

Improved Conservation of Natural Enemies with Selective Management Systems for *Bemisia tabaci* (Homoptera: Aleyrodidae) in Cotton*

STEVEN E. NARANJO¹, JAMES R. HAGLER¹ AND PETER C. ELLSWORTH²

¹USDA-ARS, Western Cotton Research Laboratory, 4135 East Broadway Road, Phoenix, AZ 85040; ²University of Arizona, Department of Entomology, Maricopa Agricultural Center, 37860 W. Smith-Enke Road, Maricopa, AZ 85239

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A large-scale study was conducted in 1996 to evaluate and demonstrate strategies for pest management of Bemisia tabaci (Gennadius) in cotton involving different insecticide regimes, application methods, and action thresholds. Here we examined the effects of the various management systems on the abundance and activity of native natural enemies. Population densities of 18 out of 20 taxa of arthropod predators were significantly higher in regimes initiated with the insect growth regulators (IGRs) buprofezin (chitin inhibitor) or pyriproxyfen (juvenile hormone analog) compared with a regime dependent on a rotation of conventional, broad-spectrum insecticides. There were no differences in predator density between the two IGR regimes, and generally no effects due to application method or action threshold level. Predator to prey ratios were significantly higher in regimes utilizing the two IGRs compared with the conventional regime, but were unaffected by application method or threshold level. Rates of parasitism by Eretmocerus eremicus Rose and Zolnerowich and Encarsia meritoria Gahan were higher in the IGR regimes compared with the conventional regime, but were unaffected by insecticide application method, or the action threshold used to initiate applications of the IGRs. Results demonstrate the selective action of these two IGRs and suggest that their use may enhance opportunities for conservation biological control in cotton systems affected by B. tabaci, especially relative to conventional insecticide alternatives.

Keywords: *Bemisia tabaci*, *Bemisia argentifolii*, arthropod predators, aphelinid parasitoids, insect growth regulators, conservation biological control, principal response curves

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Correspondence to: Steven E. Naranjo, USDA-ARS, Western Cotton Research Laboratory, 4135 E. Broadway Rd., Phoenix, AZ 85040. Tel: +1 (602) 437-0121, ext. 241; Fax: +1 (602) 437-1274; E-mail: snaranjo@wcr.ars.usda.gov

INTRODUCTION

Integrated pest management (IPM) is based on the compatible integration of multiple tactics that strive to maximize natural pest mortality by both biotic and abiotic factors (Stern *et al.*, 1959; Kogan, 1998; Ehler & Bottrell, 2000). Biological control by natural enemies represents an important element of IPM in many agricultural systems. However, its potential is rarely realized due to the widespread use of insecticides with broad toxicity to both pests and their natural enemies (e.g. Croft, 1990). This problem is especially well documented in cotton, where broad-spectrum insecticide use has been shown to disrupt the control of key pests and cause the outbreak of secondary pests (e.g. Leigh *et al.*, 1966; Eveleens *et al.*, 1973; Stoltz & Stern, 1978; Devine *et al.*, 1998; Wilson *et al.*, 1998).

Improving the compatibility between chemical and biological control depends on minimizing the effects of insecticides on natural enemies through the use of more selective materials and/or more selective approaches for application of broader-spectrum insecticides (Newsom *et al.*, 1976; Hull & Beers, 1985). The use of action thresholds may contribute to conservation of natural enemies by reducing the application of unnecessary insecticides (Gonzalez & Wilson, 1982; Sterling, 1984; Naranjo *et al.*, 2002). The use of more selective insecticides is also crucial to improving compatibility between chemical and biological controls.

Over the past decade, *Bemisia tabaci* (Gennadius) Biotype B (= *B. argentifolii* Bellows & Perring) (Homoptera: Aleyrodidae) has emerged as a key pest of cotton and various vegetable crops in the southern tier of the U.S. In cotton, feeding damage by *B. tabaci* reduces lint yields, and honeydew deposition can lead to significant reductions in lint quality from stickiness and discoloration from the growth of associated sooty molds (Hector & Hodkinson, 1989; Naranjo *et al.*, 1998). Since 1994 decision aides for insecticide use based on efficient sampling methods and action thresholds have been available to growers (Ellsworth *et al.*, 1995; Naranjo *et al.*, 1998; Ellsworth & Martinez-Carrillo, 2001). Nonetheless, over-reliance on and reduced susceptibility to pyrethroids in *B. tabaci* populations (Dennehy & Williams, 1997; Palumbo *et al.*, 2001) precipitated the issuance of an US-Environmental Protection Agency emergency exemption in 1996 for two insect growth regulators (IGRs), buprofezin and pyriproxyfen. Both of these insecticides have been successfully used in Israel, for suppression of *B. tabaci* in cotton (Ishaaya *et al.*, 1988; Ishaaya *et al.*, 1989; Ishaaya & Horowitz, 1992; Horowitz & Ishaaya, 1992). Buprofezin and pyriproxyfen are considered to be relatively safe from the standpoint of vertebrate toxicity and other qualities (Pener, 2002); however, their selectivity is species-dependent.

Buprofezin, a chitin inhibitor, is generally considered to have a relatively narrow spectrum of activity limited to homopterous insects (Ishaaya *et al.*, 1988). Laboratory bioassays with natural enemies have demonstrated mixed results. Buprofezin has been shown to be toxic to several predator and parasitoid species (Gerling & Sinai, 1994; Hattingh & Tate, 1995; Jones *et al.*, 1998; Magagula & Samways, 2000; Hoddle *et al.*, 2001; Liu & Chen, 2000; Chen & Liu, 2002), but benign to others (Balasubramani & Regupathy, 1994; Jones *et al.*, 1995; Castane *et al.*, 1996; Hoddle *et al.*, 2001). Pyriproxyfen, a juvenile hormone analog, has a comparatively broader spectrum of activity (Ishaaya *et al.*, 1988; Dhadialla *et al.*, 1998). Laboratory bioassays have demonstrated toxicity to several predator and parasitoid species (Mendel *et al.*, 1994; de Clercq *et al.*, 1995; Hattingh & Tate, 1995; Smith *et al.*, 1999). However, pyriproxyfen was found non-toxic to various other species (Peleg, 1988; Delbeke *et al.*, 1997; Liu & Stansly, 1997). In general, the effects of these IGRs on natural enemies appear to be species and stage specific indicating that testing will be needed on a case-by-case basis. Very little is known about the selectivity of these materials towards natural enemy populations in the field under typical production conditions.

