J. A. 2001. Source-sink dynamics for a generalist insect predator in a habitat with strong higher-order predation. Ecol. Monogr. 71: 93–116.

Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marios, and B. A. Jaffee. 1995. Intraguild predation among biological-control agents: theory and evidence. Biol. Control. 5: 303–335.

Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect

predators on the suppression of an herbivore population. Oecologia (Berl.). 96: 439–449.

SAS Institute. 2000. JMP statistical discovery software for Microsoft Windows, version 3.2.2. SAS Institute, Cary, NC.

Schausberger, P., and B. A. Croft. 2000. Cannibalism and intraguild predation among phytoseiid mites: are aggressiveness and prey preference related to diet specialization? Exp. Appl. Acarol. 24: 709–725.

Schausberger, P., and A. Walzer. 2001. Combined versus single species release of predaceous mites: predator-predator interactions and pest suppression. Biol. Control 20: 269–278.

Sclar, D. C., D. Gerace, and W. S. Cranshaw. 1998. Observations of population increases and injury by spider mites (Acari: Tetranychidae) on ornamental plants treated with imidacloprid. J. Econ. Entom. 91: 250–255.

Schoener, T. W. 1993. On the relative importance of direct versus indirect effects in ecological communities, pp. 365–411. *In* H. Kawanabe, J. E. Cohen, and K. Iwasaki [eds.], Mutualism and community organization: behavioral, theoretical and food web approaches. Oxford University Press, Oxford, United Kingdom

Simberloff, D., and P. Stiling. 1996. How risky is biological control? Ecology 77:1965–1974.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, 3rd ed. W. H. Freeman and Company, New York.

Snyder, W. E., and A. R. Ives. 2001. Generalist predators disrupt biological control by a specialist parasitoid. Ecology 82: 705–716.

Snyder, W. E., and A. R. Ives. 2002. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biological control. Ecology 84: 91–107.

Snyder, W. E., and D. H. Wise. 2001. Contrasting trophic cascades generated by a community of generalist predators. Ecology 82: 1571–1583.

Sunderland, K. D., J. A. Axelsen, K. Dromph, B. Freier, J. L. Hemptinne, N. H. Holst, P.J.M. Mols, M. K. Petersen, W. Powell, P. Ruggle, H. Triltsch, and L. Winder. 1997. Pest control by a community of natural enemies. Acta Jutlandica. 72: 271–326.

Tijerina-Chavez, A. D. 1991. Biological control of spider mites (Acari: Tetranychidae) on cotton through inoculative releases of predatory mites *Metaseiulus occidentalis* and *Amblyseius californicus* (Acari: Phytoseiidae) in the San Joaquin Valley of California. Ph. D. dissertation, University of California, Davis, CA.

Trichilo, P. J., and T. F. Leigh. 1986. Predation on spider mite eggs by the western flower thrips, Frankliniella occidentalis (Thysanoptera: Thripidae), an opportunist in a cotton agroecosystem. Environ. Entomol. 15: 821–825.

Trichilo, P. J., and L. T. Wilson. 1993. An ecosystem analysis of spider mite outbreaks: physiological stimulation or natural enemy suppression. Exp. Appl. Acarol. 17: 291–314.

van den Bosch, R., and K. S. Hagen. 1966. Predaceous and parasitic arthropods in California cotton fields. California Agricultural Experiment Station Bulletin 820.

Van Driesche, R. G., and T. S. Bellows. 1996. Biological control. Chapman & Hall, Inc., New York.

Von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures, pp. 113–137. *In* S. M. Scheiner and J. Gurevitch [eds.], Design and analysis of ecological experiments. Chapman & Hall Inc., New York.

Walde, S. J., J. M. Hardman, and C. N. Magagula. 1997. Direct and indirect species interactions influencing within-season dynamics of apple rust mite, *Aculus schlechtendali* (Acari: Eriophyidae). Exp. Appl. Acarol. 21: 587–614.

Wilson, L. T., P. J. Trichilo, and D. Gonzalez. 1991a. Natural enemies of spider mites (Acari: Tretranychidae) on cotton: density regulation or casual association? Environ. Entomol. 20: 849–856.

Wilson, L. T., Trichilo, P. J., and Gonzalez, D. 1991b. Spider mite (Acari: Tetranychidae) infestation rate and initiation: effect on cotton yield. J. Econ. Entomol. 84: 593–600.

Wittmann, E. J., and S. R. Leather. 1997. Compatibility of *Orius laevigatus* Fieber (Hemiptera: Anthocoridae) with *Neoseiulus* (*Amblyseius*) *cucumeris* Oudemans (Acari: Phytoseiidae) and *Iphiseius* (*Amblyseius*) *degenerans* Berlese (Acari: Phytoseiidae) in the biological control of *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae). Exp. Appl. Acarol. 21: 523–538.

Yodzis, P. 1988. The indeterminancy of ecological interactions. Ecology 69: 508–515.

Received for publication 18 January 2002; accepted 22 April 2003.