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Natural enemy impacts on *Bemisia tabaci* (MEAM1) dominate plant quality effects in the cotton system

PETER ASIIMWE,[1,†] PETER C. ELLSWORTH[1] and STEVEN E. NARANJO[2] [1]Department of Entomology, University of Arizona Maricopa Agricultural Center, Maricopa, Arizona, U.S.A. and [2]USDA-ARS, Arid-Land Agricultural Research Center, Maricopa, Arizona, U.S.A.

Abstract. 1. Plant quality (bottom-up effects) and natural enemies (top-down effects) affect herbivore performance. Furthermore, plant quality can also influence the impact of natural enemies.

2. Lower plant quality through reduced irrigation increased the abundance of the cryptic species from the *Bemisia tabaci* complex [hereafter *B. tabaci* Middle East Asia Minor 1 (MEAM1)], but not its natural enemies on cotton. It was therefore predicted that lower plant quality would diminish the impact of natural enemies in regulating this herbivore.

3. Over three cotton seasons, plant quality was manipulated via differential irrigation and natural enemy abundance with insecticides. Life tables were used to evaluate the impact of these factors on mortality of immature *B. tabaci* (MEAM1) over nine generations.

4. Mortality of *B. tabaci* (MEAM1) was consistently affected by natural enemies but not by plant quality. This pattern was driven by high levels of sucking predation, which was the primary (key) factor associated with changes in immature mortality across all irrigation and natural enemy treatments. Dislodgement (chewing predation and weather) and parasitism contributed as key factors in some cases. Analyses also showed that elimination of sucking predation and dislodgement would have the greatest effect on overall mortality.

5. The top-down effects of natural enemies had dominant effects on populations of *B. tabaci* (MEAM1) relative to the bottom-up effects of plant quality. Effects were primarily due to native generalist arthropod predators and not more host-specific aphelinid parasitoids. The findings of this study demonstrate the important role of arthropod predators in population suppression and validate the importance of conservation biological control in this system for effective pest control.

Key words. Arthropod predators, biological control, life tables, parasitoids, plant stress, whiteflies.

Introduction

Plant resources (bottom-up effects) and natural enemies (top-down effects) are important influences on insect herbivore abundance, distribution and performance, ultimately affecting population regulation in insect communities (Hunter & Price, 1992; Stiling & Rossi, 1997; Forkner & Hunter, 2000; Walker & Jones, 2001; Finke & Denno, 2002 & Richmond *et al*., 2004). The relative contributions of bottom-up and top-down effects vary with levels of plant quality (McMillin & Wagner, 1998; Dyer & Letourneau, 1999), insect feeding guild (Cornell & Hawkins, 1995), life stage (Harcourt, 1966; Walker & Jones, 2001) and spatial and temporal variation in insect densities (Hunter *et al*., 1997). Plant quality generally influences insect population dynamics through changes in fecundity, survival, dispersal, competition and natural enemy-induced mortality

Correspondence: Steven E. Naranjo, USDA-ARS, Arid-Land Agricultural Research Center, 21881 North Cardon Lane, Maricopa, Arizona, 85138, U.S.A. E-mail: Steve.naranjo@ars.usda.gov

†Current address: Monsanto Company, 800 N. Lindbergh Blvd, St. Louis, Missouri 63167, U.S.A. This article presents the results of research only. Mention of a proprietary product does not constitute endorsement or recommendation for its use by USDA; USDA is an equal opportunity employer.

(Price *et al*., 1980; Denno *et al*., 1995; Abrahamson & Weis, 1997; Williams, 1999; Lill *et al*., 2002; Walker *et al*., 2008). Insect herbivores constitute a basic resource for natural enemies. Thus, changes in host plant quality may indirectly influence the impact of the natural enemies through effects on their prey (Havill & Raffa, 2000; Giles *et al*., 2002; Harvey *et al*., 2003). For example, plant quality may influence herbivore developmental rates (Price *et al*., 1980; Clancy & Price, 1987; Loader & Damman, 1991; Benrey & Denno, 1997), their quality as prey (Harvey *et al*., 1995; Pandey & Singh, 1999; West *et al*., 2001; King, 2002), or even affect changes in prey spatial and temporal distribution (Hassell & Southwood, 1978; Damman, 1987; Walde, 1995; Stiling & Rossi, 1997; Moon & Stiling, 2002; Turlings & Wackers, 2004), all of which could affect the ability of natural enemies to find and utilise their prey as a nutritional resource. Some studies support the hypothesis that plant quality mediates natural enemy impact (Hunter & Price, 1992; Walde, 1995; Stiling & Rossi, 1997; Forkner & Hunter, 2000; Denno *et al*., 2002; Gratton & Denno, 2003), while others have found no influence of plant quality on natural enemy impact (Costamagna & Landis, 2006; Daugherty *et al*., 2007).