A commercial-scale (72 ha) study was initiated to evaluate and demonstrate strategies for pest management of *B. tabaci* in cotton based on these new IGRs. The goals of the overall project were to determine the efficacy and economics of different insecticide regimes for

suppression of *B. tabaci*, determine proper action thresholds for deploying the IGRs, compare different application methods, evaluate resistance management strategies, and examine the effects of alternative insecticide regimes on natural enemy conservation. This last goal is the focus of this study. A diverse assemblage of parasitoids and arthropod predator species inhabit cotton fields (Whitcomb & Bell, 1964; van den Bosch & Hagen, 1966), and we know that many actively attack pests in the system (Hagler & Naranjo, 1994a,b; Gerling & Naranjo, 1998). Here we contrast and compare the abundance and activity of arthropod predators and aphelinid parasitoids relative to management strategies based on the standard use of conventional insecticides and those based on the use of the IGRs buprofezin and pyriproxyfen.

MATERIALS AND METHODS

Study Site and Experimental Design

Cotton, *Gossypium hirsutum* L. was planted on 12 April 1996 at the University of Arizona, Maricopa Agricultural Center, Maricopa, AZ. The cultivar Deltapine NuCOTN 33B, a transgenic cultivar expressing the Cry1Ac insecticidal protein of *Bacillus thuringiensis* Berliner, was used and was grown according to standard agronomic practices for the area.

The experimental design was a randomized complete block with three replications. Individual plots ranged from 1.2 to 2.0 ha in size and the blocks consisted of three separate fields (total area ca. 72 ha) on the Maricopa Agricultural Center demonstration farm. Use of demonstration farm land precluded the inclusion of an untreated control within the experimental design, because proceeds from the sale of this cotton are used to finance overall farm activities. Instead, a treated control representing the commercial standard of rotated conventional insecticides was established for comparison to regimes based on the newly available IGRs. The large plot design was chosen to mimic commercial production practices, minimize inter-plot interference due to arthropod movement, and accommodate the aerial application of insecticides (see below). The experiment consisted of 14 treatments that formed an incomplete factorial design involving three main effects; insecticide treatment regime, application method, and action threshold level. There were three insecticide regimes. The first insecticide regime initially utilized the IGR buprofezin followed by the IGR pyriproxyfen if needed according to thresholds, but no sooner than 2 weeks following buprofezin. The second insecticide regime initially used pyriproxyfen followed by buprofezin as needed, but no sooner than 3 weeks following pyriproxyfen. These waiting periods between IGR use were mandated by the US-EPA Section 18 labels in force at the time. This label also permitted only a single use of each IGR per season. If additional suppression was needed in either of these IGR regimes, a uniform rotation of conventional insecticides was used. The third insecticide regime consisted of a rotation of mixtures of conventional materials (Ellsworth & Watson, 1996). These insecticide regimes are similar to those currently practiced by cotton producers in the western U.S. (Ellsworth & Martinez-Carrillo, 2001). The second main effect consisted of insecticide applications made aerially or by a tractor-mounted ground sprayer. Aerial and ground applications were made at volumes of 47 l/ha and 140 l/ha, respectively, using industry standard nozzles and configurations. The final main effect consisted of three different candidate *B. tabaci* action threshold levels for applying the IGRs. These levels were 0.5, 1.0 or 1.5 large whitefly nymphs (3rd or 4th instar) per leaf disk plus 3–5 adult whiteflies per leaf (see Whitefly Sampling below). These candidate threshold levels were chosen based on our experience that the IGRs would be most effectively deployed near the inflection point of pest population increase. A single threshold of 5 adult whiteflies per leaf (Ellsworth *et al.*, 1995) was used to schedule applications of insecticides in the conventional insecticide regime. As a result, the factorial design is incomplete for this third main effect. A threshold of five adults per leaf was also used to determine the need for additional conventional insecticide applications in the IGR regimes. The entire study site was sprayed once with oxamyl for suppression of *Lygus hesperus* Knight

on 1 August. Seasonal usage of insecticides and rates of application are summarized in Table 1.

Whitefly Sampling

Densities of eggs, nymphs, and adults of *B. tabaci* were estimated every week from mid-June through late September. Nymph and egg densities were estimated by the method of Naranjo & Flint (1994), which consists of counting individuals on a 3.88 cm² disk taken from the fifth mainstem leaf below the terminal (node 1). Nymphs were categorized as either small (1st or 2nd instar) or large (3rd or 4th instar) for the purpose of threshold implementation (see above). The densities of adults were estimated by counting individuals, *in situ*, on the underside of fifth mainstem node leaves (Naranjo & Flint, 1995). Thirty sample units were randomly examined for immature and adult stages in each plot on each sample date. Decisions to apply insecticides were based on the average densities in three replicate plots.

Natural Enemy Sampling

Arthropod predators were sampled every week with a standard 38-cm diameter sweep net from early June through mid-September. Four sets of 25 sweeps within a row were collected in each plot along a diagonal transect with a random starting point (100 sweeps total). Samples were frozen and later sorted in the laboratory. Densities of 20 taxa of arthropod predators were estimated. Only larval stages of *Chrysoperla carnea (sensu lato)* were counted. Immature and adult stages of all other species were generally pooled for analyses. *L. hesperus*, *Pseudatomoscelis seriatus* (Reuter), *Spanogonicus albofasciatus* (Reuter), and *Rhinacloa forticornis* Reuter were included, because it has been shown that these species exhibit omnivorous feeding habits (Butler, 1965; Agnew *et al.*, 1982; Hagler & Naranjo, 1994a; Hagler & Naranjo, unpublished)

The densities of immature aphelinid parasitoids (*Eretmocerus* spp. and *Encarsia* spp.) attacking *B. tabaci* were estimated by taking cotton leaf samples (30 per plot) from the 7th mainstem node from the terminal (node 1). Samples were collected each week from early July through mid-September. In the laboratory we counted all larval and pupal parasitoids of each genus and all unparasitized 4th instar whitefly nymphs on the entire leaf. Parasitoid and whitefly exuviae were not counted. The presence of visible larvae or meconia within the host mummy was used to discriminate *Encarsia* spp. from *Eretmocerus* spp. once parasitoids reached the later larval or pupal stage. Displacement of the host's mycetomes was used to determine the presence of young parasitoid larvae, but in these cases the genus of the parasitoid could not be discerned. We calculated an index of parasitism based on the proportion of 4th instar nymphs parasitized by both genera combined. A subsample of leaves (5–10) from each plot was held to determine the species composition of emerged adults and to measure treatment effects on parasitoid emergence (immature survival). Parasitized hosts were held at 27°C (~50% RH; 14:10 L:D) for two weeks.

