

Relative Influence of Plant Quality and Natural Enemies on the Seasonal Dynamics of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in Cotton

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ABSTRACT The abundance and distribution of insect herbivores is determined by, among other things, plant quality and natural enemies. These two factors vary temporally and spatially, subsequently affecting seasonal population dynamics. The relative influence of plant quality and natural enemies on the seasonal dynamics of *Bemisia tabaci* (Gennadius) was investigated in a 3-yr field study in cotton. Plant quality was manipulated through varying irrigation regimes: irrigations done at 20, 40, and 60% soil water depletions; and natural enemy densities were manipulated using broad spectrum insecticide applications that reduced their densities compared with unsprayed controls. In each year, densities of *B. tabaci* eggs, large nymphs and adults were consistently higher when natural enemy densities were reduced compared with when they were left unaltered, regardless of irrigation regime. In contrast, effects of plant quality on densities of all whitefly stages were weak and inconsistent. In addition, natural enemy densities and predator:prey ratios also were not generally affected by plant quality. Interactions between natural enemies and plant quality on whitefly dynamics were rare. In general, whitefly densities were elevated two-thirds of the time and increased two- to sixfold when natural enemy densities were reduced compared with plant quality effects which influenced whitefly densities about one-third of the time and were expressed inconsistently over the years. This indicates that natural enemies exert a comparatively greater influence on seasonal dynamics of *B. tabaci* in cotton than plant quality, as manipulated by differential irrigation.

KEY WORDS whiteflies, arthropod predators, plant stress, cotton, biological control

Plant quality, natural enemies and their interaction are known to affect the abundance, distribution, survival and movement of insect herbivores (Hairston et al. 1960, White 1984, Hunter and Price 1992, Underwood and Rausher 2000, Johnson 2008). Plant quality effects may be manifested through changes in morphology, nutrients, or host availability, and two general hypotheses have been posed to explain the effects of plant quality on the abundance and performance of insects. The plant stress hypothesis (White 1969, 1974, 1984) states that insect herbivore abundance will be higher on stressed host plants because of higher amounts of free unbound amino acids, reduced plant allocation to chemical defenses and changes in the ratio of nutrients to chemical defenses. In their meta-analysis Huberty and Denno (2004) modified this hypothesis and proposed the pulsed stress hypothesis in which phloem feeders experiencing pulsed or intermittent water stress performed better because of increased availability of nitrogen coupled with a frequent recovery of cell turgor. Alternatively, the plant vigor hypothesis

(Price 1991) predicts that vigorously growing plants are better hosts for insect herbivores, because they provide better food resources. Several subsequent studies examining these hypotheses have indicated that insect response varies with feeding guilds, plant species, stress regimes, plant ontogeny, and herbivore life stage (Koricheva et al. 1998, Mody et al. 2009). However, White (2009) suggested that the probability of either the plant stress or plant vigor hypothesis being supported would depend on whether the insect preferred to feed on young actively growing plant tissue or old senescing tissues, with the plant vigor hypothesis supporting the former and the plant stress hypothesis explaining the latter.

Natural enemy influences may be manifested through changes in density and function, and there are many examples of successful biological control (see reviews in Hassell 1978, Strong et al. 1984, Hawkins et al. 1999). The relative importance of plant quality and natural enemies on herbivore population dynamics has been widely investigated. These two factors interact to affect herbivore abundance and vary temporally and spatially (Hunter and Price 1992, Hunter et al. 1997, Forkner and Hunter 2000, Gratton and Denno 2003). Several studies have focused on the impact of nutrient effects through enhanced or re-

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duced fertilization (Cornelissen and Stiling 2005, Denno et al. 2005, Stiling and Moon 2005) or through water stress (White 1969, Larsson 1989, Flint et al. 1996, Oswald and Brewer 1997, Staley et al. 2006). While these effects have been well studied in many plant-herbivore systems, few studies have evaluated the relative influence of plant quality and natural enemies on agricultural pests, and, to our knowledge, none on whiteflies in cotton.

The sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) biotype B (=Middle East-Asia Minor one group; Dinsdale et al. 2010, DeBarro et al. 2011) is a sap-feeding pest attacking a wide range of crops in agricultural production systems of the southwestern United States (Watson et al. 1992, Butler and Henneberry 1993). In cotton, *B. tabaci* leads to a reduction in quantity and quality of yield through stunting, sticky cotton, and associated development of sooty mold (Oliveira et al. 2001). Variation in irrigation frequency affects plant quality, consequently affecting its suitability as a *B. tabaci* host (Hilje 2001). For example, Flint et al. (1996) found 45–50% lower whitefly densities in cotton that was irrigated weekly (unstressed) compared with that irrigated bi-weekly (stressed). Skinner (1996) found that oviposition rates were up to six times greater on cotton irrigated biweekly compared with weekly. These responses vary with host plant. In *Cucumis melo* (L.), there were no obvious differences in development rates between *B. tabaci* reared on stressed or unstressed plants (Isaacs et al. 1998), while Inbar et al. (2001) found a >50% reduction in whitefly oviposition rates on stressed tomato plants compared with normally watered controls.

There is a wide diversity of natural enemies, particularly predators and parasitoids, in cotton in Arizona (Gerling and Naranjo 1998, Hagler and Naranjo 1994, Naranjo et al. 2003). These natural enemies, particularly predators, play a crucial role in suppressing *B. tabaci* populations (Naranjo and Ellsworth 2005), especially after the application of selective insecticides that reduce pest populations but have little to no effect on the natural enemies (Naranjo et al. 2003, 2004; Naranjo and Ellsworth 2009). Application of these selective insecticides within an integrated pest management (IPM) framework has led to season long suppression of this pest on cotton in excess of the residual activity of the insecticides. This continued season long suppression results from the action of conserved natural enemies and other natural forces and has been defined as bioresidual (Ellsworth and Martinez-Carrillo 2001, Naranjo 2001, Naranjo and Ellsworth 2009).

However, the relative importance of plant quality and natural enemies to *B. tabaci* population dynamics and the potential for plant quality effects to mediate natural enemy densities has not been investigated in cotton. Here we used irrigation frequency and insecticide applications to simultaneously manipulate plant quality and natural enemy densities, respectively, to determine their relative contribution to *B. tabaci* population dynamics in this system. We sought to deter-

mine, 1) the comparative influence of plant quality and natural enemies on seasonal dynamics of *B. tabaci* and 2) the effects of plant quality mediated through irrigation on natural enemy densities.

Materials and Methods

Study Site and Treatment Allocation. Studies 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. Cotton was planted on 22 April 2008, 16 April 2009, and 26 April 2010 with all crops grown according to standard agronomic practices for the area. In 2008, the experiment was laid out in a north to south direction with cotton borders planted east to west, while in 2009 and 2010, it was laid out in a west to east direction with borders running south to north. Because initial *B. tabaci* populations were low in prior years, Jumbo Hales Best Cantaloupe (Willhite Seed Inc., Poolville, TX) was planted together with the cotton to augment their populations. In 2009 and 2010, the cantaloupes were planted in four row strips located on the edges immediately outside (west and east) of the experimental test area. In 2008, a single four row strip ran immediately outside the north edge of the experimental area. In all years, similar cantaloupe strips were planted within adjacent cotton fields used for unrelated studies. Cantaloupes were irrigated at the same time as the cotton and were generally dried down 2 wk before establishment of the natural enemy treatments to allow whiteflies and natural enemies to move into the adjacent cotton. A randomized complete block, split-plot design was used in all years with irrigation regime as the whole plots and natural enemy manipulation as the sub-plots (Table 1). In all years of the study we had three whole plots and two sub-plots replicated four times for a total of 24 plots. Irrigations were done at 20, 40, and 60% soil water depletion (SWD), imposing these irrigation differentials for the first time in late June of each year with a maximum of 12, 8, and 6 irrigations for each regime, respectively (Table 1).

The different irrigation regimes used in this study reflect the range of irrigation management in which full season cotton can be grown at this site, with the 20 and 60% SWD reflecting the upper and lower boundaries for commercial production. Irrigation at 40% SWD represents the standard optimal regime (normally irrigated) for cotton at our study site and over the full season received on average 153 ± 4.2 cm of water. This was supplemented with 1.5, 1.7, and 1.4 cm of rainfall in 2008, 2009, and 2010, respectively. The plants in the 20% SWD (well-irrigated) received more (191 ± 5.6 cm) and 60% SWD (deficit-irrigated) received less water than required (114 ± 7.3 cm) over the course of the season and the timing of these irrigations varied in each year (Table 1).

