

Effects of Irrigation Levels on Interactions Among *Lygus hesperus* (Hemiptera: Miridae), Insecticides, and Predators in Cotton

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Environ. Entomol. 43(2): 263–273 (2014); DOI: <http://dx.doi.org/10.1603/EN12328>

ABSTRACT Variation in plant quality and natural enemy abundance plays an important role in insect population dynamics. In manipulative field studies, we evaluated the impact of varying irrigation levels and insecticide type on densities of *Lygus hesperus* Knight and the arthropod predator community in cotton. Three watering levels were established via irrigations timed according to three levels of percent soil water depletion (SWD): 20, 40, or 60, where 40% SWD is considered standard grower practice, 60% represents a deficit condition likely to impose plant productivity losses, and 20% represents surplus conditions with likely consequences on excessive vegetative plant production. The two key *L. hesperus* insecticides used were the broad-spectrum insecticide acephate and the selective insecticide flonicamid, along with an untreated check. We hypothesized that densities of *L. hesperus* and its associated predators would be elevated at higher irrigation levels and that insecticides would differentially impact *L. hesperus* and predator dynamics depending on their selectivity. *L. hesperus* were more abundant at the higher irrigation level (20% SWD) but the predator densities were unaffected by irrigation levels. Both *L. hesperus* and its predators were affected by the selectivity of the insecticide with highest *L. hesperus* densities and lowest predator abundance where the broad spectrum insecticide (acephate) was used. There were no direct interactions between irrigation level and insecticides, indicating that insecticide effects on *L. hesperus* and its predators were not influenced by the irrigation levels used here. The implications of these findings on the overall ecology of insect-plant dynamics and yield in cotton are discussed.

KEY WORDS *Lygus hesperus*, irrigation, arthropod predator, selective insecticide, cotton

The population dynamics of insect herbivores are governed by many factors, of which plant quality and natural enemies are two of the most important (Hairston et al. 1960, Hunter and Price 1992, Walker and Jones 2001). Plant quality may affect herbivore densities directly through changes in host availability and nutrients, which in turn affect fecundity, survival, and rates of inter-species competition (Price et al. 1980, Denno et al. 1995, Abrahamson and Weis 1997). Natural enemies exert top-down control on insect herbivores through their feeding action, and their importance to herbivore population dynamics has been demonstrated in many systems (Hassell 1978, 2000; Strong et al. 1984; Hawkins et al. 1999). Plant quality and natural enemies work in concert to influence herbivore population dynamics, and their relative importance is specific to the herbivore–host plant relationship influenced by spatial and temporal variation (Hunter et al. 1997, Stiling and Rossi 1997, Hunter 2001).

Plant quality as influenced by water stress has been shown to have important effects on abun-

dance, distribution, and performance of insect herbivores (White 1969, Mattson and Haack 1987, Waring and Cobb 1992). Some studies report higher insect densities on water stressed plants (White 1969, Rhoades 1979), while others have shown increased densities on vigorously growing plants (Price 1991), but this response was dependent on feeding guild (Larsson 1989, Waring and Cobb 1992). Water stress can potentially influence pest management systems in important ways. Effects on predators include oviposition preference, the quantity of available floral resources, and the quality of the prey (Coll 1998, Corey et al. 1998, Gillespie and McGregor 2000, Seagraves et al. 2011). Insect pests that respond positively to water stress may require a greater number of insecticides for their control (Flint et al. 1996); those that respond negatively may require fewer insecticide applications (Guillebeau et al. 1989). In turn, the selectivity of the insecticide used and the potential effects of water stress on natural enemies will influence the dynamics of these beneficial arthropods in the system, and thus potentially the dynamics and suppression of the pest (Naranjo et al. 2004, Asimwe et al. 2013). Understanding the effects and interactions of plant water stress and insecticides on herbivore pests and their natural enemies could lead to improved management strategies.

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Table 1. Summary of treatment allocations for examining effects of irrigation levels and insecticides on *L. hesperus* and selected arthropod predators in cotton, 2009–2010, Maricopa, AZ

Year	Plot size (m)	Timing	Irrigation treatments			Insecticide treatments		
			20% SWD	40% SWD	60% SWD	Flonicamid	Acephate	Untreated check
2009	18 by 18.1 (0.033 ha)	Start	26 June	29 June	2 July	30 July	9 July	N/A
		End	24 Aug. (10)	31 Aug. (7)	24 Aug. (5)	30 July (1)	17 Aug. (3)	N/A (0)
2010	24 by 15.2 (0.037 ha)	Start	25 June	28 June	2 July	29 July	14 July	N/A
		End	3 Sept. (12)	9 Sept. (8)	10 Sept. (6)	21 Aug. (2)	21 Aug. (3)	N/A (0)

Numbers in parentheses after each date indicate number of irrigations or spray applications.

N/A, not applicable.

The western tarnished plant bug, *Lygus hesperus* Knight, is the most abundant and damaging species of *Lygus* in the southwestern United States (Clancy and Pierce 1966, Slosser et al. 2006), where it is typically found in alfalfa, cotton, strawberries, safflower, various weeds, and other crops (Scott 1977, Diehl et al. 1998). In cotton, *L. hesperus* feeds on several plant parts, but economic damage is primarily associated with feeding on the developing flower buds resulting in loss of possible fruiting structures (Leigh et al. 1998, Leigh and Goodell 1996, Rosenheim et al. 2004). High densities result in taller plants that set fewer bolls (Ellsworth 2000, Ellsworth and Barkley 2001, Barkley and Ellsworth 2004) leading to major economic losses to growers (Fournier et al. 2007). In Arizona, *L. hesperus* is now the most significant pest in cotton, responsible for the highest yield losses and greatest number of insecticide sprays, relative to all other pests (Ellsworth and Jones 2001, Ellsworth et al. 2012b, Fournier et al. 2007). Once thresholds are reached, insecticide control becomes imperative because of significant economic risk of yield loss (Ellsworth et al. 1998a). In Arizona, the broad-spectrum organophosphate, acephate, has historically been the most frequently used active ingredient to control *L. hesperus* and remains an effective *Lygus* control (Ellsworth 1999, 2000; Barkley and Ellsworth 2004; Fournier et al. 2007). However, this insecticide has also been shown to severely reduce the natural enemy complex (Ellsworth et al. 1998b, Naranjo et al. 2004) resulting in resurgence and secondary pest outbreaks. Recently, flonicamid, a selective pyridinecarboxamide has proven effective and been widely adopted in Arizona for *L. hesperus* control without harming the natural enemy complex (Ellsworth 2008, Ellsworth et al. 2011).