Statistical Analyses

All analyses were performed based on samples collected after the first applications of insecticides on 3–8 July. Mixed-model, repeated measures analysis of variance (SAS Proc Mixed, Littell *et al.*, 1996) was used to test for treatment effects over the season. The block variable and associated interaction terms were entered as random effects and Satterthwaite's formula was used to estimate corrected degrees of freedom for *F* tests. The first order heterogeneous autoregressive (ARH1 in SAS Proc Mixed) option was used to estimate the repeated measures covariance structure, as it consistently maximized Akaike's Information and Schwarz' Bayesian Criteria (Littell *et al.*, 1996). Pre-planned orthogonal contrasts were used to compare IGR regimes with the conventional regime, and to contrast the two IGR regimes. Treatment effects on proportional parasitism were analyzed with the GLIMMIX

TABLE 1. Insecticide application history, Maricopa Agricultural Center, Maricopa, AZ, 1996

	Treatment					
	Ground Application			Aerial Application		
	Buprofezin 1 st	Pyriproxyfen 1 st	Conventional	Buprofezin 1 st	Pyriproxyfen 1 st	Conventional
3/8 July	buprofezin (392g/ha)	pyriproxyfen (60g/ha)	endosulfan (841g/ha) + amitraz (280g/ha)	buprofezin (392g/ha)	pyriproxyfen (60g/ha)	endosulfan (841g/ha) + amitraz (280g/ha)
12/16 July			oxamyl (561g/ha) + profenophos (841g/ha)			oxamyl (561g/ha) + profenophos (841g/ha)
17/22 July	pyriproxyfen (60g/ha)		fenpropathrin (224g/ha) + acephate (561g/ha)	pyriproxyfen (60g/ha)		
24 July		buprofezin ^b (392g/ha)				
1 August	oxamyl ^a (843g/ha)	oxamyl ^a (843g/ha)	oxamyl ^a (843g/ha)	oxamyl ^a (843g/ha)	oxamyl ^a (843g/ha)	oxamyl ^a (843g/ha)
5 August					buprofezin ^b (392g/ha)	
30 August		buprofezin ^c (392g/ha)				
4/8 September			endosulfan (841g/ha) + bifenthrin (90g/ha)			fenpropathrin (224g/ha) + acephate (561g/ha)

All rates given in grams of active ingredient per hectare

^a Applied for control of *Lygus hesperus* in all plots.

^b Low threshold level only.

^c Middle threshold level; high threshold level treatment for pyriproxyfen 1st did not require an application of buprofezin within the natural enemy sampling interval.

macro (Littell *et al.*, 1996), which performs mixed-model, repeated-measures ANOVA using a binomial error structure. Depending on taxa, arthropod counts were transformed by $(x+0.5)^{0.5}$ or $\ln(x+1)$ throughout as necessary to achieve normality and homoscedasticity before analysis, but untransformed means are presented. Because the design was an incomplete factorial, two analyses were conducted. The main effects of insecticide regime and application method were tested by using only the middle threshold level (i.e., 1 large nymph/leaf disk) for the IGR regimes. The main effect of threshold was tested only for the two IGR regimes, because there was only a single threshold used in the conventional regime. We examined treatment effects on all predator taxa, proportional parasitism, and total predator:prey ratios. This ratio was calculated as the quotient of all predators combined (per 100 sweeps) to the total number of eggs, nymphs and adult whiteflies per leaf. Egg and nymph densities per leaf were estimated from a regression model relating disk to whole leaf counts (Naranjo & Flint, 1994).

To further examine seasonal effects of the treatment regimes on arthropod predator populations, we conducted a time-dependent, multivariate analysis called principal response curves (PRC) (van den Brink and Ter Braak, 1998, 1999). PRC is based on an ordination method known as partial redundancy analysis, a type of principal component analysis in which information is extracted only from the variance explained by treatment effects. PRC provide a simple means of visualizing and testing the overall response of a biological community to environmental stresses, such as the application of insecticides, by determining treatment effects relative to a control or standard. The program CANOCO 4 (Ter Braak and Smilauer, 1998) was used to perform the partial redundancy analyses, construct the PRC, and test the significance of the relationship among treatments in the composition of the arthropod predator complex using a distribution-free F type test based on sample permutation. Typically, PRC analyses would be conducted using the untreated control as the standard for comparison of treatment effects. However, because we did not have an untreated control we used the response in the treated control (conventional insecticide regime) as our standard. In CANOCO, the analyses and sample permutation can be structured to account for blocking and factorial effects and to allow statistical inference over the entire season or for individual dates. We performed contrast-like tests to compare both IGR regimes with the conventional insecticide regime, and to contrast the two IGR regimes. Arthropod count data were transformed by $\ln(x+1)$ prior to analysis.

RESULTS

Populations of *B. tabaci* grew rapidly in early July and all action thresholds in all insecticide treatment regimes were exceeded between 3 and 8 July (Table 1). Application of the second IGR was needed in most IGR treatment regimes and the timing of this application varied somewhat across different application methods and threshold levels, and also depended on which material was used initially. Generally, the second application was made within 14–31 d following the first. For the higher threshold levels in the pyriproxyfen regime, the second IGR was not needed for either aerial or ground application methods. A severe thunderstorm occurred on 26 July and appeared to have a marked effect on populations of all arthropods at our study site. This storm deposited over 2.2 cm of precipitation within several hours with maximum wind speeds exceeding 22.2 m/sec.

Whitefly Populations

Detailed analyses of the effects of various treatment variables on *B. tabaci* are presented elsewhere (Ellsworth *et al.*, 1997), and so only general results will be briefly discussed here. Based on analyses of seasonal mean densities, orthogonal contrasts indicated that densities of both eggs and adults, but not nymphs, were significantly higher ($P < 0.05$) in the IGR regimes compared with the conventional regime. This pattern was observed mainly during

the first 3–4 weeks following the initial application of insecticides. There were no significant differences ($P > 0.05$) in seasonal mean densities of any life stage between the two IGR regimes. Seasonal mean densities of eggs, but not nymphs or adults, were significantly higher ($P < 0.05$) with aerial compared with ground application of insecticides. Threshold level for applying the IGRs had no significant effect on seasonal mean densities of any life stage.