Table 1. Summary of treatment allocations for examining effects of plant quality and natural enemies on *Bemisia tabaci* in cotton, 2008–2010, Maricopa, AZ

Year	Plot size (m)	Timing	20% SWD	40% SWD	60%SWD	Acephate
2008	12 by 30.5 m (0.037 ha)	Start	20 June	23 June	27 June	8 July
		End	5 Sept. (12) ^a	8 Sept. (8)	12 Sept. (6)	2 Sept. (5)
2009	18 by 18.1 m (0.033 ha)	Start	26 June	29 June	2 July	9 July
		End	24 Aug. (10)	31 Aug. (7)	24 Aug. (5)	17 Aug. (3)
2010	24 by 15.2 m (0.037 ha)	Start	25 June	28 June	2 July	14 July
		End	3 Sept. (12)	9 Sept. (8)	10 Sept. (6)	21 Aug. (3)

^a Numbers in parentheses after each date indicate no. of irrigations or acephate spray applications.

Plant Responses. Responses to varying irrigation regimes were determined using canopy temperature obtained using an infrared thermometer placed above the top most expanded leaves for 10 plants in each irrigation regime before each irrigation (Table 2). Height and number of nodes were also determined biweekly for five representative plants in randomly selected plots representing each irrigation treatment where natural enemy densities were unaltered, using the methods described in Silvertooth (2001) (Table 2). In addition, leaves from representative plots were harvested every 2 wk and analyzed for total leaf nitrogen, using the combustion method, by a commercial laboratory (Motzz Laboratory, Tempe, AZ) (Table 2).

Natural Enemy Manipulations. Natural enemy treatments were established by reducing their abundance in one of the sub plots within a whole plot (NE-), while leaving the other unaltered as a control (NE+). Natural enemies were reduced by spray application of acephate (O,S-Dimethyl acetylphosphoramidothioate). Acephate is a broad-spectrum insecticide regularly used to control plant bugs and has been shown to reduce natural enemies (predators and parasitoids), while having minimal to no effect on all stages of whiteflies on cotton (Ellsworth et al. 1998, Fournier et al. 2008). Acephate applications were initiated and terminated at different times each year (Table 1). In all years, acephate applications were made at a full recommended rate of 1123 g active ingredient (AI)/ha with a ground sprayer every 2–3 wk to maintain low natural enemy densities. In 2010, in addition to acephate, we applied an acaricide, etoxazole (2-(2,6-difluorophenyl)-4-[4-(1,1-dimethyl-ethyl)-2-ethoxyphenyl]-4,5-dihydrooxazole), on 21 August at a rate of 80.5 g AI/ha to reduce mite outbreaks in plots receiving acephate sprays.

Whitefly Densities. The densities of all *B. tabaci* life stages were estimated weekly using methods described by Naranjo and Flint (1994, 1995) in which adults were counted on the underside of the fifth main stem node leaf from the top of the plant. Egg and nymph densities were determined by counts made on a 3.88 cm² disk from fifth main stem leaves using a dissecting microscope. Nymphs were categorized as either small (first and second instars) or large (third and fourth instars). However, data on large nymphs is presented because it is the stage used in management decisions. Fifteen to 20 and 10 to 15 leaves were used to determine adult and immature (egg and nymph) densities, respectively, on each sample date. All density data were collected from the middle three to four rows and was collected weekly from mid July to early September in all years.

Natural Enemy Densities. Fifty sweeps in each plot were used to determine natural enemy densities using a 38 cm diameter sweep net. The sweeps were made on two separate but centrally located rows, with 25 sweeps in each row, and were collected weekly between mid July and early September. Collections were held in plastic bags, which were frozen before sorting in the laboratory using a dissecting microscope. In total, 19 taxa of arthropod predators were identified, based on known morphological characteristics, and counted for each plot at each sampling date. Densities of both subimago and adult stages for each taxa, in each plot, were pooled for analysis.

Predator:Prey Ratios. Predator:prey ratios were measured by dividing the density of all predators (from 50 sweeps) on a particular sampling date by the sum of *B. tabaci* eggs, nymphs and adults per sample on the same date (Naranjo et al. 2004). *Lygus* spp. and *Pseudatomoscelis seriatus* (Reuter) were excluded

Table 2. Summary of parameters measured in each treatment to evaluate effects of plant quality and natural enemies on *Bemisia tabaci* in cotton, 2008–2010, Maricopa, AZ

Parameter ^a	20% SWD NE+	20% SWD NE-	40% SWD NE+	40% SWD NE-	60% SWD NE+	60% SWD NE-
Plant responses ^b	+		+		+	
Whitefly densities	+	+	+	+	+	+
Natural enemy densities	+	+	+	+	+	+
Predator:prey ratios	+	+	+	+	+	+
Yield	+	+	+	+	+	+

+ Indicates treatment plots where samples were collected for each parameter.

^a Plant responses measured bi-weekly; insect densities and ratios measured weekly.

^b Plant responses include ht, no. of nodes, canopy temp, and leaf nitrogen.

Table 3. Mean (\pm SEM) of plant quality parameters for cotton irrigated at 20, 40, and 60% SWD

Irrigation regime	Height (cm)	No. of nodes	Height to node ratio	Canopy temp ($^{\circ}$ C)	Leaf N (%)
20% SWD	41.51 (2.369)a	24.27 (1.108)a	1.71 (0.057)a	34.28 (0.887)a	3.20 (0.165)a
40% SWD	38.18 (2.519)a	23.42 (1.312)b	1.62 (0.048)a	35.26 (0.474)a	3.47 (0.137)a
60% SWD	33.52 (2.199)b	22.61 (0.957)b	1.48 (0.063)b	36.06 (1.018)a	3.35 (0.171)a

Different letters within a column indicate significant differences among irrigation regimes ($n = 9$).

from the analysis, because they are primarily plant feeding taxa.

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 yield estimates, expressed as lint in kilograms per hectare, for each plot.

Statistical Analyses. A mixed-model repeated measures analysis of variance (ANOVA) (Littell et al. 1996) was used to determine effects of irrigation regime, natural enemy treatment, and their interaction on plant and *B. tabaci* density parameters. The block variable and its interaction terms were entered as random effects while sampling dates were entered as repeated measures. The Kenward–Roger formula was used to calculate the corrected degrees of freedom for the type III F tests. The first order heterogeneous autoregressive option (ARH1) was used to estimate the covariance structure of the repeated measures as it consistently maximized both Akaike's information and Schwarz' Bayesian Criteria (Littell et al. 1996). Insect response analyses were conducted separately for each year. Significant differences among or between main effects were examined using mean separations in 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). All densities were log transformed (\ln) to meet normality and homogeneity of variance although untransformed means are presented. Plant response analyses were conducted with date within year as the random factor and sampling date as the repeated measure. Interactions between irrigation regime and year were analyzed within each year using the SLICE option of the LSMEANS statement. Treatment effects on yield were analyzed separately for each year using ANOVA with block as the random factor. All analyses were conducted in the PROC MIXED platform of SAS (SAS Institute, Cary, NC).

Further analyses to determine treatment effects on the predator community were carried out using a multivariate, redundancy analysis known as principal response curves (PRC) (Van den Brink and Ter Braak 1998, 1999). 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 natural enemies unaltered. The redundancy analyses were performed using CANOCO 4.5 (Ter Braak and Smlauer, 1998). PRCs were constructed and differences in community composition because of all established treatments were determined for each year. Tests of significance were estimated by permutation-based F-tests and analyses were structured to contrast effects because of plant quality or natural enemy abundance.

Results

Plant Responses. There was a significant effect of irrigation regimes on seasonal plant height ($F = 9.30$; $df = 2, 12$; $P = 0.0036$) and number of nodes ($F = 5.25$; $df = 2, 12$; $P = 0.0230$). The deficit-irrigated plants were significantly shorter than plants in the other irrigation regimes (Table 3). The number of nodes was significantly higher in the well-irrigated regime (20% SWD) compared with the other irrigation regimes. The higher number of nodes in the well-irrigated regime translated to a higher number of leaves and potential fruiting structures in this treatment compared with the normal (40% SWD) and deficit-irrigation (60% SWD) regime. There were also significant effects of irrigation regime on overall plant vigor indicated in height to node ratios ($F = 12.87$; $df = 2, 12$; $P = 0.001$) with significantly higher ratios in the well and normally irrigated regimes compared with the deficit-irrigated regime (Table 3). In general, plant growth and canopy development was greatest in the well-irrigated and lowest in the deficit-irrigation regime. There were no significant effects of irrigation regime on canopy temperature or total leaf nitrogen ($P > 0.05$; Table 3).