Most of these studies have been conducted in natural and forest ecosystems with only a few conducted in managed agro-ecosystems (e.g. Dyer & Stireman, 2003; Costamagna & Landis, 2006) and some under different climatic scenarios (e.g. McKenzie *et al*., 2013; Ryalls *et al*., 2015). In managed row-crop agro-ecosystems, plant quality is typically high for productivity purposes and can be manipulated easily through varying water and/or nitrogen inputs. Water as an input plays an important role in abundance of insect herbivores through its influence on plant quality (White, 1969; Mattson & Haack, 1987; Waring & Cobb, 1992). The response of herbivores to water stress could vary with feeding guild; for example, gall formers responded negatively (Larsson 1989), while leaf miners and phloem feeders benefited from drought stress (Huberty and Denno 2004). In agro-ecosystems, water stress can influence oviposition and nutritional resources for pests and natural enemies (Gillespie & McGregor, 2000, Seagraves *et al*., 2011), as well as the herbivore's microenvironment (Ellsworth *et al*., 1992). Similarly, insect pests and natural enemies are more consistently abundant in agro-ecosystems and both can be manipulated through the application and timing of specific insecticide inputs. Agro-ecosystems could therefore provide useful insights into the relative influences of plant quality and natural enemies on insect herbivores.

The invasive, polyphagous cryptic species of the *Bemisia tabaci* complex [here after referred to as *B. tabaci* Middle East Asia Minor 1 (MEAM1); Dinsdale *et al*., 2010] is a key pest of several crops throughout the world and, in Arizona, it is a key pest of cotton causing potential losses in quantity and quality (Naranjo & Ellsworth, 2009b). Several studies have examined the separate effects of plant quality, manipulated via water stress or nitrogen fertility, and natural enemies on abundance and performance of *B. tabaci*. Higher *B. tabaci* densities have been found on water-stressed plants (Flint *et al*., 1994; 1996; Skinner, 1996a) and under high nitrogen application (Bentz *et al*., 1996; Bi *et al*., 2001; 2003; 2005). Natural enemies have been shown to play a key role in mortality of immature *B. tabaci* (Naranjo & Ellsworth, 2005; Asiimwe *et al*., 2007; Karut & Naranjo, 2009). The potential influence of water stress on natural enemies may influence their population dynamics and consequently their potential contribution to pest suppression (Naranjo *et al*., 2009; Asiimwe *et al*., 2013). No study has simultaneously manipulated plant quality and natural enemies to investigate their interactive and competing effects on the factors that influence mortality in populations of *B. tabaci* (MEAM1).

Life tables are a useful tool for understanding the factors governing population dynamics in the field (Stiling, 1988; Cornell, 1990; Cornell & Hawkins, 1995; Cornell *et al*., 1998), the relative importance of different insect mortality factors, and the role that bottom-up and top-down forces play in regulating insect populations (Preszler & Price, 1988; Cornell, 1990; Cornell & Hawkins, 1995; Stein & Price, 1995; Cornell *et al*., 1998; McMillin & Wagner, 1998). A combination of manipulative experiments and life tables could potentially provide a much better understanding of the relative importance of bottom-up and top-down forces on insect populations (Hunter, 2001; Walker & Jones, 2001; Gripenberg & Roslin, 2007). The sessile nature of immatures of *B. tabaci* (MEAM1) makes it an ideal system for using life table methods, because life stages can be readily identified, the fate of individuals can be followed over time, and natural enemies in our system typically leave a permanent record of their activity.

We manipulated plant quality by varying irrigation levels and used an insecticide to create contrasted natural enemy densities in central Arizona cotton fields. We examined the population dynamics and interaction of whiteflies and natural enemies relative to plant quality and insecticide treatments in a companion study (Asiimwe *et al.*, 2013). Here, we used an *in situ*, life table method to evaluate the relative influences of plant quality and natural enemies on sources and rates of mortality of individual cohorts of *B. tabaci* (MEAM1) in cotton over three seasons. In particular, we sought to understand whether plant quality effects indirectly influenced the impact of natural enemies on *B. tabaci* (MEAM1) or directly affected the overall survival of immature *B. tabaci* (MEAM1) in cotton. We predicted that the impact of natural enemies in regulating populations of *B. tabaci* (MEAM1) would be diminished on plants of lower quality, because *B. tabaci* densities have been higher on water-stressed cotton with lower plant productivity, i.e. poorer quality plants (Flint *et al*., 1994; 1996; Skinner *et al*., 1996a) while abundance and function of natural enemies do not accompany changes in prey density (Naranjo & Ellsworth, 2005; 2009a).