Predator Populations and Predator:Prey Ratios

Over the entire experimental area, predator population densities were relatively high in early July, declined from late July to early August and then increased again towards the end of August. In general, the decline was associated with insecticide applications for *B. tabaci* throughout much of July (particularly the conventional materials), a single application of the carbamate oxamyl for suppression of *L. hesperus* in early August, and a severe thunderstorm that occurred in late July. Many of the predator taxa occurred at relatively low densities, including the beetles, most spiders, and several heteropterans. The most abundant spider was the crab spider *Misumenops celer* (Hentz). *Orius tristicolor* (White) and *Geocoris pallens* Stål were among the most common predaceous heteropterans. The omnivorous heteropterans, *P. seriatus*, *S. albofasciatus*, and especially *L. hesperus*, occurred at relatively high densities. Larval *C. carnea s.l.* and an empidid fly, *Drapetis nr. divergens* were also relatively abundant. Populations of most spiders, beetles, predaceous heteropterans and *C. carnea s.l.* remained at lower density levels following initial declines in late July to early August. Densities of *M. celer*, the assassin bug *Zelus renardii* Kolenati, *L. hesperus*, and *D. nr. divergens* rebounded strongly in late August, and the latter two species accounted for much of the increase in overall predator density in the late season.

Seasonal population densities were significantly higher ($P < 0.05$) in the IGR regimes compared with the conventional regime for 18 of the 20 predator taxa monitored in this study (Table 2). For half of these 18 taxa, the pattern of significantly higher densities in the IGR regimes was observed on at least 50% of the sampling dates. There was no significant difference ($P > 0.05$) in seasonal mean densities of any predator taxa between the two IGR regimes, and this pattern was consistent over the vast majority of sampling dates. Densities of most predator taxa changed significantly over sampling dates, and there were significant insecticide regime by date interactions for about half of the taxa examined. In most instances, these interactions were due to changes in the differences between the two IGR regimes or small changes among all treatments at low predator densities on mid to late season sampling dates.

Seasonal mean densities of predators were unaffected by insecticide application method or the threshold level used to initiate IGR applications (Table 3). The one exception was *Hippodamia convergens* Guérin-Ménéville. Densities of this predator were higher when IGRs were applied at the medium threshold compared with a lower or higher threshold. This was largely the result of population patterns one sampling date in the early part of the season.

Predator:prey ratios varied widely over the season, but were generally higher in the IGR regimes compared with the conventional regime (Figure 1). Insecticide regime main effects were significant ($P < 0.05$) on 4 of 8 sampling dates and orthogonal contrasts indicate significantly higher predator:prey ratios in IGR regimes averaged over the season (Table 2). There was no significant ($P > 0.05$) difference detected between the two IGR regimes. Predator:prey ratios were unaffected by application method, or the threshold level used for applying the IGRs (Table 3).

The time-dependent effect of insecticide regime on the overall arthropod predator community was further examined using PRC analysis that quantified population patterns in IGR regimes relative to the conventional regime (Figure 2a). The PRC based on the first axis of the redundancy analysis were highly significant ($P = 0.008$) and explained 73.3% of the variation due to insecticide regime. The second axis of the redundancy analysis was not significant ($P > 0.05$). Positive canonical coefficients indicate that populations of predators

TABLE 2. Seasonal mean densities of arthropod predators (per 100 sweeps), and seasonal mean predator:prey ratios and parasitism relative to three different insecticide regimes for management of *B. tabaci*, Maricopa, AZ, 1996

Taxon	Treatment regime			Orthogonal contrasts ^d	
	Buprofezin	Pyriproxyfen	Conventional	IGR vs Conven.	Bup vs Pyr
<i>Dictyna reticulata</i>	0.26 ± 0.05	0.24 ± 0.04	0.02 ± 0.02	42.5** (5)	0.39 (1)
<i>Misumenops celer</i>	2.67 ± 0.55	3.01 ± 0.39	0.58 ± 0.17	219** (6)	0.05 (0)
Jumping spiders	0.14 ± 0.03	0.20 ± 0.03	0.06 ± 0.04	9.13** (3)	0.02 (0)
Other spiders	0.03 ± 0.01	0.06 ± 0.04	0.02 ± 0.02	9.11** (2)	0.02 (0)
<i>Collops vittatus</i>	0.57 ± 0.22	0.74 ± 0.22	0.52 ± 0.14	4.48* (1)	0.81 (0)
<i>Hippodamia convergens</i>	0.29 ± 0.04	0.23 ± 0.04	0.13 ± 0.04	4.51* (2)	0.75 (0)
Anthicidae	0.10 ± 0.03	0.13 ± 0.06	0.10 ± 0.04	0.12 (0)	0.37 (0)
Other coccinellids	0.23 ± 0.04	0.14 ± 0.01	0.06 ± 0.01	6.52* (4)	0.16 (0)
<i>Geocoris punctipes</i>	0.83 ± 0.22	0.92 ± 0.31	0.25 ± 0.10	23.2** (4)	0.02 (0)
<i>Geocoris pallens</i>	2.85 ± 0.31	3.11 ± 0.59	0.46 ± 0.08	79.2** (4)	0.33 (0)
<i>Orius tristicolor</i>	17.1 ± 3.70	18.2 ± 3.51	11.8 ± 1.93	17.4** (3)	1.26 (0)
<i>Nabis alternatus</i>	0.80 ± 0.30	1.06 ± 0.22	0.33 ± 0.06	59.0** (5)	0.34 (0)
<i>Zelus renardii</i>	0.67 ± 0.28	0.40 ± 0.21	0.17 ± 0.02	15.2** (5)	3.37 (1)
<i>Sinea</i> spp.	0.10 ± 0.02	0.14 ± 0.07	0.04 ± 0.04	4.26 (0)	0.12 (1)
<i>Lygus hesperus</i>	20.4 ± 4.47	18.8 ± 2.48	13.0 ± 2.44	19.2** (4)	0.28 (0)
<i>Pseudatomoscelis seriatus</i>	5.01 ± 1.85	4.49 ± 1.48	1.13 ± 0.17	41.4** (3)	0.01 (0)
<i>Spanogonicus albofasciatus</i>	5.03 ± 0.24	4.88 ± 0.35	4.31 ± 0.93	5.46* (3)	0.23 (0)
<i>Rhinacloa forticornis</i>	0.06 ± 0.02	0.03 ± 0.01	0.02 ± 0.02	12.4** (4)	0.52 (0)
<i>Chrysoperla carnea s.l.</i>	6.03 ± 0.64	5.86 ± 0.36	4.73 ± 0.23	5.94* (3)	1.43 (0)
<i>Drapetis</i> nr. <i>divergens</i>	12.8 ± 1.58	16.5 ± 1.03	13.5 ± 2.15	4.94* (3)	0.53 (0)
Predator:Prey ratio ^b	0.52 ± 0.07	0.51 ± 0.04	0.37 ± 0.05	21.3** (4)	0.06 (0)
Proportional parasitism ^c	0.17 ± 0.03	0.19 ± 0.04	0.12 ± 0.02	7.37* (3)	0.92 (2)