Yield. In 2008, there were no significant effects of irrigation regime or natural enemy treatment ($P > 0.05$) on lint yield (Table 4). In 2009, there was a significant effect of irrigation regime ($F = 12.59$; $df =$

Table 4. Main effect mean (\pm SEM) lint yield (kg/ha) from cotton irrigated at 20, 40, and 60% SWD and for natural enemy densities unaltered (NE+) or reduced (NE-)

Treatment	2008	2009	2010
20%SWD	733.7 (47.2)a	1468.1 (62.1)a	1623.4 (76.1)b
40%SWD	771.4 (43.8)a	1286.5 (24.6)b	1802.3 (106.9)a
60%SWD	694.9 (25.4)a	1215.9 (51.9)b	1626.8 (62.7)b
NE+	767.8 (35.5)a	1384.0 (56.3)a	1866.9 (55.5)a
NE-	698.9 (27.1)a	1262.9 (35.5)a	1501.5 (33.2)b

Different letters within a main effect and column indicate significant differences ($P < 0.05$) among treatments in each year.

2, 12; $P = 0.0011$) but not natural enemy treatment ($P > 0.05$) on lint yields. Yields were significantly higher in the well-irrigated compared with either the normal or deficit-irrigated regimes (Table 4). In 2010, there was a significant effect of both irrigation regime ($F = 4.50$; $df = 2, 9$; $P = 0.0442$) and natural enemy treatment ($F = 45.04$; $df = 1, 9$; $P < 0.0001$). Yields were higher in the normally irrigated regime compared with the other two irrigation regimes and yields were higher in the natural enemy control (Table 4). There were no significant interactions between irrigation regime and natural enemy treatment on yields in any year ($P > 0.05$).

Whitefly Densities. 2008. Egg densities were significantly affected by natural enemy treatment ($F = 24.21$; $df = 1, 20.3$; $P < 0.0001$) and sampling date ($F = 33.48$; $df = 7, 40.4$; $P < 0.0001$). There was no significant effect of irrigation regime ($P > 0.05$). There were significant interactions only between sampling date and natural enemy treatment ($F = 15.87$; $df = 7, 40.3$; $P < 0.0001$), and sampling date and irrigation regime ($F = 3.36$; $df = 14, 52.2$; $P = 0.0007$) but not between irrigation regime and natural enemy treatment ($P > 0.05$). Seasonal mean egg density was higher in the reduced natural enemy treatment compared with the control plots resulting from consistently higher densities in the reduced natural enemy treatment on multiple dates (Fig. 1; Table 5). Irrigation effects were variable, with egg densities initially higher in the well and normally irrigated regimes compared with the deficit-irrigated regime, but reversed by the last sampling date (Fig. 1; Table 5).

Similarly large nymph densities were significantly affected by natural enemy treatment and sampling date ($F = 28.68$; $df = 1, 8.86$; $P = 0.0005$ and $F = 49.94$; $df = 7, 38.6$; $P < 0.0001$) but not irrigation regime ($P > 0.05$) (Fig. 1). There were significant interactions only between irrigation regime and natural enemy treatment ($F = 4.78$; $df = 2, 8.86$; $P = 0.0390$), and between irrigation regime and date ($F = 2.12$; $df = 14, 49.8$; $P = 0.0264$) but not between irrigation regime and natural enemy treatment ($P > 0.05$). Seasonal mean densities were numerically higher in the reduced natural enemy treatment compared with the controls regardless of irrigation regimes, but significantly higher densities ($F = 32.0$; $df = 1, 8.6$; $P = 0.0004$) were only observed in the deficit-irrigated regime with reduced natural enemies compared with its control. Higher densities were observed between the reduced natural enemy treatment and the controls on multiple dates (Fig. 1; Table 5). Deficit-irrigated plants had significantly higher densities of large nymphs than the well-irrigated plants on only a single late-season date (Fig. 1).

Adult densities were also significantly affected by natural enemy treatments and sampling date ($F = 85.47$; $df = 1, 16.1$; $P < 0.0001$ and $F = 40.59$; $df = 7, 39.5$; $P < 0.0001$, respectively) but not irrigation regime ($P > 0.05$). There were significant interactions only between sampling date and natural enemy treatments and between and sampling date and irrigation regime ($F = 5.28$; $df = 7, 39.5$; $P = 0.0003$ and $F = 2.54$; $df = 14, 51$; $P = 0.0079$, respectively) but not between

irrigation regime and natural enemy treatment ($P > 0.05$). Seasonal mean densities were significantly higher in the reduced natural enemy treatments compared with the controls as a result of higher densities in this treatment on multiple dates (Fig. 1; Table 5). Significantly higher adult densities were found in the well and normally irrigated plants on two July dates (Fig. 1; Table 5).

2009. Egg densities were significantly affected by natural enemy treatment, irrigation regime and sampling date ($F = 72.03$; $df = 1, 9.2$; $P < 0.0001$, $F = 7.91$; $df = 2, 6.25$; $P = 0.0194$ and $F = 5.87$; $df = 6, 37.1$; $P = 0.0002$, respectively). There were significant interactions only between sampling date and natural enemy treatment ($F = 12.10$; $df = 6, 37.1$; $P < 0.0001$) but not between sampling date and irrigation regimes or between irrigation regimes and natural enemy treatments ($P > 0.05$). Seasonal mean densities were significantly higher in the reduced natural enemy treatment compared with the controls and densities were significantly lower in the well-irrigated regime compared with the normal and deficit-irrigated regime ($P < 0.05$) (Fig. 2; Table 5). Egg densities were higher in the reduced natural enemy treatment on several dates (Fig. 2).

Large nymph densities were significantly affected by natural enemy treatment and sampling date ($F = 60.3$; $df = 1, 18.4$; $P < 0.0001$ and $F = 12.4$; $df = 6, 35.5$; $P < 0.0001$, respectively) but not irrigation regime ($P > 0.05$). There were significant interactions only between sampling date and natural enemy treatment ($F = 7.21$; $df = 6, 35.4$; $P < 0.0001$) but not between sampling date and irrigation regime or irrigation regime and natural enemy treatment ($P > 0.05$). Seasonal mean densities were significantly higher in the reduced natural enemy treatment than the controls resulting from higher densities in the reduced natural enemy treatment on several dates (Fig. 2; Table 5).

Adult densities were significantly affected by natural enemy treatments and sampling date ($F = 62.12$; $df = 1, 17.7$; $P < 0.0001$ and $F = 6.22$; $df = 6, 34.2$; $P = 0.0002$, respectively) but not irrigation regime ($P > 0.05$; Fig. 2). There were significant interactions only between sampling date and natural enemy treatment and irrigation regime and natural enemy treatment ($F = 19.27$; $df = 6, 34.2$; $P < 0.0001$ and $F = 3.85$; $df = 2, 17.7$; $P = 0.0408$, respectively) but not between sample date and irrigation regime ($P > 0.05$). Seasonal mean densities were significantly higher in the reduced natural enemy treatment compared with the controls resulting from higher densities on several dates in August (Fig. 2; Table 5). Within the natural enemy reduced treatment, significantly higher densities were observed in the normally irrigated regime compared with the deficit-irrigated regime ($F = 2.33$; $df = 2, 17.5$; $P = 0.0321$) while, in the natural enemy control, significantly higher densities were found in the deficit-irrigated compared with the well-irrigated regime ($F = 2.48$; $df = 2, 17.5$; $P = 0.0237$; Fig. 2).

2010. Egg densities were significantly affected by natural enemy treatment and sampling date ($F = 152.1$; $df = 1, 19.7$; $P < 0.0001$ and $F = 206.0$; $df = 9,$