The impact of irrigation regimes on the effectiveness of these *Lygus* chemical control tactics has not been investigated. Leigh et al. (1974), and subsequently Munk and Goodell (2002), showed that variation in irrigation levels affects *L. hesperus* densities, with higher densities occurring in more vigorous well-watered plants compared with smaller water-stressed plants. While the effects of irrigation regime and chemical controls have been investigated separately, no study has simultaneously manipulated irrigations and chemical controls to determine their relative impact on seasonal population dynamics of *L. hesperus* and the arthropod predator community. Our objec-

tives here were to evaluate the influence of varying irrigation levels, insecticide regimes, and their interaction on the density of *L. hesperus* and the predator complex in cotton. We hypothesized that higher *L. hesperus* abundance and higher densities of its associated predators would be observed with higher irrigation levels and that insecticides would differentially impact pest and natural enemy dynamics depending on their selectivity.

Materials and Methods

Experimental Design. The experiments were conducted on the Demonstration Farm of the University of Arizona's Maricopa Agricultural Center, Maricopa, AZ. Genuity Bollgard II with Roundup Ready Flex cotton varieties (Monsanto Company, St. Louis, MO) that confer resistance to lepidopteran insects and glyphosate herbicides were used each year; DP164B2RF in 2009 and DP1044B2RF in 2010. Cotton was planted on 16 April 2009 and 26 April 2010 with planting, fertilization, and other agronomic practices based on standard grower practices in central Arizona. Briefly, this includes dry planting followed by uniform field irrigation 2 d later, a postemergence glyphosate application for weed control, three split applications of urea applied through irrigation water and routine tillage until the canopy closes. The experimental design was a randomized complete block, split-plot design with nine treatments (three whole plots by three subplots) and four replications for a total of 36 plots each year (Table 1). Irrigation treatment was applied to whole plots while *Lygus* insecticides were applied to subplots. We used three irrigation levels with water applied at 20, 40, or 60% soil water depletion (SWD) (Martin 2001). Irrigation at 40% SWD represents the standard (normal) for cotton at our study site (Martin 2001) and over the full season received on average 153 cm of water. This was supplemented with 1.5–1.7 cm of rainfall each year. The plants in the 20% SWD (well-irrigated) received more (191 cm) and 60% SWD (deficit-irrigated) received less water than required (114 cm) over the course of the season, and the timing of these irrigations varied each year (Table 1). Plant responses to varying irrigation levels were estimated by canopy temperature obtained using an infrared thermometer placed above the topmost expanded leaves for 10 plants in the unsprayed plots of each irrigation level (Jackson 1982, Martin 2001).

Height and number of nodes were also determined biweekly for five representative plants in randomly selected plots of the unsprayed treatment, representing a single plot from each irrigation whole plot, using the methods described by Silvertooth (2001). Five leaves were also collected biweekly in each irrigation level in these same plots and analyzed for total leaf nitrogen by a commercial laboratory using the combustion method (Motzz Laboratory, Tempe, AZ).

Subplots consisted of two different *Lygus* insecticides and an untreated check. The insecticide treatments included acephate at a full, recommended rate of 1,123 g active ingredient (a.i.)/ha, and flonicamid at a full recommended rate of 99 g a.i./ha. Both were ground applied with a tractor mounted ground sprayer at 187 liters/ha. Acephate applications were scheduled as part of a companion study, and a total of three applications were made, every 2–3 wk, to maintain low *L. hesperus* densities (Table 1). This frequency and interval represent typical historical grower practice in Arizona when chronic economic levels of *Lygus* were present (Ellsworth 1999, Naranjo et al. 2004). Flonicamid applications were made when *Lygus* densities reached recommended thresholds of 15 total *Lygus* with at least four nymphs per 100 sweeps (Ellsworth 2000, Ellsworth and Barkley 2001). One flonicamid application was made in 2009 and two in 2010 (Table 1). In 2010, we also applied the miticide, etoxazole, at a low rate of 80.5 g a.i./ha on 21 August, together with acephate to reduce mite outbreaks in plots of this treatment.

Lygus and Natural Enemy Densities. *L. hesperus* and natural enemy densities were determined through weekly sampling in each plot using a 38-cm-diameter sweep net. In 2009, 25 sweeps were taken in each of the two rows; in 2010, 15 sweeps were taken in each of the three rows because of shorter length of the subplots. All plots were sampled weekly between mid-July and early September, and collections were held in plastic bags and frozen before sorting in the laboratory using a dissecting microscope. Arthropods sampled included *L. hesperus* adults and nymphs, and the following eight known *Lygus* predators: *Geocoris punctipes* Say, *Geocoris pallens* Stal, *Orius tristicolor* White, *Misumenops celer* Hentz, *Dictyna reticulata* Gertsch and Ivie, *Zelus renardii* Kolenati, *Nabis alternatus* Parshley, and *Sinea* spp. These predators are generalists and also feeding on other pests in cotton, but have been shown to feed on *L. hesperus* (Ruberson and Williams 2000, Hagler 2011). *L. hesperus* and predator counts were scaled up to 100 sweeps to reflect densities at which management decisions are made. For predators, densities of adult and subimago stages of each taxon were pooled for analysis.