Materials and methods

Study site and experimental design

The studies were conducted in Maricopa, Arizona using Genuity Bollgard II with Roundup Ready Flex cotton (Monsanto Company, St Louis, Missouri) that confers protection against lepidopteran insect damage and tolerance to glyphosate herbicides. Seeds were planted in mid-April each year. Study design was a randomised complete block ($n = 4$), split-plot design with irrigation level as the whole plots and natural enemy manipulation as the subplots. Irrigations were done at

20%, 40% and 60% soil water depletion (SWD), where 40% SWD represents the standard regime for cotton at our study site. Chemical exclusion with acephate was used to manipulate natural enemy levels. Acephate has been shown to reduce natural enemies (predators and parasitoids) while having minimal to no effect on any stage of whiteflies (Ellsworth *et al.*, 1998; Naranjo *et al.*, 2004b; Naranjo & Ellsworth, 2009a). Pest and natural enemy densities were measured in a companion study according to standard methods (Asiimwe *et al.*, 2013). Briefly, natural enemies were measured with 38-cm-diameter sweep nets, and densities of *B. tabaci* (MEAM1) were monitored with leaf or leaf disk sample units.

Plant responses

The effect of irrigation regimes on plant responses was estimated through infrared thermometer measurements of the topmost expanded leaves for 10 plants in each irrigation regime immediately before each irrigation. Higher canopy temperatures indicate elevated levels of water stress. We also estimated plant height and number of nodes biweekly for five randomly selected plants in plots of each irrigation treatment according to the methods described in Silvertooth (2001).

Cohort establishment

We used naturally occurring populations to establish cohorts of eggs and settled first-instar nymphs on the undersides of leaves in the central two to three rows of each plot following Naranjo & Ellsworth (2005). Freshly laid eggs and recently settled first-instar nymphs were located using an 8X Peak loupe lens (Light Impressions, Brea, California). New eggs were identified by their creamy white colour and usually found on the third and fourth fully expanded leaf down from the main-stem terminal. Settled first-instar nymphs were identified by their translucent colour, almost flush with the leaf surface, and were mostly found on the fourth to seventh fully expanded leaves below the main-stem terminal. A non-toxic, ultra-fine-point black or blue permanent marker was used to draw a small tight circle around identified eggs or nymphs. Each circle contained usually one, but no more than four, eggs, or one settled first-instar nymph. Eggs and nymphs were marked on separate leaves and a small numbered tag was placed on the petiole of each leaf containing marked eggs and nymphs. Brightly coloured flagging tape was tied on to the main stem just below the tagged leaf to facilitate relocation of marked individuals. No more than seven eggs or nymphs were marked per leaf and no more than one leaf was marked per plant. A minimum of 40 eggs and 40 settled first-instar nymphs were marked in each plot for a minimum of 960 individual eggs and first-instar nymphs in each cohort over the entire experiment. As many as 20–30 evenly spaced plants were used in each plot depending on insect densities at the time of establishment. To ensure that settled first-instar nymphs and not mobile crawlers were marked, each marked nymph was re-examined after 1–3 h. Cohorts were established on 16 July, 12 August and 4 September in 2008, 9 July, 5 August and 4 September in 2009, and 16 July, and 4 and 27 August in 2010. All cohorts were generally established on a single day between 06.00 and 09.00 hours, although low insect densities during establishment of several cohorts required setup times to be extended into the early afternoon hours. Here, we use the term cohort and generation interchangeably because we are measuring mortality from the egg to adult stage.

Determination of mortality factors

After cohorts had been established, each marked nymph was observed in the field (three times a week) using a 15X peak loupe (Light Impressions, Brea, California) until that individual died, disappeared or emerged as an adult. We found it difficult to determine the fate of the eggs in the field, even with a 15X lens, so all leaves containing marked eggs were harvested after 10 days and taken to the laboratory where they were examined under a dissecting microscope. Eggs typically take 5–7 days to hatch into nymphs under summer temperatures in central Arizona. During each observation date, the instar and state of each nymph were recorded and categorised as alive, dislodged, preyed upon, parasitised or dead due to unknown causes. Mortality in the egg stage was due to dislodgement, predation or physiological inviability. The sessile nymphs were categorised as alive based on size, shape, colour and the presence and location of symmetrical bacteriosomes. Dislodgement was recorded when a marked individual observed as alive on the previous observation date was absent without leaving a trace on the subsequent observation date. Dislodgement was mainly due to weather and chewing predation (Naranjo & Ellsworth, 2005). Predation was most often observable as being due to sucking predators and was characterised by a sunken, usually translucent, empty or partially empty nymph cadaver or egg chorion. Parasitism was only observed in nymphs and was characterised by the displacement of bacteriosomes or presence of parasitoid larvae, pupae or meconium within fourth-instar cadavers. Eggs were categorised as inviable when they appeared mature (with a dark brown colour) but failed to eclose after 10 days. When an individual was observed to be dead, yet it was not obvious that mortality was due to any of the above factors, mortality was categorised as unknown. This source of mortality was rarely observed and provided insufficient data for analysis. Once all marked individuals on a leaf had either died or emerged, the leaf was harvested and returned to the laboratory where cause of death was verified on individuals still on the leaf using a dissecting microscope. A single person determined cause of death for both the eggs and nymphs throughout the study, ensuring consistency in determining sources of mortality. Mortality of first-instar crawlers was not explicitly measured in this study; however, given that the duration between eclosion and settling is 3–6 h (Price & Taborsky, 1992; Simmons, 2002) and crawler mortality on cotton is negligible (Naranjo, 2007; Karut & Naranjo, 2009), we did not expect mortality during this stage to significantly affect generational mortality.