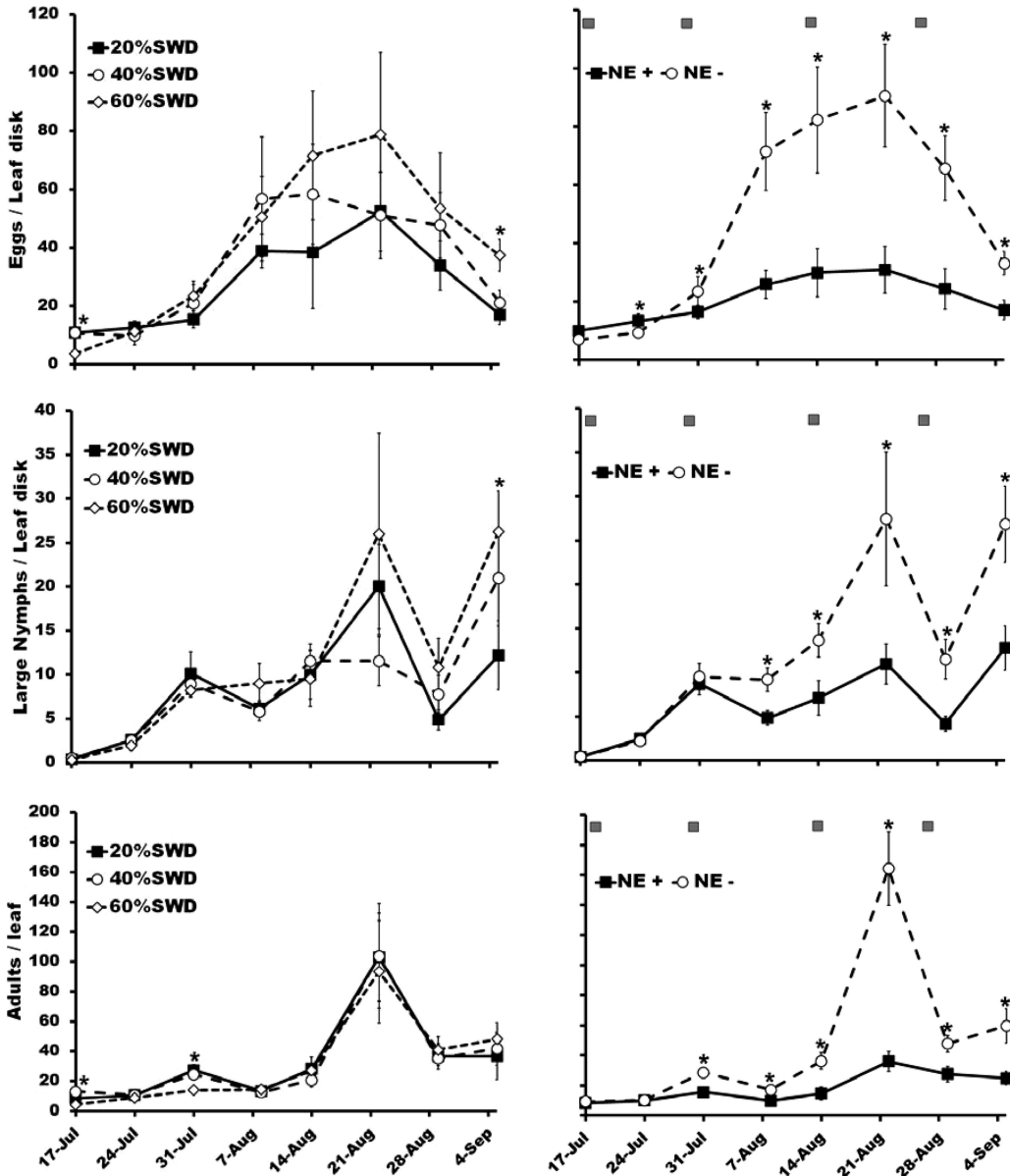


Fig. 1. Main effect mean densities of *B. tabaci* eggs per leaf disk (3.88 cm²) (top row), large nymphs per leaf disk (3.88 cm²) (middle row), and adults per leaf (bottom row) on cotton irrigated at 20, 40, and 60% soil water depletion (SWD), for natural enemy densities unaltered (NE+) or reduced (NE-), in 2008, Maricopa, AZ. Asterisks (*) indicate significant differences ($P < 0.05$) at each sampling date. Symbols (■) at the top of the first row of graphs represent the timing of each acephate application. Error bars indicate SEM.

51.9; $P < 0.0001$, respectively). There was no significant effect of irrigation regime. There were significant interactions only between sampling date and natural enemy treatment, and between sampling date and irrigation regime ($F = 32.2$; $df = 9, 51.9$; $P < 0.0001$ and $F = 8.57$; $df = 18, 67.9$; $P < 0.0001$, respectively) but not between irrigation regime and natural enemy treatment. Seasonal mean densities were significantly higher in the reduced natural enemy treatment compared with the controls ($P < 0.05$) as a result of higher

densities in the reduced natural enemy treatment on multiple dates (Fig. 3; Table 5). Densities were significantly higher ($P < 0.05$) in the normally irrigated plants compared with the well or deficit-irrigated plants on several dates (Fig. 3; Table 5).

Large nymph densities were significantly affected by natural enemy treatments, irrigation regime and sampling date ($F = 98.97$; $df = 1, 48.6$; $P < 0.0001$, $F = 7.39$; $df = 2, 12.4$; $P = 0.0077$ and $F = 184.71$; $df = 9, 53.8$; $P < 0.0001$, respectively). There were significant

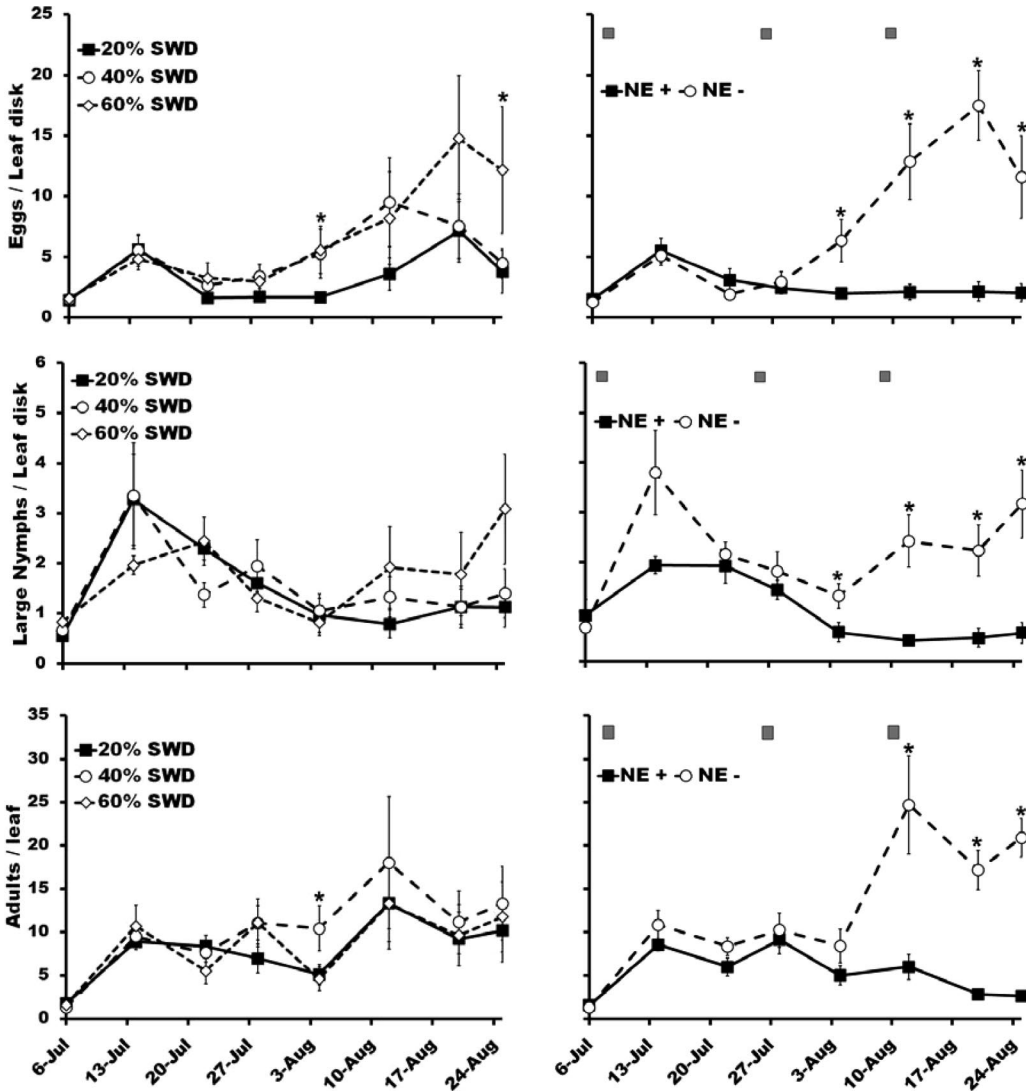


Fig. 2. Main effect mean densities of *B. tabaci* eggs per leaf disk (3.88 cm²) (top row), large nymphs per leaf disk (3.88 cm²) (middle row), and adults per leaf (bottom row) on cotton irrigated at 20, 40, and 60% SWD, for natural enemy densities unaltered (NE+) or reduced (NE-), in 2009, Maricopa, AZ. Asterisks (*) indicate significant differences ($P < 0.05$) at each sampling date. Symbols (■) at the top of the first row of graphs represent the timing of each acephate application. Error bars indicate SEM.