Yield. At the end of each growing season, seed cotton was machine picked in the middle four rows of each plot, bagged, and weighed. Grab samples were then randomly selected from each bag and ginned in a small-scale research gin. Lint and seed fractions derived were then weighed and lint turnouts calculated for each grab sample (plot). These turnouts were

used to derive lint yield estimates, expressed as kilogram per hectare, for each plot.

Statistical Analyses. We used a mixed model, repeated-measures analysis of variance (ANOVA; Littell et al. 1996) in the PROC MIXED platform (SAS, Cary, NC) to examine the main and interactive effects of irrigation levels and insecticide treatment on densities of *L. hesperus* and predators during each year. Yield was analyzed using ANOVA in PROC MIXED. The block variable (replicates) and its associated interaction terms with irrigation level and insecticides were entered into the model as random effects, and the Kenward–Roger method was used to estimate the corrected degrees of freedom. The covariance structure of the repeated measures was estimated using the first order autoregressive heterogeneous function, because it consistently maximized both Akaike's information and Schwarz' Bayesian criteria (Littell et al. 1996) for our dataset. Significant differences among or between main effects were examined by mean separations using the DIFF option of the LSMEANS statement, while significant interaction terms were further analyzed at each level of one of the main effects using the SLICE option of the LSMEANS statement. A Bonferroni adjustment to the *P* values was used to determine significance at the alpha level (0.05). Data were transformed ($\ln [x + 1]$) to achieve normality and homogeneity before analyses, although untransformed means are presented. Analyses of treatment effects were conducted on *L. hesperus* nymphs and total *L. hesperus* densities (nymphs + adults), because these are the two parameters used for management decisions (Ellsworth 2000, 2010). Irrigation effects on plant height, number of nodes, height to node ratios, and canopy temperatures were examined with date within year as the random factor and sampling date as the repeated measure.

Multivariate, redundancy analyses known as principal response curves (PRC) were used to examine treatment effects on densities of predators (van den Brink and Ter Braak 1998, 1999). The PRC provides a means of estimating the response of a biological community to different stresses by looking at treatment effects relative to the untreated control, which in our case was the 40% SWD with no insecticides applied. The redundancy analyses were performed using CANOCO 4.5 (Ter Braak and Smilauer, 1998). PRCs were conducted separately for each year. Tests of significance were estimated by permutation-based *F*-tests, and analyses were structured to contrast effects due to irrigation levels and insecticide treatment.

Results

Plant Responses. Irrigation level had significant effects on the number of nodes ($F = 8.25$; $df = 2, 8$; $P = 0.011$). The well-irrigated plants (20% SWD) had significantly more nodes than plants in the other irrigation treatments. Because each node in cotton generates a sympodial branch and a subtending mainstem leaf, a greater number of nodes in the well-irrigated treatment would translate to more potential fruiting

Table 2. Mean (\pm SEM) of plant parameters for cotton irrigated at 20, 40, and 60% SWD

Irrigation levels	Height (cm)	No. of nodes	Height to node ratio	Canopy temp ($^{\circ}$ C)	Leaf N (%)
20% SWD	40.29 (3.087)a	24.83 (1.614)a	1.62 (0.030)a	34.28 (0.887)a	3.20 (0.165)a
40% SWD	37.20 (2.900)a	22.95 (1.810)b	1.63 (0.065)a	35.26 (0.474)a	3.47 (0.137)a
60% SWD	33.41 (2.611)a	22.83 (1.163)b	1.46 (0.087)a	36.06 (1.018)a	3.35 (0.171)a

Different letters within a column indicate significant differences among irrigation levels, $n = 6$.

sites. There were no significant effects of irrigation levels on plant height, height to node ratios, or canopy temperatures ($P > 0.05$; Table 2), although ordinal responses consistent with irrigation levels were apparent. There was no significant effect of irrigation levels on total leaf nitrogen. No significant effects of year or its interaction with irrigation treatment were observed for any of the parameters measured ($P > 0.05$).

Yield. In both years, yields were significantly influenced by irrigation (2009: $F = 30.04$; $df = 2, 18$; $P <$

0.0001 ; 2010: $F = 4.71$; $df = 2, 7.52$; $P = 0.047$) and insecticide treatments (2009: $F = 47.89$; $df = 2, 6$; $P = 0.0002$; 2010: $F = 27.58$; $df = 2, 7.74$; $P = 0.0003$), but only in 2009 was there an interaction between these two factors ($F = 3.31$; $df = 4, 18$; $P = 0.034$). Yields were generally highest in plots sprayed with flonicamid and lowest in those sprayed with acephate (Fig. 1A and B). Results were less consistent for irrigation treatments. In 2009, yields were significantly higher in the 20 and 40% SWD irrigated plants sprayed with flonicamid compared with the other