Values are main-effect seasonal means ± SE based on eight post-treatment sample dates in three replicate plots ($n = 3$).

^a F -values based on mixed-model, repeated-measures ANOVA; $P < 0.05^*$; $P < 0.01^{**}$. Values in parentheses indicate the number of sample dates (out of 8 total) on which the F -value was significant ($P < 0.05$).

^b Quotient of all arthropod predators per 100 sweeps to all *B. tabaci* life stages per leaf.

^c Proportion of 4th instar *B. tabaci* nymphs parasitized per leaf.

were generally higher in the IGR regimes compared with the conventional regime from mid to late July and again in early September. The density of predators in the IGR regimes declined rapidly beginning in late July, and from early to mid-August predator densities were similar in all insecticide regimes. This decline was coincident with declining adult whitefly densities, which is representative of whitefly densities overall (Figure 2b), and a severe thunderstorm in late July. The species weight denotes the contribution of each predator taxa to the pattern of the overall response curve. The higher the value the more the response of a taxon resembles the PRC diagram. Negative weights indicate an opposite pattern and values between -0.5 and 0.5 indicate a weak response or a response unrelated to the PRC (van den Brink & Ter Braak, 1999). Species weights suggest that the PRC are most representative of *P. seriatus*, *M. celer*, *G. pallens*, *O. tristicolor*, *L. hesperus*, *G. punctipes*, *D. nr. divergens*, *S. albofasciatus*, *N. alternatus*, and *C. carnea s.l.* (Figure 2a). The weight for species k (b_k) and the canonical coefficient, c_{dt} , for a given treatment (d) and time (t) can be further used to infer the effect of a treatment relative to the standard by $\exp(b_k c_{dt})$. For example, on the second post-spray sampling date densities of *M. celer* were 6.7 times higher in the buprofezin regime, and 6.4 times higher in the pyriproxyfen regime compared with the conventional regime. On the final sampling this species is 2.4 to 2.6 times higher in the IGR compared with the conventional regimes.

TABLE 3. Seasonal mean densities of arthropod predators (per 100 sweeps), and seasonal mean predator:prey ratios and parasitism relative to insecticide application method and three different action thresholds for management of *B. tabaci*, Maricopa, AZ, 1996

Taxon	Application Method			Action Threshold ^b			
	Aerial	Ground	F ^a	0.5 nymphs	1.0 nymphs	1.5 nymphs	F ^a
<i>Dictyna reticulata</i>	0.19±0.04	0.16±0.02	1.61 (0)	0.21±0.05	0.33±0.06	0.22±0.04	0.19 (0)
<i>Misumenops celer</i>	2.20±0.45	1.98±0.29	1.56 (0)	2.48±0.26	3.15±0.34	2.90±0.48	1.61 (0)
Jumping spiders	0.14±0.02	0.13±0.04	0.05 (0)	0.18±0.04	0.13±0.04	0.21±0.07	0.77 (1)
Other spiders	0.03±0.01	0.04±0.03	0.05 (0)	0.04±0.02	0.05±0.02	0.04±0.02	0.77 (1)
<i>Collops vittatus</i>	0.62±0.24	0.60±0.14	1.26 (0)	0.81±0.31	0.35±0.05	0.79±0.19	1.73 (0)
<i>Hippodamia convergens</i>	0.28±0.03	0.15±0.04	1.59 (2)	0.23±0.06	0.31±0.10	0.24±0.06	5.43* (1)
Anthicidae	0.12±0.02	0.10±0.04	0.13 (0)	0.09±0.04	0.06±0.02	0.18±0.05	0.54 (1)
Other coccinellids	0.09±0.01	0.19±0.03	0.13 (1)	0.23±0.13	0.18±0.06	0.15±0.05	2.84 (0)
<i>Geocoris punctipes</i>	0.63±0.10	0.70±0.21	0.04 (0)	0.86±0.25	0.99±0.16	0.77±0.17	1.51 (0)
<i>Geocoris pallens</i>	2.42±0.17	1.87±0.22	0.09 (0)	3.44±0.35	2.65±0.29	2.86±0.45	0.65 (1)
<i>Orius tristicolor</i>	15.8±2.41	15.6±3.65	0.19 (1)	17.3±1.68	18.7±1.93	16.9±1.91	1.78 (0)
<i>Nabis alternatus</i>	0.77±0.13	0.69±0.25	0.00 (0)	0.95±0.17	0.93±0.21	0.89±0.19	1.68 (0)
<i>Zelus renardii</i>	0.39±0.18	0.44±0.17	0.81 (1)	0.58±0.14	0.63±0.17	0.39±0.09	1.47 (1)
<i>Sinea</i> spp.	0.06±0.03	0.13±0.06	0.72 (0)	0.08±0.04	0.14±0.05	0.15±0.08	1.88 (1)
<i>Lygus hesperus</i>	17.9±2.71	16.8±3.32	0.42 (1)	18.9±1.72	21.9±2.49	18.1±1.69	1.21 (1)
<i>Pseudatomoscelis seriatus</i>	3.50±1.02	3.57±1.19	4.07 (2)	4.58±0.62	5.28±1.06	4.38±0.93	0.82 (2)
<i>Spanogonicus albofasciatus</i>	5.67±0.47	3.81±0.27	0.69 (1)	5.56±0.57	4.16±0.45	5.16±0.55	0.25 (0)
<i>Rhinacloa forticornis</i>	0.03±0.01	0.04±0.02	0.29 (0)	0.02±0.02	0.05±0.04	0.06±0.03	1.83 (0)
<i>Chrysoperla carnea</i> s.l.	5.48±0.37	5.60±0.44	0.11 (0)	5.30±0.34	5.97±0.52	6.57±0.46	2.26 (1)
<i>Drapetis</i> nr. <i>divergens</i>	13.9±0.41	14.7±1.56	0.11 (0)	12.9±1.67	13.5±2.11	17.6±1.74	1.62 (0)
Predator:Prey ratio ^c	0.45±0.04	0.49±0.05	1.60 (1)	0.45±0.04	0.48±0.08	0.49±0.07	0.07 (0)
Prop. Parasitism ^d	0.16±0.05	0.16±0.04	3.44 (1)	0.19±0.03	0.19±0.03	0.15±0.02	3.80 (0)

Values are main-effect seasonal means ±SE based on eight post-treatment sample dates in three replicate plots. For action threshold levels, only insect growth regulator regimes are analyzed, because conventional insecticides were applied on the basis of a single threshold level.