The species weights indicate the strength of the response of each taxon to the observed pattern (Fig. 4). The higher the value is, the closer the response of a given taxon reflects the pattern of the PRC with negative weights indicating an opposite pattern. Weights between -0.5 and 0.5 reflect a weak response unrelated to the observed PRC pattern (van den Brink and Ter Braak 1999). In all years the PRC patterns were most representative of the sit-and-wait crab spider *Misumenops celer* (Hentz), *Geocoris punctipes* (Say), *Orius tristicolor* (White), *Zelus renardii* (Kolenati), *G. pallens* (Stal), and *Rhinacloa forticornis* (Reuter).

Predator:Prey Ratios. In 2008, there was a significant effect of natural enemy treatment, sampling date and

their interaction on predator:prey ratios ($F = 98.92$; $df = 1, 18.6$; $P < 0.0001$, $F = 12.72$; $df = 6, 36.6$; $P < 0.0001$ and $F = 6.35$; $df = 6, 36.6$; $P = 0.0001$, respectively). Ratios were consistently higher in the natural enemy controls compared with the reduced natural enemy treatment resulting from higher ratios on multiple dates (Fig. 5A; Table 5).

In 2009, there was a significant effect of natural enemy treatment, irrigation regime, and sampling date on predator:prey ratios ($F = 88.3$; $df = 1, 14.6$; $P < 0.0001$, $F = 4.55$; $df = 2, 14.6$; $P = 0.029$ and $F = 26.38$; $df = 5, 30.5$; $P < 0.0001$, respectively). Only sampling date interactions with irrigation regime and natural enemy treatment were significant ($F = 2.50$; $df = 10, 38.4$; $P = 0.0201$ and $F = 18.76$; $df = 5, 30.5$; $P < 0.0001$,

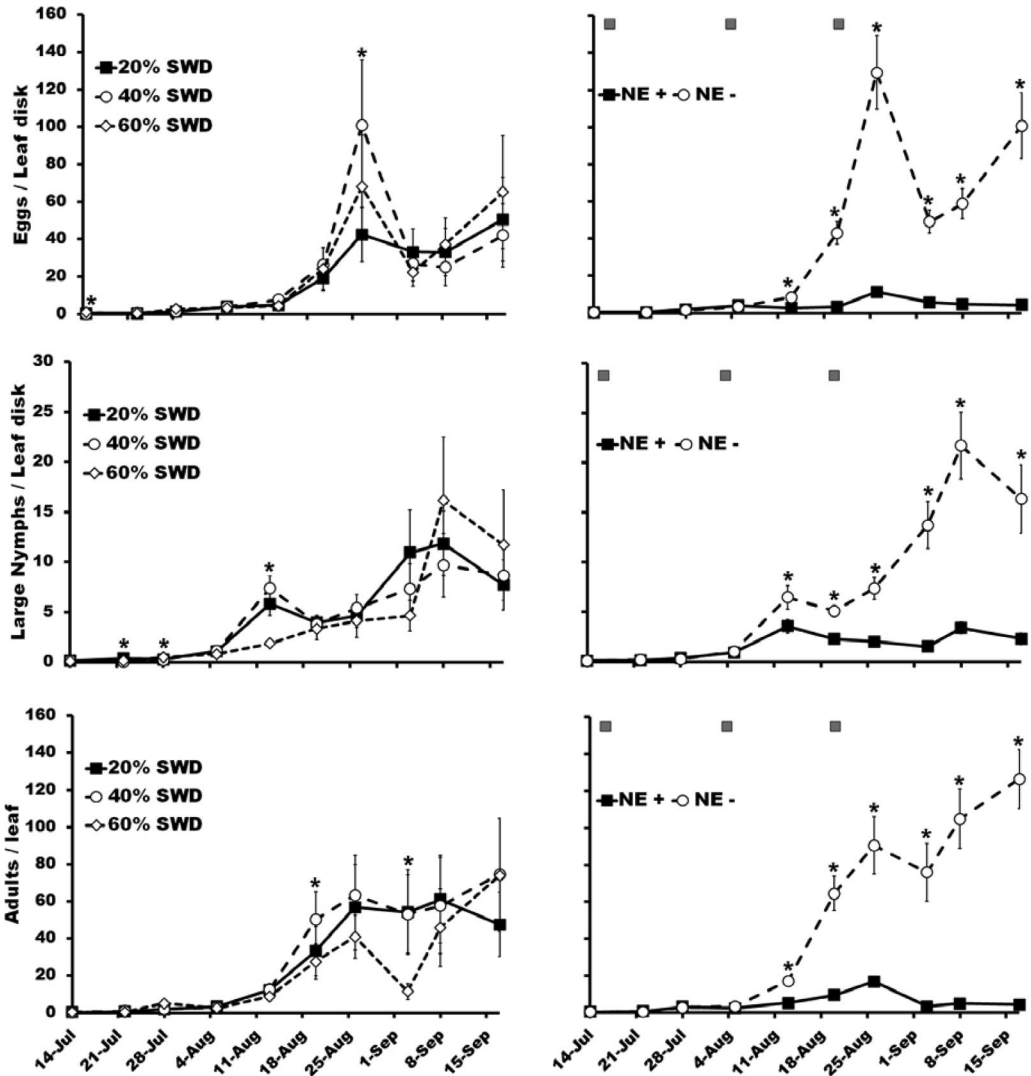


Fig. 3. Main effect mean densities of *B. tabaci* eggs per leaf disk (3.88 cm²) (top row), large nymphs per leaf disk (3.88 cm²) (middle row), and adults per leaf (bottom row) on cotton irrigated at 20, 40, and 60% SWD, for natural enemy densities unaltered (NE+) or reduced (NE-), in 2010, Maricopa, AZ. Asterisks (*) indicate significant differences ($P < 0.05$) at each sampling date. Symbols (■) at the top of the first row of graphs represent the timing of each acephate application. Error bars indicate SEM.

respectively). Ratios were significantly higher in the well-irrigated compared with the other irrigation regimes on a single date in August and higher in the natural enemy controls compared with the reduced natural enemy treatment on several mid-season dates (Fig. 5B; Table 5).

In 2010, there were only significant effects of natural enemy treatment, sampling date, and their interaction on predator:prey ratios ($F = 170.8$; $df = 1, 10.3$; $P < 0.0001$, $F = 328.8$; $df = 8, 45.4$; $P < 0.0001$ and $F = 25.5$; $df = 8, 45.4$; $P < 0.0001$, respectively). Ratios were significantly higher in natural enemy controls resulting from differences on multiple dates (Fig. 5C; Table 5).

Discussion

We used different irrigation regimes to vary plant quality using 20, 40, and 60% soil water depletion and manipulated natural enemies by reducing their densities using biweekly applications of a broad spectrum insecticide compared with unsprayed controls. The irrigation regimes used affected the characteristics and physiology of the plants, as indicated by differences in height, number of nodes and overall plant vigor, all of which potentially impact the quality of the plant relative to whiteflies (Hilje et al. 2001). In cotton, plant height has an effect on *B. tabaci* densities (Chilcutt et al. 2005), while number of nodes reflects