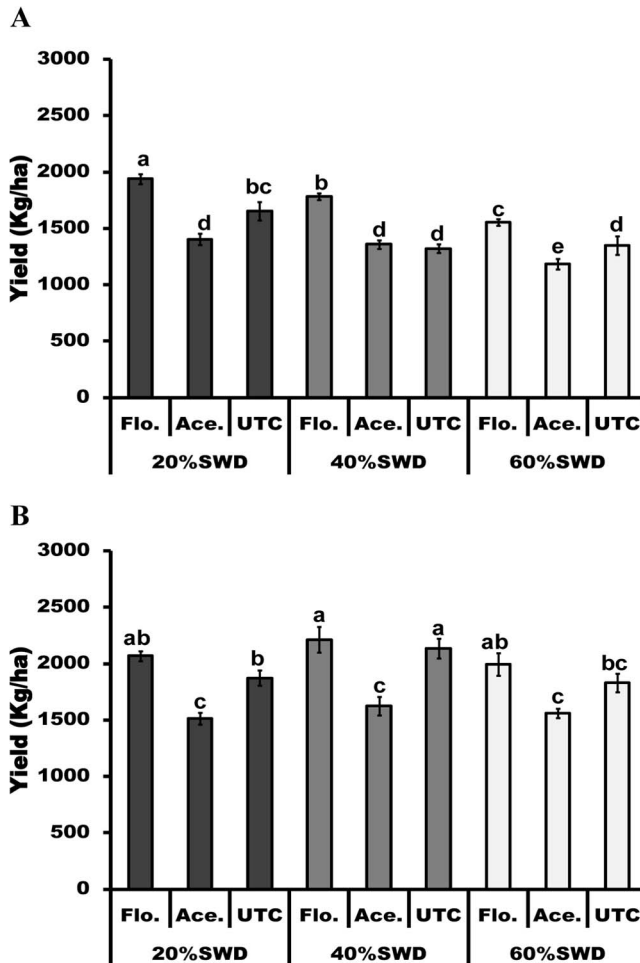


Fig. 1. Cotton lint yields (\pm SEM) showing the effects of irrigation levels (20, 40, and 60% SWD), and insecticide treatment (Flo. = flonicamid; Ace. = acephate; UTC = untreated check) in 2009 (A) and 2010 (B), Maricopa, AZ. Columns not sharing a letter indicate significant differences between those means ($P < 0.05$).

Table 3. ANOVA examining the effects of irrigation and insecticide treatments on *L. hesperus* nymphs and total nymph and adults in cotton, 2009–2010, Maricopa, AZ

Year	<i>L. hesperus</i> nymphs				Total <i>L. hesperus</i> (nymphs + adults)			
	Effect	df	F-value	P value	Effect	df	F-value	P value
2009	Irrigation	2, 6.2	2.69	0.15	Irrigation	2, 6.5	7.24	0.02
	Insecticides	2, 19	2.13	0.15	Insecticides	2, 21.6	5.59	0.01
	Irr*Insect	4, 19	1.24	0.33	Irr*Insect	4, 21.6	0.74	0.58
	Date	6, 54.8	41.92	<0.001	Date	6, 53.7	59.87	<0.001
	Irr*Date	12, 72.1	2.95	0.002	Irr*Date	12, 70.5	5.06	<0.001
	Insect*Date	12, 72.1	5.69	<0.001	Insect*Date	12, 70.5	3.44	0.0005
	Irr*Insect*Date	24, 87.4	1.58	0.07	Irr*Insect*Date	24, 85.2	1.61	0.06
	2010	Irrigation	2, 5.6	15.30	0.005	Irrigation	2, 32.9	32.26
Insecticides		2, 8.1	6.65	0.01	Insecticides	2, 9.7	6.89	0.01
Irr*Insect		4, 77.9	1.05	0.39	Irr*Insect	4, 24.8	0.39	0.82
Date		8, 77.2	64.2	<0.001	Date	8, 77.3	70.53	<0.001
Irr*Date		16, 103	1.47	0.16	Irr*Date	16, 102	1.02	0.44
Insect*Date		16, 103	4.33	<0.001	Insect*Date	16, 102	2.76	0.001
Irr*Insect*Date		32, 124	0.68	0.90	Irr*Insect*Date	32, 123	0.45	0.99

Irr, Irrigation; Insect, Insecticides.

treatment combinations ($P < 0.05$) (Fig. 1A). In 2010, the highest yields were obtained from the 40% SWD plants and the lowest in the 60% SWD plants (Fig. 1B).

***L. hesperus* Densities.** Seasonal densities of nymphs were inconsistently affected by irrigation and insecticides. In 2010, densities were affected by both irrigation and insecticide treatment, while neither of these factors affected nymphs in 2009 (Table 3). There were no interactions between irrigation and insecticides in either year ($P > 0.050$; Table 3). Nymphs differed significantly by sampling date and the interactions of date and insecticides were significant in both years (Table 3). In 2009, sampling date by irrigation was also significant. Nymph densities were generally lowest in the flonicamid sprayed plots mid- to late-season in 2009 and throughout most of the season in 2010 (Figs. 2 and 3). Nymphs were also more abundant in the 20 and 40% SWD plots mid- to late-season compared with the 60% SWD plants in both years (Figs. 2 and 3).

The influence of treatment factors on densities of nymphs and adults combined was more consistent. In both years, irrigation and insecticide treatments affected the abundance of total *L. hesperus* (Table 3). Again, there were no interactions between main effect treatments ($P > 0.05$; Table 3). Densities of *L. hesperus* were generally highest in the 20% SWD and lowest in the 60% SWD plots (Figs. 2 and 3). They also were generally lower in plots sprayed with flonicamid compared with acephate and the untreated control. In both years, *L. hesperus* varied over sample date, and the interactions of date and insecticide treatment were also significant. In 2009, the interaction of date and irrigation was significant as well. Differences in abundance were generally observed mid- to late-season for both irrigation and insecticide effects (Figs. 2 and 3).

Predator Densities. We used a multivariate analysis (PRC) to test for treatment effects on the predator community. In both years, there were significant effects of insecticides (2009: $F = 2.386$, $P = 0.002$; 2010:

$F = 1.819$, $P = 0.002$), but not irrigation treatments on the predator community. The community was significantly reduced by applications of acephate, but communities in plots sprayed with flonicamid did not differ from the untreated control (Fig. 4). In both years, species weights indicated that the observed patterns were driven most by the sit-and-wait crab spider *M. celer* and the big-eyed bug *G. punctipes*. Overall, the PRCs based on the first axes of the redundancy analysis explained 54–62% of the variation in treatment effects.

ANOVA was used to further assess the general patterns from the PRC analyses. In both years, there were significant effects of insecticides but not irrigation or their interactions on most or all predator taxa (Table 4). As expected, acephate sprays consistently reduced predator densities, whereas flonicamid had no effect compared with the untreated control. Among the more abundant predators, *M. celer* declined by 56–82%, *G. punctipes* declined by 75–76%, *Z. renardii* declined by 44%, and *O. tristicolor* declined by 23% in acephate plots compared with the untreated control (Table 4). The effects of irrigation were limited to two taxa. Densities of *N. alternatus* were most abundant in 60% SWD plots and least abundant in 20% SWD plots in 2009. In 2010, *D. reticulata* was most abundant in 60% SWD plots (Table 4). There were no significant irrigation by insecticide treatment interactions on densities of any taxon.