Data analyses

Determination of mortality rates. The concepts originally proposed by Royama (1981) and later elaborated and expanded on by Buonaccorsi & Elkinton (1990), Elkinton *et al.* (1992) and Naranjo & Ellsworth (2005) were used to determine stage-specific marginal rates of mortality based on observed (apparent) mortality rates for each treatment. Because any single stage could be possibly affected by three mortality factors that do not act in any obvious sequence, but are instead contemporaneous, marginal mortality rates are needed. The marginal rate estimates the level of mortality from a single factor assuming that factor was the only one operating at the time. Because dislodgement cannot be obscured by any other factor, it is the only mortality factor for which the apparent rate of mortality is equal to the marginal mortality rate. We used the simplified equation from Naranjo & Ellsworth (2005) to calculate marginal mortality rates, where

$$M_A = d_A / \left(1 - d_B\right),$$

and M_A is the marginal rate of mortality for factor A, d_A is the apparent (observed) rate of mortality from factor A, and d_B is the sum of apparent mortalities from all other competing contemporaneous factors. Thus, the marginal rates of egg inviability, nymphal parasitism and unknown mortality were estimated by accounting for apparent rates of predation and dislodgement, marginal rates of predation accounted for the apparent rate of dislodgement and the marginal rate of dislodgement was the same as the apparent rate.

Irreplaceable mortality. Irreplaceable mortality was calculated for each treatment using the methods of Carey (1989) and Naranjo & Ellsworth (2005). Irreplaceable mortality is that portion of total generational mortality that would not occur if a given mortality factor was eliminated (Southwood, 1978). The simplified general equation is

$$I_C = D - \left[1 - \left(1 - M_A\right)\left(1 - M_B\right)\right]$$

where

$$D = \left[1 - \left(1 - M_A\right)\left(1 - M_B\right)\left(1 - M_C\right)\right]$$

and M_x is the marginal mortality for generalised factor or stage A, B, or C. I_C is the irreplaceable mortality for factor or stage C and excludes the marginal mortality of the factor or stage of interest (which, in this example, is C). This estimate assumes that mortality factors are density-independent.

Key factor analysis. Mortality was expressed as *k*-values [where $k = -\ln(1 - M)$], and *M* is the marginal mortality rate for a given factor in a given stage. *k*-values are convenient for calculating mortality because they are additive across stages and mortality factors (Varley & Gradwell, 1960). The method of Podoler & Rogers (1975) was used to evaluate key factors by regressing individual *k*-values on total *K*. This method identifies the key factor as that with the largest regression coefficient (slope). The method of Smith (1973) was then used to determine the relative importance of each factor by sequentially eliminating each key factor based on the regression coefficient until all but one or two factors remained in most of the stages.

Statistical analyses

Linear regression analysis was conducted to assess the relationship between irrigation levels and various estimates of plant quality (canopy temperature, plant heights, number of nodes, height to node ratios). Plant quality metrics, standardised for each year, were regressed on differential levels of total water (cm) applied to the three irrigation treatments after establishment of the crop (see Asiimwe *et al.*, 2013). Mixed-model ANOVA (Littell *et al.*, 1996) was used to determine effects of plant quality (irrigation levels), natural enemies and their interaction on levels of marginal mortality, generational survivorship and irreplaceable mortality. The block and cohort within-year variables and their associated interaction terms were random effects; natural enemy and irrigation treatments, year and associated interactions were fixed effects. The Kenward–Roger's formula was used to estimate corrected degrees of freedom. Data were transformed using square root or arcsine-square root as needed to meet the assumptions of ANOVA. Pre-planned orthogonal contrasts for plant quality compared 20% and 40% SWD to 60% SWD and 20% SWD to 40% and 60% SWD. Key factor analyses were conducted using data from all nine generations (three per year for 3 years).