^aF-values based on mixed-model repeated-measures ANOVA; $P < 0.05^*$; $P < 0.01^{**}$. Values in parentheses indicate the number of sample dates (out of 8 total) on which the F-value was significant ($P < 0.05$).

^bNumber of large (3rd or 4th instar) *B. tabaci* nymphs per leaf disk plus 3–5 adults per leaf.

^cQuotient of all arthropod predators per 100 sweeps to all *B. tabaci* life stages per leaf.

^dProportion of 4th instar *B. tabaci* nymphs parasitized per leaf.

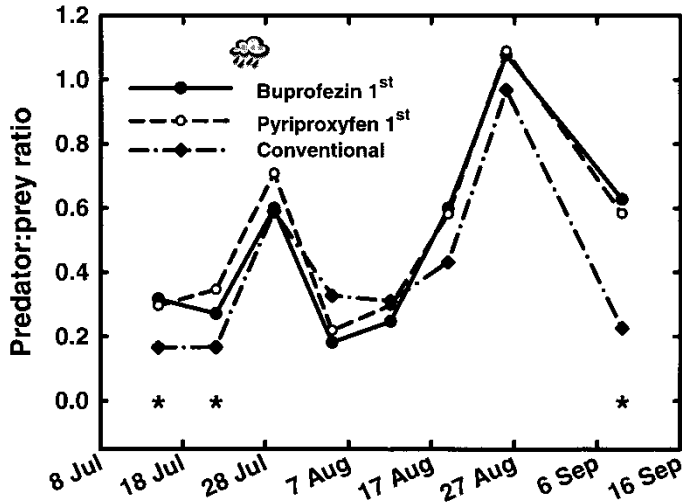


FIGURE 1. Effect of insecticide regime on total predator:prey ratios over the season, 1996, Maricopa, AZ. Only post-application dates for whitefly insecticides are shown. The predator-prey ratio is estimated as the quotient of all arthropod predators (per 100 sweeps) to all *B. tabaci* life stages per leaf. Asterisks along the bottom of each graph denote dates on which significant ($P < 0.05$) treatment differences were observed. The rain-cloud symbol denotes the timing of a severe thunderstorm. ● Buprofezin 1st, ○ Pyriproxyfen 1st, ◆ Conventional.

Parasitoid Populations and Parasitism

Eretmocerus eremicus Rose and Zolnerowich and *Encarsia meritoria* Gahan were the two primary species of aphelinid parasitoids found attacking *B. tabaci* at our study site. Of these, *E. eremicus* was dominant, comprising over 83% (range 69 to 100% per sample date) of all parasitoids sampled. There were no significant ($P > 0.05$) changes in species composition due to insecticide regime, application method or threshold level. Parasitoid densities peaked in mid-July and declined during August and September at the study site. This pattern generally paralleled the density of host whitefly populations, which declined steadily after the first insecticide applications in early July. The proportion of hosts parasitized varied widely over time and was unrelated to host density in any treatment regime. Parasitism rates averaged from about 0.45 in the pyriproxyfen regime to near or less than 0.10 during several dates in all insecticide regimes (Figure 3). There were significant insecticide effects on rates of parasitism on 3 of 8 sampling dates. In all these instances, the rate was significantly ($P < 0.05$) lower in the conventional insecticide regime. Averaged over the season, rates of parasitism were higher in plots treated with IGRs compared with those treated with conventional materials (Table 2). The interaction between insecticide regime and date was significant ($P < 0.05$), and resulted primarily from variable differences between the two IGR regimes over time. Rates of parasitism were unaffected by insecticide application method or the threshold level used to trigger IGR applications (Table 3).

Rates of immature survival from subsamples held in the laboratory averaged 79.8% for *E. eremicus* and 76.2% for *E. meritoria* over all treatments and sample dates. A date by date analysis was not possible due to extremely small sample sizes on some dates, but data pooled over the entire season indicated no significant ($P > 0.05$) effects for any of the main-effect variables on adult emergence of either parasitoid species.