Discussion

We hypothesized that *L. hesperus* would be more abundant in cotton subject to higher levels of irrigation and this pattern was generally supported in our 2-yr field study. We showed that plots receiving less water than optimal for plant productivity and yield supported fewer *L. hesperus* than standard or well-watered irrigation regimes. However, we did not see a corresponding increase in a community of generalist arthropod predators that are known to attack *L. hesperus*. Predators were not generally influenced by ir-

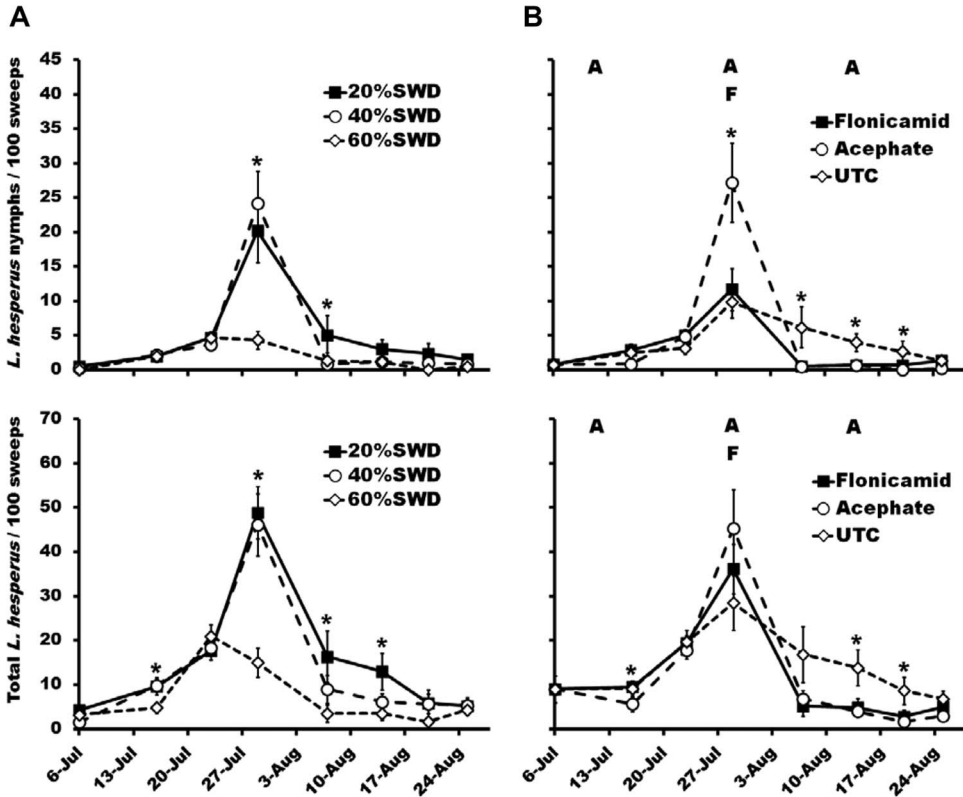


Fig. 2. Main effect mean densities (\pm SEM) of *L. hesperus* nymphs per 100 sweeps and total *L. hesperus* per 100 sweeps showing effects of different irrigation levels (20, 40, and 60% SWD) (A) and insecticide treatments (A = acephate; F = flonicamid) (B) on cotton in 2009, Maricopa, AZ. Asterisk symbols (*) indicate significant differences ($P < 0.05$) at each sampling date. Letters at the top of graph represent the timing of each insecticide application.

rigation levels, but they were strongly and consistently affected by insecticide applications, and more specifically, affected relative to the differential selectivity of insecticides used. This ultimately contributed to differential dynamics of *L. hesperus* and other pests in the system, although apparently independent of irrigation effects directly. We did not observe any interactions between irrigation and insecticides on the pest or its natural enemies but did observe such an interaction in one yr for cotton yields. Several factors could have contributed to this outcome as discussed below.

The effects of irrigation levels on *L. hesperus* population dynamics were expected based on similar findings in other studies of this insect (Leigh et al. 1970, 1974; Flint et al. 1996; Munk and Goodell 2002). Such effects have also been observed in another mirid, *Pseudatomoscelis seriatus* Reuter, which was found in higher densities in plots irrigated more frequently compared with those receiving the regular schedule of irrigations (Brett et al. 1946). In our study, these effects were more pronounced mid- to late-season when established thresholds for *L. hesperus* were exceeded. At this point, densities on the well- and normally irrigated plants were two to four times higher than on the deficit-irrigated plants. This pattern was likely because of more potential feeding sites for *L. hesperus*

available in well-watered conditions, as indicated by the increased number of nodes, vis-à-vis sympodial branches, on the well-irrigated plants. More nodes are also indicative of bigger plants with more leaves potentially providing a better habitat for oviposition and shelter from natural enemies, but our results for this parameter showed only weak trends with regard to plant height. The bigger plants could also have compromised the ability of the insecticides to reach their target pest, leading to the observed higher densities in well-irrigated plants. Reductions in nodes, and thus potential fruiting structures, likely contributed to the consistently lower lint yield observed in the deficit-irrigated plants despite lower *L. hesperus* pressure.