Results

Increasing levels of irrigation were associated with increasing plant height [$F(1, 25) = 6.0$, $P = 0.021$], increasing height to node ratios [$F(1, 25) = 18.3$, $P = 0.0002$] and declining canopy temperature [$F(1, 69) = 9.6$, $P = 0.0028$], but no differences were found in number of nodes ($P = 0.378$). A companion study examined population dynamics and predator–prey interactions (Asiimwe *et al.*, 2013). Briefly, broad-spectrum insecticide applications resulted in lower natural enemy densities relative to the untreated control and lower predator:prey ratios, but there were no effects of plant quality on natural enemy abundance or these ratios. Densities of *B. tabaci* eggs, nymphs and adults were higher when natural enemies were reduced compared with the controls, regardless of irrigation level (Asiimwe *et al.*, 2013). Whitefly densities were higher two-thirds of the time and increased two- to six-fold when natural enemies were reduced. Plant quality effects on *B. tabaci* densities were expressed about one-third of the time and were generally inconsistent across years.

Marginal mortality

Results were not affected by year of study [$F(2, 6) < 2.00$, $P > 0.22$]. Marginal mortalities for parasitism [$F(1, 6.6) = 1.10$, $P = 0.33$] were unaffected by natural enemy treatment, while results for dislodgement ($F(1, 31.9) = 0.37$, $P = 0.055$) were marginally significant (Fig. 1A). Rates of predation were greater in control plots than in plots where natural enemy densities were reduced [$F(1, 6) = 60.23$, $P = 0.0002$], but the opposite was observed for rates of egg inviability, which were very low [$F(1, 20.6) = 7.61$, $P = 0.012$]. Marginal rates of mortality factors were not affected by plant quality [$F(2, 9.8–15.2) < 0.76$,

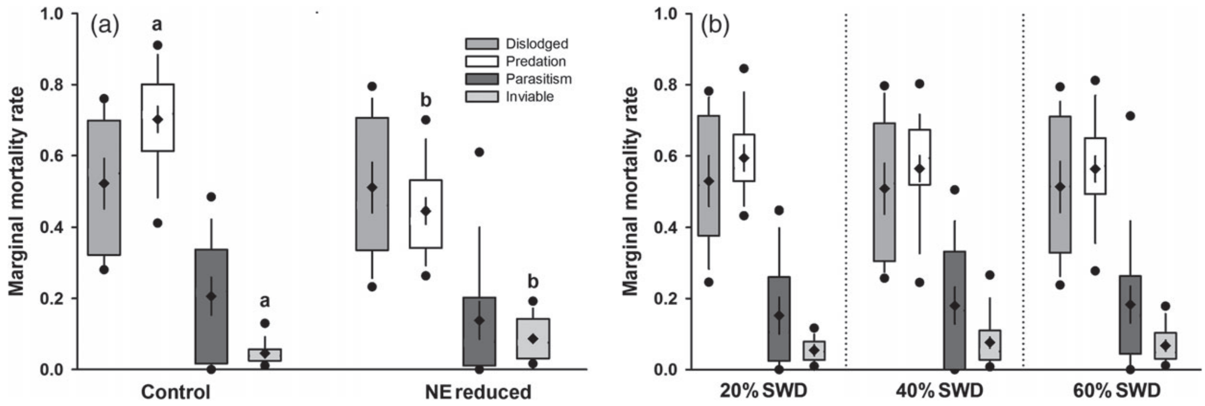

Fig. 1. Main effect box plots for marginal mortality rates for immature *Bemisia tabaci* (MEAM1) caused by various factors, over nine generations in 3 years (2008–2010). (a) Natural enemy treatments; (b) cotton irrigation regimes [20%, 40% and 60% soil water depletion (SWD)]. Different letters within a mortality factor denote statistical significance ($P < 0.05$); bars without letters did not differ significantly. Control, natural enemies unaltered; NE reduced, natural enemies reduced with acephate sprays. For plots, diamonds with error bars denote the mean and SEM, the box denotes the 25th and 75th percentiles, whiskers denote the 10th and 90th percentiles and points depict the 5th and 95th percentiles.