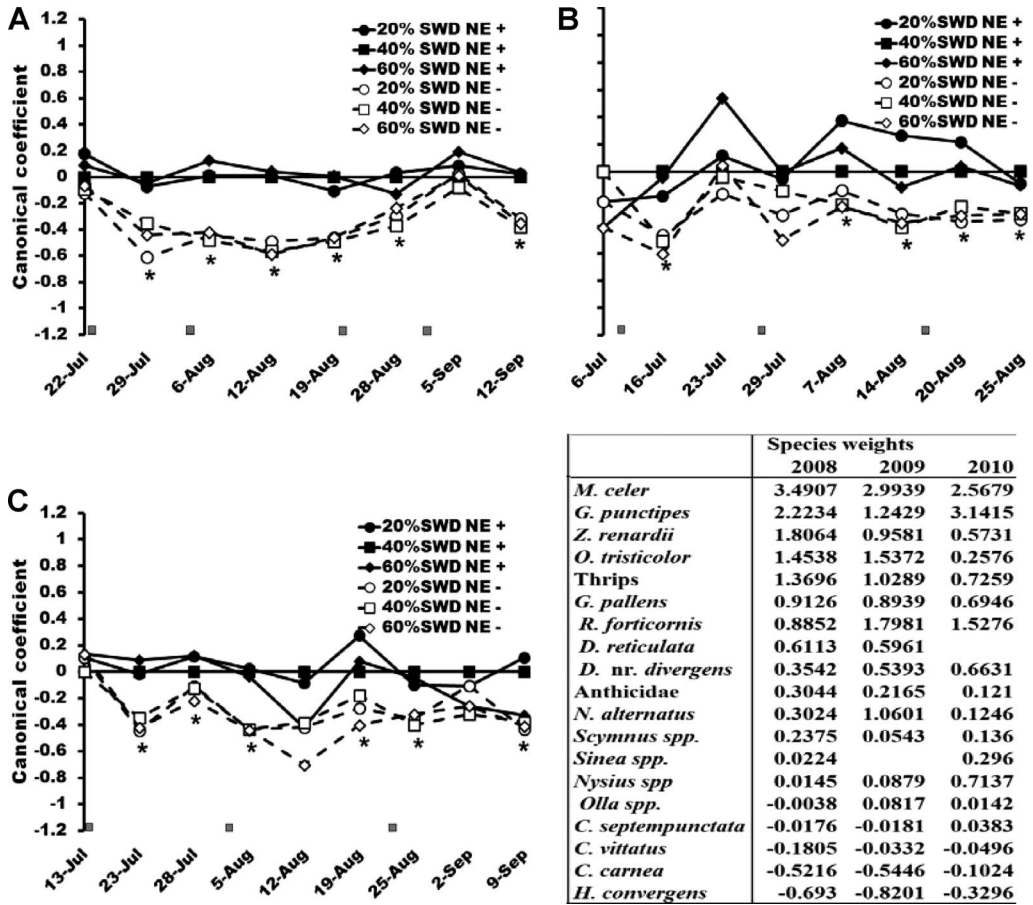


Fig. 4. Principal Response Curves (PRC) showing the effects of different irrigation regimes (20, 40, and 60% SWD) and applications of the broad spectrum insecticide, acephate, on the predatory arthropod community in cotton in (A) 2008, (B) 2009, and (C) 2010, Maricopa, AZ. Symbols (■) at the bottom of each graph represent the timing of each acephate application. Asterisks (*) represent significant differences at each date ($P < 0.05$). 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 (40% SWD NE+).

potential total leaf number, total leaf area, and potential flower numbers and fruiting sites, indirectly affecting densities of *B. tabaci* and its natural enemies.

We observed significant increases in whitefly densities after the reduction of natural enemies, and these increases were consistent across all irrigation regimes in all years. When natural enemies were reduced, densities of all whitefly stages were elevated two-thirds of the time (Table 5) with densities increased two- to sixfold over controls. In contrast, plant quality effects imposed by differential irrigation were observed less than one-third of the time. This overall pattern is consistent with previous studies in cotton showing significant increases in whitefly densities after application of the broad spectrum insecticide, acephate (Ellsworth et al. 1998).

In general, the effects of plant quality on seasonal whitefly population density were relatively minor and inconsistent in this study. Higher egg densities were only observed in the deficit-irrigated regime $\approx 8\%$ of the time and lower egg densities were observed in the

well irrigated regime only $\approx 15\%$ of the time over the 3 yr (on 2 of 26 and 4 of 26 sampling dates, respectively; Table 5). Flint et al. (1996) also observed higher egg densities in cotton irrigated biweekly (more stressed; equivalent to 60% SWD used in this study) compared with that irrigated weekly (equivalent to 20% SWD of this study), even though they did not attempt to alter or measure natural enemy densities in their study. Adult densities were significantly depressed in the deficit-irrigated regime 19% of the time compared with the normally irrigated regime (on 5 of 26 sampling dates; Table 5). In contrast, no consistent trends emerged for large nymph densities in our study with respect to irrigation regime (Table 5). Interactions between irrigation regimes and natural enemy manipulations were similarly rare indicating that the influence of either plant quality or natural enemies on densities seldom depended on the level of manipulation in the other factor. The year to year inconsistencies in our results, particularly with respect to plant quality effects on *B. tabaci* densities, could also be

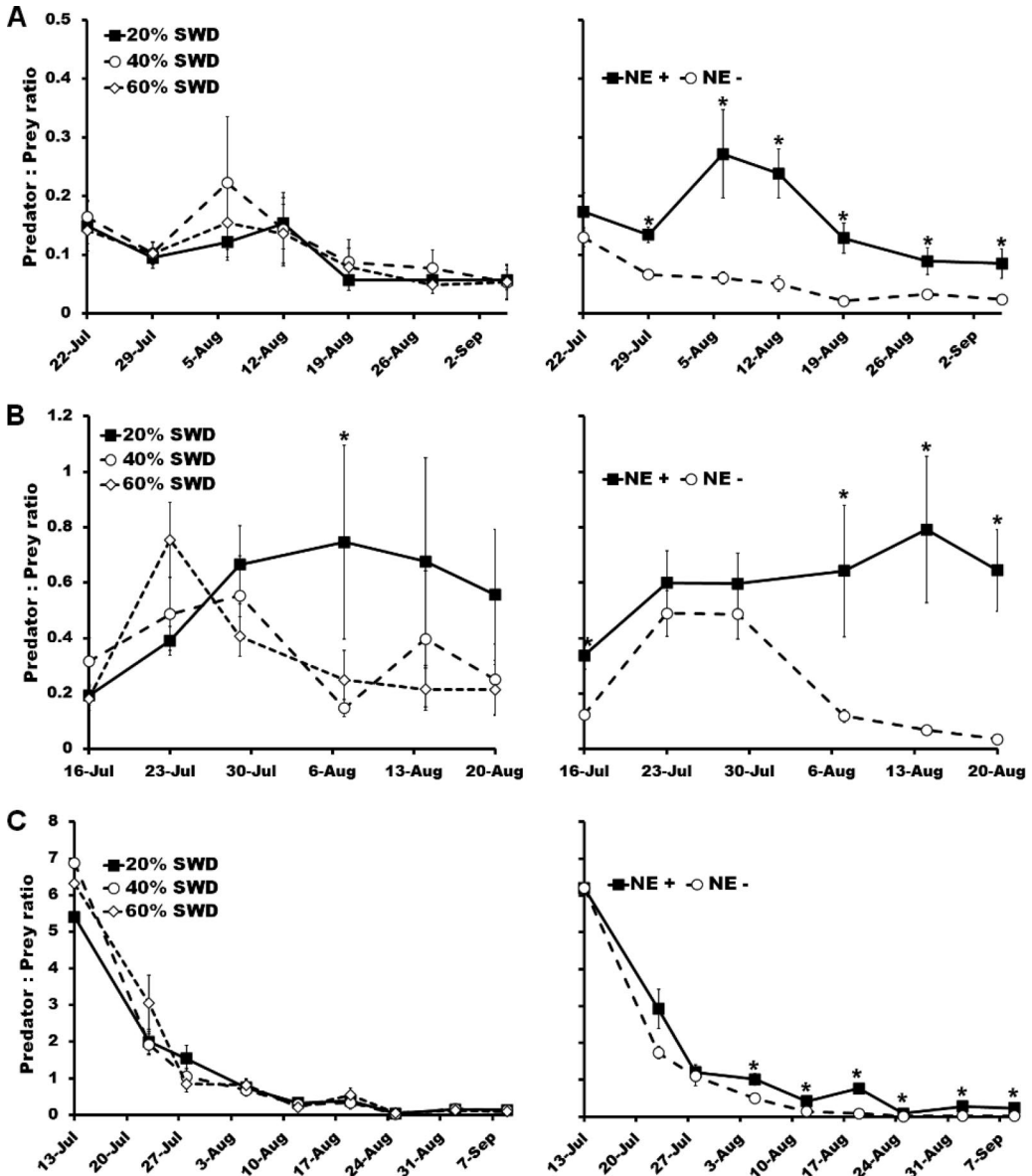


Fig. 5. Main effect of predator:prey ratios for three irrigation regimes (20, 40, and 60% SWD) and for natural enemy densities unaltered (NE+) or reduced (NE-) in (A) 2008, (B) 2009, and (C) 2010, Maricopa, AZ. Asterisks (*) represent significant differences at each date ($P < 0.05$); error bars indicate SE.

because of among year variation in environmental and crop management factors that affect the nature of the crop. For example, year to year variation in temperatures leads to variation in heat stress that, depending on the stage of growth when the crop experienced peak heat stress, could have affected the overall development of the crop. In addition, a different field location was used in 2008 compared with the other years. This could have led to variations in residual soil nitrogen and therefore affected the crop's response to irrigation and could explain the particularly low yields observed in 2008. However, the fact that we observed consistent effects of natural enemy treatments on all

B. tabaci stages, in every year, indicates the strong influence natural enemies have on *B. tabaci* dynamics. Once released from biological control, especially after the second acephate application, both whiteflies and spider mites broke out later in the season. However, Naranjo et al. (2004) have shown that even a single early season acephate application is enough to produce season long suppression of natural enemies. The combination of whitefly and spider mite outbreaks caused feedback effects on the plant resulting in further reductions in plant quality that were largely expressed in lower lint yields and premature plant defoliation. These effects were more severe in the

deficit-irrigated regime probably because of the already poor physiological condition of these plants and their higher temperature. Water stress and high canopy temperature have previously been associated with spider mite outbreaks (English-Loeb 1989, 1990). Here, these outbreaks resulted in a greater and more rapid decline in plant quality in the deficit-irrigation regimes. In addition, because whiteflies and spider mites occupy the same niche in cotton, outbreaks of both pests on the same leaves could have led to competition and/or affected the recruitment of predators that could have also had an unmeasured effect on plant quality. *Lygus hesperus* (Knight), the other key pest of cotton in Arizona, was also observed occurring at higher densities in the well-irrigated regime compared with the deficit-irrigated regime (Asiimwe 2011). These differential *L. hesperus* densities could have affected fruiting patterns and consequently plant quality among irrigation regimes. All these factors, individually and collectively, somewhat confounded our assessment of plant quality effects in this study. In general, the patterns and trends in yield responses suggest that natural enemy effects are more consistent than those influenced by plant quality manipulations (see Table 4).