The role of the broad-spectrum insecticide acephate as both a *Lygus* control agent and a potential disruptor of biological control of *L. hesperus* and other pests in the system is clearly indicated here. In both years, higher densities of nymph and total *L. hesperus* were observed in the acephate sprayed plots, regardless of irrigation level, compared with those receiving flonicamid or left untreated. Acephate has historically been an effective *L. hesperus* control for growers in Arizona (Ellsworth 1998, 2000; Barkley and Ellsworth 2004). Here, as part of a companion study focused on *Bemisia tabaci* (MEAM1) (Gennadius), acephate ap-

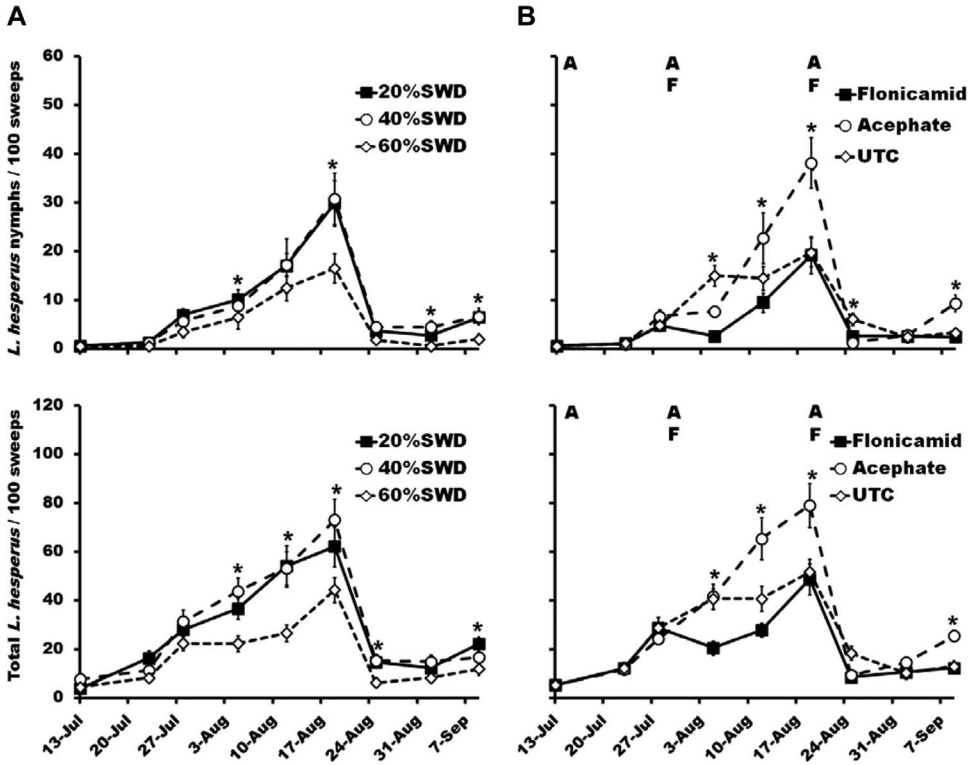


Fig. 3. Main effect mean densities (\pm SEM) of *L. hesperus* nymphs per 100 sweeps and total *L. hesperus* per 100 sweeps showing effects of different irrigation levels (20, 40, and 60% SWD) (A) and insecticide treatments (A = acephate; F = flonicamid) (B) on cotton in 2010, Maricopa, AZ. Asterisk symbols (*) indicate significant differences ($P < 0.05$) at each sampling date. Letters at the top of graph represent the timing of each insecticide application.

plications were made every 2–3 wk, a pattern similar to what commercial growers in the region would follow based on thresholds (Ellsworth 2000). Despite fewer sprays, flonicamid plots generally had lower *L. hesperus* densities than acephate sprayed plots and, more importantly, had lower nymph and total densities than the untreated check mid- to late-season when cotton is blooming and particularly susceptible to economic damage from *L. hesperus*. Although both insecticides are used to effectively control *L. hesperus* in Arizona, the differences in *L. hesperus* densities observed relative to insecticide treatments were most likely because of their effects on natural enemies. Acephate lowered predator densities, while flonicamid selectively reduced *L. hesperus* densities without disrupting natural enemies. Loss of coincident *L. hesperus* suppression by natural enemies in the acephate plots ultimately resulted in higher densities of this pest independent of irrigation levels. Our findings are similar to studies by Leigh and Gonzalez (1976), who found up to a 76% reduction in densities of *L. hesperus* due to the action of the natural predator complex, compared with when this complex was reduced using broad spectrum insecticides.

The predators evaluated here are generalist predators that also feed on whiteflies (*B. tabaci*) and spider mites, which are important pests of cotton in Arizona and were present in this study. In fact, acephate ap-

plications released these pests from biological control, resulting in whitefly and spider mite outbreaks and subsequently leading to premature defoliation in these treatment plots (Asimwe et al. 2013). These outbreaks probably caused negative feedback effects on the plant that we did not directly quantify in this study, potentially limiting our inferences about direct effects of irrigation on *Lygus* and the predators present. The outbreaks and subsequent defoliation occurred more rapidly and more severely in the deficit-irrigated plants and could have contributed to the lack of *L. hesperus* preference for these plants. Densities of predators were rarely impacted by irrigation levels, regardless of the insecticide used, indicating that predators did not appear to respond numerically to higher *L. hesperus* densities in the well-irrigated plots. Plant water stress can have direct effects on natural enemy recruitment through changes in host plant physiology. Predators can be affected through differences in the levels of amino acids, turgor pressure, and floral resources in deficit compared with well irrigated plants (Yokoyama 1978, Stone et al. 1984, Coll 1998). Water stress also has been shown to affect oviposition choice of predators with some preferring stressed plants (Seagraves et al. 2011) and others preferring well-watered plants (Anderson 1962, Chu 1969, Frampton et al. 2000). We did not observe any consistent direct or indirect effects of irrigation on predators in our