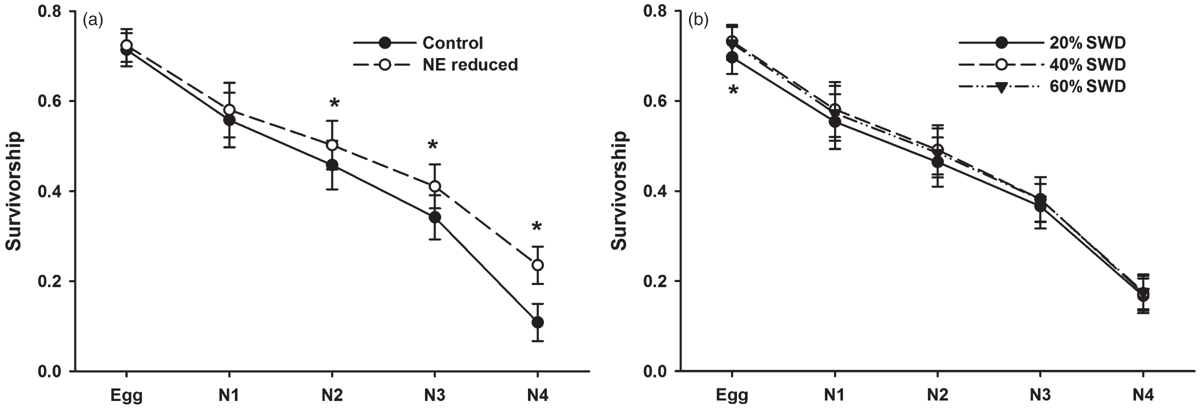

Fig. 2. Survivorship curves for *Bemisia tabaci* (MEAM1) relative to natural enemy (a) and cotton irrigation regimes [20%, 40% and 60% soil water depletion (SWD)] (b), over nine generations in 3 years (2008–2010). Asterisks denote significant differences as measured cumulatively through the indicated life stage ($P < 0.05$). Control, natural enemies unaltered; NE reduced, natural enemies reduced with acephate sprays. Error bars represent SEM. N1 through N4 denote the four nymphal stadia.

$P > 0.49$] (Fig. 1B) and there were no interactions between natural enemy and plant quality treatments for any mortality factor [$F(2, 12–45) < 1.31$, $P > 0.28$].

Generational survival

Year was not a significant factor and survivorship was similar across years [$F(2, 6) < 0.72$, $P > 0.52$]. Natural enemy levels did not affect cumulative survival of up to the first nymphal stadium [$F(1, 6) < 2.29$, $P > 0.18$] but was higher for insects in the second to fourth stadia when natural enemy densities were reduced compared with the control [$F(1, 6) > 12.4$, $P < 0.009$] (Fig. 2A). Plant quality affected survival during the egg stage [$F(2, 183) = 3.72$, $P = 0.026$], but not cumulatively through the remainder of the nymphal stadia [$F(2, 21.1) < 1.33$, $P > 0.33$] (Fig. 2B). Eggs on plants subject to 40–60% SWD had marginally higher survival than those on plants with 20% SWD [$F(1, 183) = 7.33$, $P = 0.07$].

Key factors

The key factors were consistently associated with mortality during the fourth stadium regardless of plant quality or natural enemy treatment (Tables 1 and 2). Predation was the dominant key factor followed by parasitism and then dislodgement in various life stages.

Irreplaceable mortality

Levels of irreplaceable mortality due to various sources did not generally vary across years [$F(2, 6) < 2.49$, $P > 0.16$]. Predation, dislodgement and inviability were affected by natural enemy levels (Fig. 3A). Predation was higher in the natural enemy control [$F(1, 6.55) = 18.78$, $P = 0.004$] and the other two factors were higher when natural enemy densities were reduced. [dislodgement, $F(1, 6.12) = 24.48$, $P = 0.003$; inviability, $F(1, 34) = 21.42$, $P < 0.0001$]. Plant quality did not affect

Table 1. Key factor analysis of life tables over nine generations of immature *Bemisia tabaci* (MEAM1) pooled over all natural enemy treatments for each plant quality treatment: cotton irrigated at 20%, 40% and 60% soil water depletion (SWD), Maricopa, Arizona.

		Iteration				
Stage	Factor	1	2	3	4	5
20% SWD						
Egg	Dislodgement	0.075	0.115	0.184	0.236	0.257
	Predation	0.002	0.006	0.017	0.015	0.048
	Inviability	0.004	0.013	0.026	0.03	0.028
First instar	Dislodgement	0.126	0.207	0.232	**0.419**	
	Predation	0.014	0.019	0.031	0.055	0.049
Second instar	Dislodgement	−0.002	−0.002	−0.003	0.002	−0.005
	Predation	0.003	0.012	0.006	0.031	0.066
Third instar	Dislodgement	0.047	0.071	0.193	0.11	**0.422**
	Predation	0.048	0.064	0.088	0.129	0.169
Fourth instar	Dislodgement	0.079	0.119	**0.242**	–	–
	Predation	**0.354**	–	–	–	–
	Parasitism	0.259	**0.388**	–	–	–
40% SWD						
Egg	Dislodgement	0.06	0.216	0.176	0.341	**0.358**
	Predation	0.011	0.019	0.011	0.035	0.055
	Inviability	−0.004	−0.002	−0.014	−0.019	0.0
First instar	Dislodgement	0.111	**0.272**	–	–	–
	Predation	−0.003	−0.005	0.001	0.000	−0.066
Second instar	Dislodgement	−0.011	−0.023	−0.028	−0.052	−0.042
	Predation	0.004	−0.029	−0.037	−0.002	−0.199
Third instar	Dislodgement	0.037	0.251	**0.450**	–	–
	Predation	0.037	0.036	0.027	0.148	0.329
Fourth instar	Dislodgement	0.045	0.266	0.416	**0.557**	–
	Predation	**0.35**	–	–	–	–
	Parasitism	**0.363**	–	–	–	–
60% SWD						
Egg	Dislodgement	0.065	0.108	0.192	0.279	0.272
	Predation	0.001	0.005	0.009	0.008	0.025
	Inviability	0.016	0.038	0.05	0.064	0.083
First instar	Dislodgement	0.112	0.162	0.192	**0.344**	
	Predation	0.009	0.002	0.004	0.012	0.036
Second instar	Dislodgement	0.004	0.018	0.027	0.037	0.013
	Predation	0.013	0.015	0.001	0.027	0.035
Third instar	Dislodgement	0.049	0.105	0.207	0.152	**0.425**
	Predation	0.052	0.052	0.049	0.068	0.104
Fouth instar	Dislodgement	0.09	0.162	**0.263**	–	–
	Predation	**0.363**	–	–	–	–
	Parasitism	0.222	**0.327**	–	–	–