Several studies have evaluated the effects of different irrigation regimes on *B. tabaci* densities, without manipulating natural enemy densities (Mor 1983, 1987; Mattson and Haack 1987; Flint et al. 1994, 1996; Gencsoy et al. 2003), and have found higher densities on stressed plants, or plants receiving less than adequate amounts of water. However most of these studies did not account for the potential variation in leaf area on densities. The higher densities observed on stressed plants could have been because of a greater concentration of the population on a smaller resource. In our study, plant quality effects were generally uncommon and variable. These minor and inconsistent plant quality effects coupled with the much larger natural enemy effects means we cannot draw any conclusive evidence in support of either the plant stress or plant vigor hypothesis from this study.

In general, plant quality effects on predator densities and predator:prey ratios were rare ($\approx 5\%$ of the time; Table 5) indicating minimal influence of plant quality in predator:prey dynamics. This is consistent with findings in Flint et al. (1994) who, except for *N. alternatus* (Parshley), found no significant differences in densities of 11 predator species between cotton plots irrigated weekly and biweekly. However, in 2010, we found significantly higher densities of predators in the well-irrigated regime compared with the deficit regime. This could have been a numerical response to increased prey densities reflected by higher large nymph densities, which are most susceptible to predation (Naranjo and Ellsworth 2005), or to the presence of a different assemblage of prey items.

Although this study does not eliminate the possibility of a chemically induced increase in fecundity, we found that natural enemies are the dominant factor in regulating *B. tabaci* densities in cotton. We used an 'insecticide check' method (DeBach 1946) to reduce

natural enemies with the application of acephate, a broad-spectrum organophosphate. This method has been used in similar field studies to investigate the role of predators in spider mite (Wilson et al. 1998) and aphid (Wilson et al. 1999) outbreaks in cotton. Although this method has been criticized (Morse and Zareh 1991, Morse 1998), we found it to be particularly useful in reducing and keeping natural enemy densities low, hence allowing us to measure their relationship with *B. tabaci* abundance. Pesticide induced outbreaks of *B. tabaci* after application of broad spectrum insecticides have previously been shown in cotton (Eveleens 1983, Ditttrich et al. 1985, Devine et al. 1998). It has been hypothesized that these outbreaks are because of a reduction in natural enemies or stimulatory effects of insecticides on the crop and/or *B. tabaci*. We conducted cohort-based life table measurements on immature *B. tabaci* in these plots (Asiimwe 2011) and found major reductions in predation and overall natural enemy induced mortality during immature stages of *B. tabaci* after acephate applications, and these reductions were most pronounced mid to late season coinciding with the period when adult whitefly densities reached outbreak levels. In addition, nutritional analysis of total leaf nitrogen on leaves harvested from both acephate sprayed and unsprayed plots showed no significant differences.

This study has confirmed the important role that natural enemies play in reducing densities of *B. tabaci* in cotton in Arizona (Naranjo et al. 2004, Naranjo and Ellsworth 2005, Naranjo and Ellsworth 2009). Most studies on the relative influence of plant quality and natural enemies have focused on manipulating available nutrients and predation pressure with relatively few studies simultaneously manipulating plant quality through available plant water, and natural enemies. Morris (1992) manipulated these factors and found that natural enemies were the predominant factor influencing densities of *Aphis varians* (Patch) on fireweed. Similarly, Hanks and Denno (1993) found that natural enemies had a greater impact than plant water status on densities of *Pseudaulacaspis pentagona* (Targioni) in Mulberry trees. Our findings are consistent with these studies. We have shown that regardless of irrigation regime, natural enemies remain an important component of the overall management strategy for *B. tabaci* in cotton. Natural enemies have a much greater influence on *B. tabaci* population dynamics than the plant-based factors investigated in this study.

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References Cited

- Asimwe, P. 2011. Relative influence of plant quality and natural enemies on population dynamics of *Bemisia tabaci* and *Lygus hesperus* in cotton. PhD. dissertation. University of Arizona, Tucson, AZ.
- Butler Jr., G. D., and T. J. Henneberry. 1993. Sweetpotato whitefly natural enemies: parasite surveys in urban areas and cotton fields and identification of a new predator, pp. 256–257. In Cotton, A College of Agriculture Report, Series P-94, University of Arizona, Tucson, AZ.
- Chilcutt, C. F., L. T. Wilson, R. Lascano, K. F. Bronson, and J. Booker. 2005. Scaling and the effects of plant, soil and landscape characteristics on sap-feeding herbivores in cotton. *Environ. Entomol.* 34: 75–86.
- Cornelissen, T., and P. Stiling. 2005. Perfect is best: low leaf fluctuating asymmetry reduces herbivory by leaf miners. *Oecologia* 142: 46–56.
- DeBach, P. 1946. An insecticidal check for measuring the efficacy of entomophagous insects. *J. Econ. Entomol.* 39: 695–697.
- De Barro, P. J., S. S. Liu, L. M. Boykin, and A. B. Dinsdale. 2011. *Bemisia tabaci*: a statement of species status. *Annu. Rev. Entomol.* 56: 1–19.
- Denno, R. F., D. Lewis, and C. Gratton. 2005. Spatial variation in the relative strength of top-down and bottom-up forces: causes and consequences for phytophagous insect populations. *Ann. Zool. Fenn.* 42: 295–311.
- Devine, G. J., I. Ishaaya, A. R. Horowitz, and I. Denholm. 1998. Effects of piperonyl butoxide on *Bemisia tabaci* Genn. (Homoptera: Aleyrodidae): mortality, development, parasitism and predation in Israeli cotton fields. *Crop Prot.* 17: 717–726.
- Dinsdale, A., L. Cook, C. Riginos, Y. M. Buckley, and P. De Barro. 2010. Refined global analysis of *Bemisia tabaci* (Hemiptera: Sternorrhyncha: Aleyrodoidea: Aleyrodidae) mitochondrial cytochrome oxidase 1 to identify species level genetic boundaries. *Ann. Entomol. Soc. Am.* 103: 196–208.
- Dittrich, V., S. O. Hassan, and G. H. Ernst. 1985. Sudanese cotton and the whitefly: a case study of the emergence of a new primary pest. *Crop Prot.* 4: 161–176.
- Ellsworth, P. C., and J. L. Martinez-Carrillo. 2001. IPM for *Bemisia tabaci*: a case study from North America. *Crop Prot.* 20: 853–869.
- Ellsworth, P. C., S. E. Naranjo, S. J. Castle, J. R. Hagler, and T. J. Henneberry. 1998. Whitefly management in Arizona: looking at the whole system, pp. 311–318. In Cotton, A College of Agriculture Report, Univ. Arizona, Tucson, Series P112.
- English-Loeb, G. M. 1989. Non-linear responses of spider mites to drought-stressed host plants. *Ecol. Entomol.* 14: 45–55.
- English-Loeb, G. M. 1990. Plant drought stress and outbreaks of spider mites: a field test. *Ecology* 71: 1401–1411.
- Eveleens, K. G. 1983. Cotton-insect control in the Sudan Gezira: analysis of a crisis. *Crop Prot.* 2: 273–287.
- Flint, H. M., F. D. Wilson, D. Hendrix, J. Leggett, S. Naranjo, T. J. Henneberry, and J. W. Radin. 1994. The effect of plant water stress on beneficial and pest insects including the pink bollworm and the sweetpotato whitefly in two short-season cultivars of cotton. *Southwest. Entomol.* 19: 11–22.
- Flint, H. M., S. E. Naranjo, J. E. Leggett, and T. J. Henneberry. 1996. Cotton water stress, arthropod dynamics and management of *Bemisia tabaci*. *J. Econ. Entomol.* 89: 1288–1300.
- Forkner, R. E., and M. D. Hunter. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* 81: 1588–1600.
- Fournier, A., P. C. Ellsworth, and V. M. Barkley. 2008. Economic impact of *Lygus* in Arizona cotton: a comparative approach. In P. B. Goodell and P. C. Ellsworth. 2008. Second International *Lygus* Symposium. *J. Insect. Sci.* 8: 49. (insectscience.org/8.49).
- Gencsoylu, I., A. R. Horowitz, F. Sezgin, and C. Oncuer. 2003. Effect of drip and furrow irrigation methods on *Bemisia tabaci* populations in cotton fields. *Phytoparasitica* 31: 139–143.
- Gerling, D., and S. E. Naranjo. 1998. The effect of insecticide treatments in cotton fields on the levels of parasitism of *Bemisia tabaci* (Gennadius) sl. *Biol. Control* 12: 33–41.
- Gratton, C., and R. F. Denno. 2003. Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. *Oecologia* 134: 487–495.
- Hagler, J. R., and S. E. Naranjo. 1994. Determining the frequency of heteropteran predation on sweet-potato whitefly and pink-bollworm using multiple ELISAs. *Entomol. Exp. Appl.* 72: 59–66.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *Am. Nat.* 94: 421–425.
- Hanks, L. M., and R. F. Denno. 1993. Natural enemies and plant water relations influence the distribution of an armoured scale insect. *Ecology* 74: 1081–1091.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton, NJ.
- Hawkins, B. A., N. J. Mills, M. A. Jervis, and P. W. Price. 1999. Is the biological control of insects a natural phenomenon? *Oikos* 86: 493–506.
- Hilje, L., H. S. Costa, and P. A. Stansly. 2001. Cultural practices for managing *Bemisia tabaci* and associated viral diseases. *Crop Prot.* 20: 801–812.
- Huberty, A. F., and R. F. Denno. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology* 85: 1383–1398.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders-heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 724–732.
- Hunter, M. D., G. C. Varley, and G. R. Gradwell. 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proc. Natl. Acad. Sci. U.S.A.* 94: 9176–9181.
- Inbar, M., H. Doostdar, and R. T. Mayer. 2001. Suitability of stressed and vigorous plants to various insect herbivores. *Oikos* 94: 228–235.
- Isaacs, R., D. N. Byrne, and D. L. Hendrix. 1998. Feeding rates and carbohydrate metabolism on different quality phloem sap. *Physiol. Entomol.* 23: 241–248.
- Johnson, M.T.J. 2008. Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology* 89: 145–154.
- Koricheva, J., S. Larsson, and E. Haukioja. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. *Annu. Rev. Entomol.* 43: 195–216.
- Larsson, S. 1989. Stressful times for the plant stress-insect performance hypothesis. *Oikos* 56: 277–283.
- Littell R.C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute, Cary, NC.
- Mattson, W. J., and R. A. Haack. 1987. The role of drought in outbreaks of plant eating insects. *Biosciences* 37: 110–118.
- Mody, K., D. Eichenberger, and S. Dorn. 2009. Stress magnitude matters: different intensities of pulsed water stress