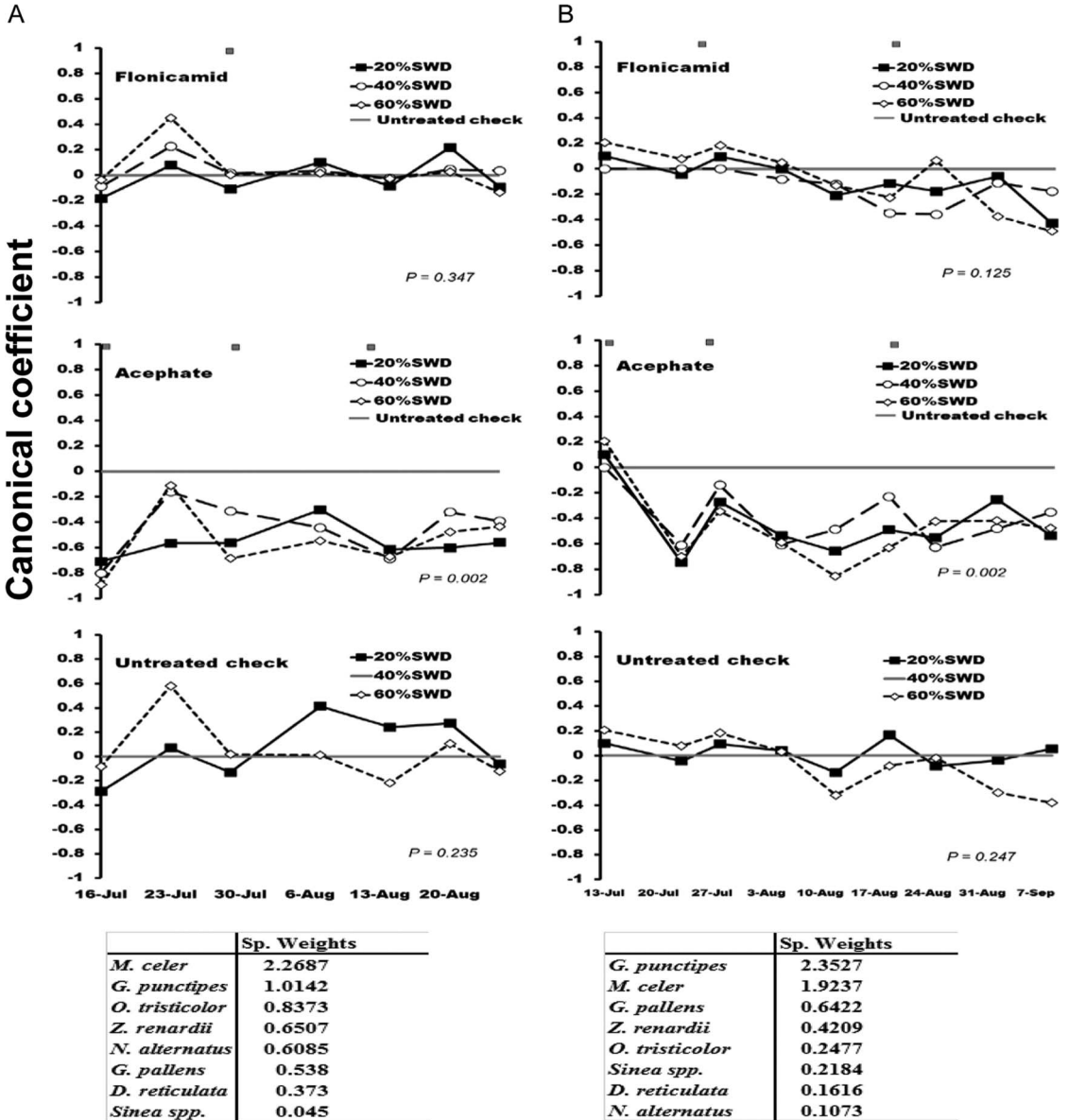


Fig. 4. PRC showing the effects of different irrigation levels (20, 40, and 60% SWD) and flonicamid, acephate, and the untreated check on the predators known to attack *L. hesperus* in 2009 (A) and 2010 (B), Maricopa, AZ. Symbols (■) at the top of each graph represent the timing of insecticide applications. Species weights indicate the strength of the response of each taxon relative to the observed trend. The product of the species weight and the canonical coefficient equals the natural log change in density of that taxon relative to the control (the line $y = 0$; 40% SWD untreated check, appears on each chart). $P < 0.05$ indicates significant differences from the control (40% SWD, Untreated check).

study. Our findings are similar to studies by Flint et al. (1994) who generally found no significant differences in predator densities between cotton irrigated weekly or biweekly. Thus, our hypothesis that natural enemies would increase in well-watered cotton in association with *Lygus* prey was not supported. This could be attributed to the following: 1) the decoupled nature of the relationship between generalist predator and one of their many prey, 2) the lack of response by this specific predator community to plant quality cues, and

3) to the unmeasured counterbalancing effects of outbreak levels of alternative prey (i.e., whiteflies and spider mites). Given the lack of response of these predators to our irrigation levels coupled with their consistent and predictable response to the insecticides, it is not surprising that we observed no interaction between irrigation and insecticide treatments for natural enemies in this study.

Our irrigation levels and *L. hesperus* controls encompass the full range of conditions that growers may

Table 4. Mean (\pm SEM) seasonal densities (per 100 sweeps) of predators in cotton irrigated at 20, 40, and 60% SWD and sprayed with flonicamid, acephate, or left untreated, Maricopa, AZ, 2009–2010