Values represent the slope of the regression of individual k-values on total K (−ln of generational survival). The factor with the highest slope (key factor in bold type) is eliminated in each subsequent step in order to estimate the relative effect of each factor on overall variation in generational survival.

irreplaceable mortality from any mortality factor [$F(2, 34) < 2.41$, $P > 0.10$] (Fig. 3B) and there were no interactions between natural enemy and plant quality treatments [$F(2, 45) < 1.86$, $P > 0.18$].

Discussion

We used a combination of experimental manipulation and life table analyses to evaluate the relative impact of the top-down influences of natural enemies and the bottom-up effects of plant quality on mortality of *B. tabaci* (MEAM1). We show that natural enemies, mainly predators and, to a much lesser extent, parasitoids, are exerting significant top-down mortality on *B. tabaci* (MEAM1) in cotton regardless of levels of plant quality. These effects translated into increased survivorship of *B. tabaci* (MEAM1) when natural enemy densities were reduced, irrespective of plant quality. Irrigation changed the plant environment in important ways, and we presume these changes are reflected in the quality of the plant relative to whitefly biology. Such changes have been shown to influence whitefly behaviour and population dynamics (Hilje *et al*., 2001; Chilcutt *et al*., 2005). However, plant quality effects on whitefly population dynamics were weak and observed only one-third of the time, mostly as elevated densities on deficit-irrigated plants (Asiimwe *et al*., 2013). The lack of interaction between

Table 2. Key factor analysis of life tables over nine generations of immature *Bemisia tabaci* (MEAM1) pooled over all plant quality treatments for each natural enemy treatment (Maricopa, Arizona).

		Iteration				
Stage	Factor	1	2	3	4	5
Control						
Egg	Dislodgement	0.066	0.265	0.239	**0.443**	–
	Predation	0.004	0.011	0.02	0.021	0.047
	Inviability	0.004	0.006	−0.011	0.004	0.011
First instar	Dislodgement	0.154	**0.392**	–	–	–
	Predation	0.004	0.029	0.035	0.058	0.069
Second instar	Dislodgement	−0.006	−0.018	−0.022	−0.028	0.103
	Predation	0.001	0.001	−0.021	0.022	0.129
Third instar	Dislodgement	0.015	0.101	**0.336**	–	–
	Predation	0.035	0.09	0.121	0.186	0.293
Fourth instar	Dislodgement	0.035	0.126	0.317	0.31	**0.489**
	Predation	**0.348**	–	–	–	–
	Parasitism	**0.339**	–	–	–	–
Natural enemies reduced						
Egg	Dislodgement	0.084	0.115	0.136	0.209	0.202
	Predation	−0.007	0.012	0.012	0.024	0.039
	Inviability	0.024	0.036	0.046	0.081	0.087
First instar	Dislodgement	0.1	0.15	0.274	**0.312**	–
	Predation	−0.008	−0.008	−0.008	−0.002	−0.004
Second instar	Dislodgement	0.006	0.013	0.024	0.043	0.013
	Predation	−0.014	−0.016	−0.011	−0.008	0.018
Third instar	Dislodgement	0.142	0.18	0.124	0.306	**0.615**
	Predation	0.026	0.031	0.046	0.043	0.034
Fourth instar	Dislodgement	0.198	**0.249**	–	–	–
	Predation	**0.256**	–	–	–	–
	Parasitism	0.18	0.239	**0.362**	–	–

Values represent the slope of the regression of individual *k*-values on total *K* (−ln of generational survival). The factor with the highest slope (key factor in bold type) is eliminated in each subsequent step in order to estimate the relative effect of each factor on overall variation in generational survival.

plant quality and natural enemy treatments further indicates that plant quality did not influence natural enemy impacts. Thus, our prediction that lower plant quality would negatively affect herbivore regulation as supplied by natural enemy mortality was not supported.