- produce non-monotonic resistance responses of host plants to insect herbivores. *Ecol. Entomol.* 34: 133–143.
- Mor, U. 1983. Cotton yields and quality as affected by *Bemisia tabaci* under different regimes of irrigation and pest control. *Phytoparasitica* 11: 64.
- Mor, U. 1987. *Bemisia tabaci* and cotton physiology: a 5-year summary of the influence of water stressed plants on the pest population. *Phytoparasitica* 15: 261.
- Morris, W. F. 1992. The effects of natural enemies, competition, and host plant water availability on an aphid population. *Oecologia* 90: 359–365.
- Morse, J. G. 1998. Agricultural implications of pesticide-induced hormesis of insects and mites. *Hum. Exp. Toxicol.* 17: 266–269.
- Morse, J. G., and N. Zareh. 1991. Pesticide-induced hormoligosis of citrus thrips (Thysanoptera, Thripidae) fecundity. *J. Econ. Entomol.* 84: 1168–1174.
- Naranjo, S. E. 2001. Conservation and evaluation of natural enemies in IPM systems for *Bemisia tabaci*. *Crop Prot.* 20: 835–852.
- Naranjo, S. E., and H. M. Flint. 1994. Spatial distribution of pre-imaginal *Bemisia tabaci* (Homoptera: Aleyrodidae) in cotton and development of fixed-precision sampling plans. *Environ. Entomol.* 23: 254–266.
- Naranjo, S. E., and H. M. Flint. 1995. Spatial-distribution of adult *Bemisia tabaci* (Homoptera, Aleyrodidae) in cotton and development and validation of fixed-precision sampling plans for estimating population-density. *Environ. Entomol.* 24: 261–270.
- Naranjo, S. E., and P. C. Ellsworth. 2005. Mortality dynamics and population regulation in *Bemisia tabaci*. *Entomol. Exp. Appl.* 116: 93–108.
- Naranjo, S. E., and P. C. Ellsworth. 2009. The contribution of conservation biological control to integrated control of *Bemisia tabaci* in cotton. *Biol. Control* 51: 458–470.
- Naranjo, S. E., J. R. Hagler, and P. C. Ellsworth. 2003. Improved conservation of natural enemies with selective management systems for *Bemisia tabaci* (Homoptera: Aleyrodidae) in cotton. *Biocontrol Sci. Technol.* 13: 571–587.
- Naranjo, S. E., P. C. Ellsworth, and J. R. Hagler. 2004. Conservation of natural enemies in cotton: role of insect growth regulators in management of *Bemisia tabaci*. *Biol. Control* 30: 52–72.
- Oliveira, M.R.V., T. J. Henneberry, and P. Anderson. 2001. History, current status, and collaborative research projects for *Bemisia tabaci*. *Crop Prot.* 20: 739–765.
- Oswald, C. J., and M. J. Brewer. 1997. Aphid-barley interactions mediated by water stress and barley resistance to Russian wheat aphid (Homoptera: Aphididae). *Environ. Entomol.* 26: 591–602.
- Price, P. W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62: 244–251.
- Silvertooth, J. C. 2001. Determining height to node ratios in cotton. University of Arizona Cooperative Extension Bulletin No. AZ1210.
- Skinner, R. H. 1996. Response of *Bemisia argentifolii* (Homoptera: Aleyrodidae) to water and nutrient stressed cotton. *Environ. Entomol.* 25: 401–406.
- Staley, J. T., S. R. Mortimer, G. J. Masters, M. D. Morecroft, V. K. Brown, and M. E. Taylor. 2006. Drought stress differentially affects leaf mining insects. *Ecol. Entomol.* 31: 460–469.
- Stiling, P., and D. C. Moon. 2005. Quality or quantity: the direct and indirect effects of host plants on herbivores and their natural enemies. *Oecologia* 142: 413–420.
- Strong, D. R., J. H. Lawton, and T.R.E. Southwood. 1984. *Insects on plants*. Blackwell, Oxford, United Kingdom.
- Ter Braak, C.J.F. and P. Smilauer. 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY.
- Underwood, N., and M. D. Rausher. 2000. The effects of host plant genotype on herbivore population dynamics. *Ecology* 81: 1565–1576.
- van den Brink, P. J., and C.J.F. Ter Braak. 1998. Multivariate analysis of stress in experimental ecosystems by Principle Response Curves and similarity analysis. *Aquat. Ecol.* 32: 163–178.
- van den Brink, P. J., and C.J.F. Ter Braak. 1999. Principle response curves: analysis of time-dependent multivariate responses of biological communities to stress. *Environ. Toxicol. Chem.* 18: 138–148.
- Watson, T. F., J. C. Silvertooth, A. Tellez, and L. Lastra. 1992. Seasonal dynamics of sweet potato whitefly in Arizona. *Southwest. Entomol.* 17: 149–167.
- White, T.C.R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of Psyllids in Australia. *Ecology* 50: 905–909.
- White, T.C.R. 1974. Hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologia* 16: 279–301.
- White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63: 90–105.
- White, T.C.R. 2009. Plant vigour versus plant stress: a false dichotomy. *Oikos* 118: 807–808.
- Wilson, L. J., L. R. Bauer, and D. A. Lally. 1998. Effect of early season insecticide use on predators and outbreaks of spider mites (Acari: Tetranychidae) in cotton. *Bull. Entomol. Res.* 88: 477–488.
- Wilson, L. J., L. R. Bauer, and D. A. Lally. 1999. Insecticide induced increases in aphid abundance in cotton. *Aust. J. Entomol.* 38: 242–243.

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