Taxa	Main effects				Main effects			
	20% SWD	40% SWD	60% SWD	F, P ^a	Flonicamid	Acephate	Untreated	F, P ^b
2009^c								
<i>D. reticulata</i>	1.84 \pm 0.28	1.10 \pm 0.18	1.28 \pm 0.18	2.12, 0.192	1.36 \pm 0.20	0.90 \pm 0.18*	1.96 \pm 0.26	8.0, 0.006
<i>M. celer</i>	11.78 \pm 1.10	11.72 \pm 1.04	11.80 \pm 1.30	0.82, 0.469	15.72 \pm 0.98	3.02 \pm 0.44*	16.58 \pm 1.20	127.41, <0.0001
<i>C. punctipes</i>	3.00 \pm 0.40	3.12 \pm 0.38	3.28 \pm 0.40	0.36, 0.703	4.30 \pm 0.40	1.02 \pm 0.22*	4.08 \pm 0.42	47.05, <0.0001
<i>G. pallens</i>	0.88 \pm 0.18	1.46 \pm 0.30	1.70 \pm 0.32	2.92, 0.061	1.72 \pm 0.30	0.72 \pm 0.18*	1.58 \pm 0.34	5.71, 0.019
<i>O. tristicolor</i>	12.54 \pm 1.82	15.26 \pm 2.48	17.1 \pm 2.76	0.15, 0.863	15.26 \pm 2.32	12.9 \pm 2.36*	16.75 \pm 2.48	4.66, 0.04
<i>Z. renardii</i>	1.96 \pm 0.26	1.76 \pm 0.22	1.76 \pm 0.26	0.24, 0.787	2.04 \pm 0.24	0.96 \pm 0.18*	2.46 \pm 0.26	11.89, <0.0001
<i>Sinea</i> spp.	0.04 \pm 0.04	0.08 \pm 0.04	0.02 \pm 0.02	0.55, 0.592	0.04 \pm 0.04	0	0.10 \pm 0.04	2.50, 0.09
<i>N. alternatus</i>	0.98 \pm 0.24*	1.28 \pm 0.30	4.44 \pm 0.38*	7.05, 0.001	1.74 \pm 0.36	0.74 \pm 0.22*	2.00 \pm 1.04	8.30, 0.0001
2010^c								
<i>D. reticulata</i>	1.21 \pm 0.64	0.55 \pm 0.11	1.34 \pm 0.18*	5.64, 0.008	1.67 \pm 0.64	0.59 \pm 0.11	0.86 \pm 0.13	2.47, 0.091
<i>M. celer</i>	21.12 \pm 2.09	20.72 \pm 1.98	17.58 \pm 1.49	0.69, 0.520	23.34 \pm 1.94	10.45 \pm 0.95*	23.65 \pm 2.15	60.02, <0.0001
<i>C. punctipes</i>	7.96 \pm 0.88	7.85 \pm 0.81	7.39 \pm 0.75	0.36, 0.728	8.64 \pm 0.77	2.79 \pm 0.39*	11.79 \pm 0.92	88.05, <0.0001
<i>G. pallens</i>	2.35 \pm 0.31	1.80 \pm 0.26	3.98 \pm 0.64	2.92, 0.071	3.34 \pm 0.48	1.69 \pm 0.37*	3.10 \pm 0.46	6.61, 0.004
<i>O. tristicolor</i>	8.18 \pm 0.99	5.48 \pm 0.55	5.48 \pm 0.33	2.33, 0.151	6.49 \pm 0.68	6.71 \pm 0.88	5.92 \pm 0.59	0.39, 0.686
<i>Z. renardii</i>	5.35 \pm 0.39	4.62 \pm 0.42	4.0 \pm 0.11	3.37, 0.102	4.91 \pm 0.37	4.05 \pm 0.39*	5.02 \pm 0.35	5.18, 0.007
<i>Sinea</i> spp.	0.72 \pm 0.18	0.42 \pm 0.11	0.42 \pm 0.15	0.79, 0.496	0.70 \pm 0.154	0.22 \pm 0.07	0.15 \pm 0.15	2.94, 0.128
<i>N. alternatus</i>	0.41 \pm 0.11	0.55 \pm 0.11	0.68 \pm 0.59	1.29, 0.281	0.64 \pm 0.13	0.44 \pm 0.11	0.59 \pm 0.13	1.09, 0.342

Asterisk (*) indicates significant differences ($P < 0.05$) within irrigation main effect in comparison to the 40% SWD treatment, or within insecticide main effect in comparison to the untreated check.

^a F-value and probability; numerator df = 2 in all instances, denominator df ranged from 6.77 to 72.4.

^b F-value and probability; numerator df = 2 in all instances, denominator df ranged from 8.04 to 84.3.

^c Seasonal means per 100 sweeps based on seven sampling dates in both 2009 and 2010 over four replicate plots ($n = 4$).

experience in Arizona cotton production systems. In general, the effects of the insecticides on *L. hesperus* and its predators were not influenced by the irrigation levels used here. However, we have shown that growers need to pay attention to both irrigation practices and choices in chemical control options for managing *L. hesperus*. The economic and ecological outcomes of reduced natural enemy abundance provide a clear example of how disruption of the food web in cotton, made up of a diverse suite of generalist natural enemies, can destabilize the natural controls of multiple pests. The combination of *L. hesperus* resurgence and premature defoliation due to secondary outbreaks of whiteflies and spider mites led to lower yields in the acephate treatment, regardless of irrigation level. Any benefits of *L. hesperus* control provided by acephate were lost because of the potentially accompanying loss in predator function in controlling resurgent *L. hesperus* or secondary outbreaks of whiteflies and spider mites. Conversely, use of flonicamid to suppress *L. hesperus* avoided pest resurgences, produced the highest yields, and did so by providing for an ecological balance among natural enemies and pest prey that favored the predator function and associated pest control dynamics irrespective of irrigation level. This suggests a greater role of natural enemies in the seasonal dynamics of *L. hesperus* and other important pests, such as *B. tabaci*, compared with any changes in plant characteristics because of differential irrigation.

Acknowledgments

We thank Y. Carrière, G. Wang, R. Kaggwa-Asiimwe, and two anonymous reviewers for helpful comments on earlier drafts of this manuscript. E. Martin provided guidance on establishing the irrigation regimes. M. Stefanek, V. Barkley,

G. Castro, F. Bojorquez, B. Stuart, J. Trejo, A. Slade, L. Rodarte, and A. Sonoqui provided expert field and laboratory technical assistance. We also appreciate the funding support of the Maricopa Agricultural Center, U.S. Department of Agriculture–Agricultural Research Service, and grants from the U.S. Department of Agriculture–Risk Avoidance and Mitigation Program, Cotton Incorporated, AZ Cotton Growers Association, and the Cotton Foundations.

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Received 19 November 2012; accepted 20 December 2013.