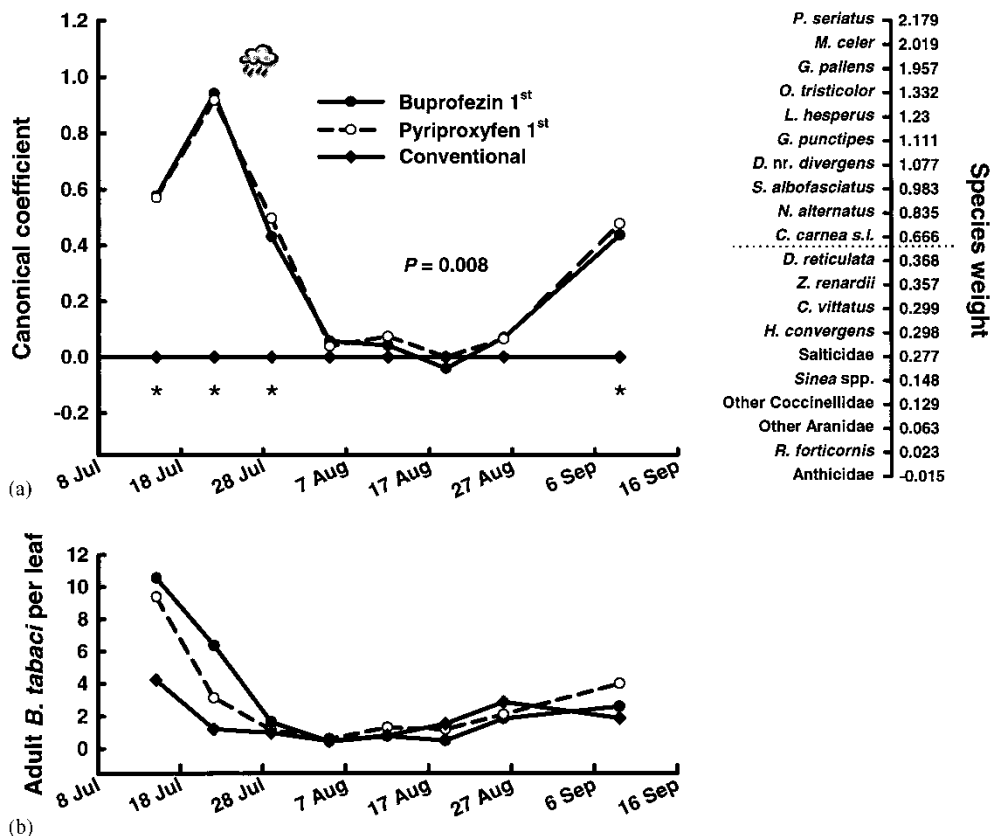


FIGURE 2. a) Principal response curves (PRC) showing the effect of insecticide regime on the predatory arthropod community over the season, 1996, Maricopa, AZ. Only post-application dates for whitefly insecticides are shown. The PRC show the effect of each IGR regime relative to the conventional regime (treated control) which is represented by the y = 0 line. The greater the species weight the more the response for that species resembles the PRC. Negative weights indicate an opposite pattern and weights between -0.5 and 0.5 indicate a weak response or a response unrelated to the PRC. The P-value denotes the overall significance of the PRC and the asterisks denote the significance ($P < 0.05$) of the contrast between IGR and conventional regimes on each sample date. b) Mean density of adult *B. tabaci* over the season (representative of whitefly populations overall). The rain-cloud symbol denotes the timing of a severe thunderstorm. ● Buprofezin 1st, ○ Pyriproxyfen 1st, ◆ Conventional.

DISCUSSION

When insecticides are a necessary tactic in pest management, the use of insecticides with physiological and/or ecological selectivity is a fundamental component of an integrated control strategy (Stern *et al.*, 1959; Newsom *et al.*, 1976). Our field study showed that the IGRs buprofezin and pyriproxyfen exhibited selectivity when compared with conventional insecticides in managing *B. tabaci* in cotton. All insecticide regimes were equally effective in suppressing populations of *B. tabaci* over the season. However, three to four applications of conventional mixtures were required to achieve the same level of suppression as two applications of IGRs regardless of which IGR was used first. The constraint of conducting this study on a demonstration farm, did not allow for an untreated control. Therefore we cannot precisely estimate the overall control efficacy of any insecticide regime. However, severe outbreaks of *B. tabaci* developed in unsprayed cotton research plots throughout the

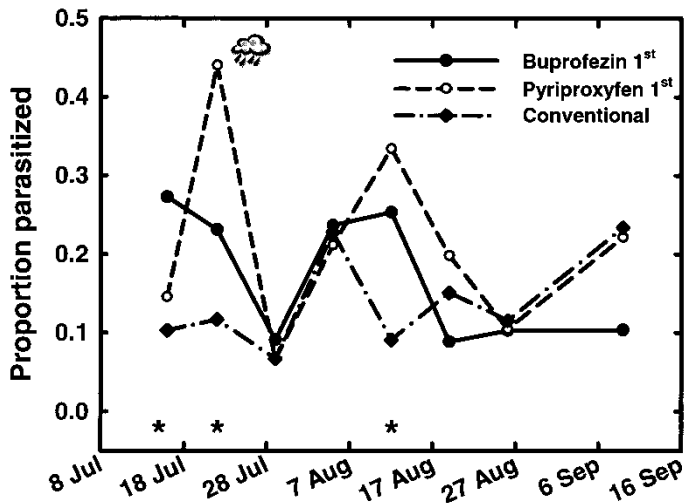


FIGURE 3. Effect of insecticide regime on parasitism (proportion of 4th instar *B. tabaci* nymphs parasitized per leaf) by aphelinid parasitoids attacking *B. tabaci* over the season, 1996, Maricopa, AZ. Only post-application dates for whitefly insecticides are shown. Asterisks along the bottom of each graph denote dates on which significant ($P < 0.05$) treatment differences were observed. The rain-cloud symbol denotes the timing of a severe thunderstorm. ● Buprofezin 1st, ○ Pyriproxyfen 1st, ◆ Conventional.

Maricopa Agricultural Center leaving little doubt that insecticides played an essential role in pest suppression (see also Naranjo *et al.*, 1998).

These insecticide regimes had very different effects on the natural enemy fauna. Seasonal rates of parasitism by two aphelinid parasitoids were higher in fields treated with one or the other of the IGR regimes compared with fields treated with conventional insecticides. Likewise, population densities of 18 predator taxa out of 20 that we examined were significantly higher in fields using IGRs compared with fields treated with conventional insecticides. The two groups that did not differ among the insecticide regimes, anthicid beetles and assassin bugs of the genus *Sinea*, both occurred at very low densities. The comparative selectivity of the IGRs also led to predator:prey ratios more favorable for biological control, a direct result of high efficacy and selectivity of these materials against *B. tabaci*. In no instance was there a difference in densities of predators, predator:prey ratios, or rates of parasitism between the two IGR regimes suggesting that both strategies conserved natural enemies relative to the use of conventional insecticides.

Our multivariate analyses indicated a sharp decline in predator populations in fields treated with IGRs in late July, and during most of August predator densities were similar among all insecticide treatment regimes (see Figure 2a). Predator populations then rebounded in the IGR regimes near the end of the growing season. This decline was coincident with IGR applications, declining whitefly populations in the IGR regimes, and the occurrence of a severe thunderstorm. All factors may have affected predator population dynamics, however, the rebound in predator densities in early September without the concomitant increase in whitefly densities or further insecticide applications suggests that weather may have played a greater role in the patterns observed.

Without an untreated control we cannot accurately determine the presence or extent of any negative effects of buprofezin or pyriproxyfen on the natural enemy fauna. Although IGRs are known to have a narrower spectrum of activity compared with many conventional synthetic insecticides, results from laboratory bioassay studies have been equivocal.

Buprofezin, and especially pyriproxyfen, have been found toxic to various predators in laboratory bioassays (Mendel *et al.*, 1994; Hattingh & Tate, 1995; de Clercq *et al.*, 1995; Smith *et al.*, 1999; Magagula & Samways, 2000). Many of these reports deal with coccinellid predators found in citrus with effects ranging from interference of adult emergence to inhibition of egg hatch from exposed adults. Hattingh & Tate (1995) and Smith *et al.* (1999) further showed that residues of pyriproxyfen can be long-lived in the field, leading to prolonged detrimental effects on pupation and reproduction of several species of coccinellids. Coccinellids were relatively rare at our study and we observed no larvae in any treatment. However, both *H. convergens* and a group comprising all other coccinellids were significantly higher in the IGR fields than in fields treated with mixtures of conventional materials. It is difficult to directly compare results from bioassays to those based on changes in population density over time in the field as the latter integrates many factors influencing survival, movement, reproduction and changing exposure levels. Nonetheless, if these coccinellid species were negatively affected by the use of either buprofezin or pyriproxyfen, the effect must have been smaller than that resulting from the use of broader-spectrum insecticides.

Bioassay results from other predator groups have been more variable. Pyriproxyfen was found toxic to all stages of *C. rufilabris* (Burmeister) (Chen & Liu, 2002), and buprofezin reduced survival and prolonged development in 1st stage larvae (Liu & Chen, 2000). However, Balasubramani & Regupathy (1994) reported no effect of buprofezin on larval *C. carnea*. The effects of buprofezin or pyriproxyfen have been examined on relatively few heteropteran predators. Castane *et al.* (1996) reported no effects of pyriproxyfen on nymphs of the predator *Dicyphus tamaninii* Wagner, and Delbeke *et al.* (1997) found no reduction in adult emergence of *Orius laevigatus* (Fieber) from oral or residual exposure. However, pyriproxyfen suppressed egg hatch in the predator *Elatophilus hebraicus* Pericart (Mendel *et al.*, 1994), and adult emergence of *Podisus maculiventris* (Say) was strongly suppressed by this IGR (de Clercq *et al.*, 1995). Again, if *C. carnea s.l.* or heteropteran predators were negatively affected by IGRs in our study, the effect was smaller than that resulting from the use of conventional insecticides.

Several aphelinid parasitoids attacking *B. tabaci*, including *E. luteola* Howard, *E. formosa* Gahan, *E. eremicus*, and *E. tejanus* Rose and Zolnerowich, have been shown to be affected by the IGRs studied here (Gerling & Sinai, 1994; Jones *et al.*, 1998; Liu & Stansly, 1997; Hoddle *et al.*, 2001). In general, effects were manifested mainly from exposures during early developmental stages and most likely reflect not only direct impacts of the insecticides, but also their indirect effects on host survival and quality. Other laboratory studies have found buprofezin and/or pyriproxyfen to be non-toxic to species such as *E. transvena* (Timberlake), *E. pergandiella* Howard, and *E. mundus* Mercet (Jones *et al.*, 1995, 1998; Liu & Stansly, 1997). We did not directly estimate populations of adult parasitoids in this study, but we can infer from parasitism rates that female densities were higher in IGR-treated fields or alternatively that sublethal effects of broad-spectrum insecticides reduced searching and/or oviposition behaviors of female parasitoids in the conventional regime. Based on the emergence of adults in the laboratory from immatures exposed in the field, we found no differences in mortality of immature parasitoids between IGR and conventional insecticides regimes.

This study also examined two important operational factors related to insecticide use; application method and whitefly threshold levels for applying the IGRs. Population densities of predators, predator:prey ratios, and rates of parasitism were unaffected regardless of whether applications were made by ground or by air. This has two important implications. First, it suggests that the same relative selectivity of the IGRs will be realized regardless of how the materials are applied. Second, it suggests that research findings, which are most commonly achieved with ground-spraying equipment, are directly applicable to commercial production systems that mainly utilize aerial application methods. The lack of differences

relative to changing action threshold levels can be largely explained by the sudden increases in pest density across the entire study site leading to almost simultaneous application of the first IGR in all fields. Only five days separated treatment initiation for all three thresholds (see Table 1). Naranjo *et al.* (2002) showed that any delay in the application of conventional insecticides can help to conserve arthropod predators. However, given the relative selectivity of the IGRs demonstrated here, it seems unlikely that a delay in application afforded by use of higher thresholds would significantly improve natural enemy conservation.

The significant impact of severe weather on populations of natural enemies and *B. tabaci* was clearly observed in our study (see Figures 1–3) and is worthy of note. Central Arizona typically experiences thunderstorms and high winds during July and August. A particularly severe storm occurred 26 July with high winds and heavy precipitation being associated with rapid declines in all arthropods examined. For *B. tabaci* this decline was the result of direct mortality through the dislodgment of eggs and nymphs from the leaf surface observed in ongoing life table studies (Naranjo, 2001; Naranjo & Ellsworth, unpublished). Populations of *B. tabaci* and natural enemies began to recover somewhat by mid to late August, but this weather event probably reduced the overall number of insecticide treatments that would have been necessary for *B. tabaci* otherwise. It is likely that these annual weather events are important elements of the natural control of *B. tabaci*. However, they may also contribute to disruption of the natural enemy complex.

Since their introduction in 1996 through an emergency exemption, buprofezin and pyriproxyfen have been widely adopted for suppression of *B. tabaci* in western U.S. cotton production systems (Agnew & Baker, 2001; Ellsworth & Jones, 2001). Pyriproxyfen was granted full registration in 1998 and buprofezin in 2002. These materials form an integral part of an insecticide resistance management plan and an overall cost-effective system for managing economic populations of *B. tabaci* in cotton (Ellsworth *et al.*, 1996; Dennehy & Williams, 1997; Ellsworth & Martinez-Carrillo, 2001). Relative to the commercial standard of using broad-spectrum insecticides, our results also demonstrate that the use of these IGRs contributes significantly to conservation of naturally occurring parasitoids and arthropod predators that may play an important role in augmenting suppression of *B. tabaci* and other pests in cotton. Because these results were based on a large-scale experiment that closely mimicked a real production setting, we would expect our findings to have broad applicability to commercial farming operations. Further field research involving the use of untreated controls will be needed to definitively evaluate the selectivity of buprofezin and pyriproxyfen and to establish their utility as part of a more biologically-based IPM strategy for cotton in the western U.S.

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