Marginal mortality rates, key factor and irreplaceable mortality analyses collectively provided further insight into the relative importance of individual sources of mortality to immature mortality. Sucking predation supplied the highest rates of marginal and irreplaceable mortality across all levels of plant quality but was diminished in treatments where natural enemies were deliberately reduced with insecticides. Consistent with this, key factor analyses showed that predation was generally the primary mortality factor responsible for changes in immature mortality across all treatments. Parasitism was the secondary key mortality factor followed by dislodgement of various life stages. These findings corroborate those of Naranjo & Ellsworth (2005) in unsprayed cotton at the same general study location. Consistent with the current study, predation was due to the action of sucking predators, while dislodgement reflected the effects of chewing predators and weather, particularly rain and dust storms (Naranjo & Ellsworth, 2005). The reduction of natural enemy densities due to insecticides and consequent decline in predation rates led to increased survivorship and concomitant outbreak levels of *B. tabaci* (Asiimwe *et al.*, 2013), indicating the important role that predators play in conservation biological control of this pest in cotton (Naranjo & Ellsworth, 2009a, 2009b).

Our results emphasised the greater role that predation plays over parasitism in this system. The sucking predators typical in this system are generalists feeding on a suite of prey, including *Lygus hesperus* (Knight) (Miridae) and spider mites, which were prevalent in this study (Asiimwe *et al.*, 2013; 2014). Any accompanying changes in the dynamics of these alternative prey might alter the functional contribution of these predators to whitefly suppression either positively or negatively. We observed higher densities of *L. hesperus* in the well-irrigated plants (Asiimwe *et al.*, 2014), and higher spider mite densities in the deficit-irrigated plants (Asiimwe *et al.*, 2013), both of which potentially make these respective treatments more attractive for the generalist predators. This is in contrast to aphelinid parasitoids, which lack alternate hosts due to their specialisation on whiteflies, and are relatively poor dispersers (Naranjo *et al.*, 2009).

Life table methods have been used to understand the relative roles that plant factors or natural enemies play in mortality of insect herbivores (Hunter, 2001; Walker & Jones, 2001). These studies have produced varying results depending on feeding site, with natural enemies having a greater influence on exophytic insect herbivores and plant factors dominating

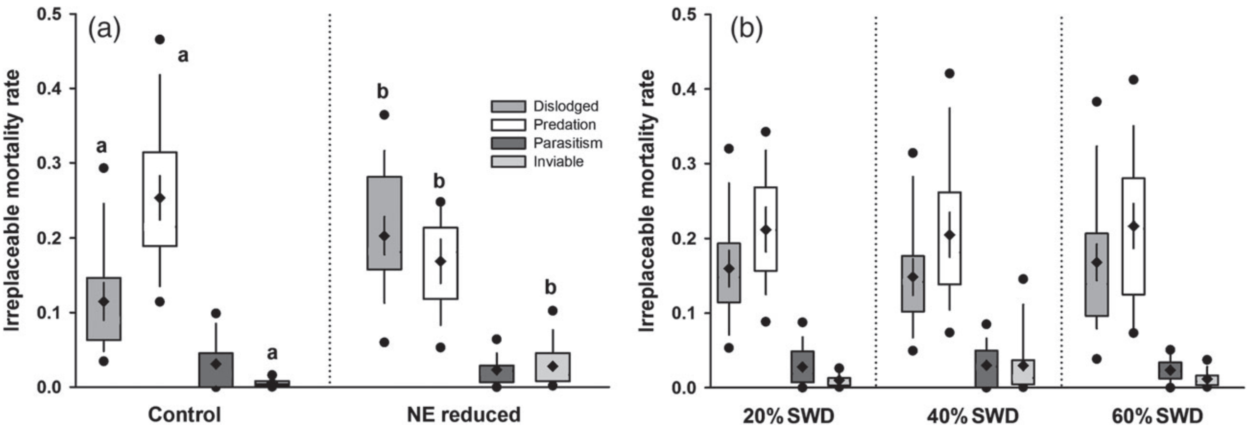

Fig. 3. Main effect box plots for irreplaceable mortality rates for immature *Bemisia tabaci* (MEAM1) caused by various factors. Natural enemy treatments (a) and cotton irrigation regimes [20%, 40% and 60% soil water depletion (SWD)] (b) shown over nine generations in 3 years (2008–2010). Different letters within a mortality factor denote statistical significance ($P < 0.05$); bars without letters did not differ significantly. Control, natural enemies unaltered; NE reduced, natural enemies reduced with acephate sprays. For plots, diamonds with error bars denote the mean and SEM, the box denotes 25th and 75th percentiles, whiskers denote 10th and 90th percentiles and points depict 5th and 95th percentiles.

in endophytic herbivores (Cornell & Hawkins, 1995). This pattern holds here, where mortality of the exophytic *B. tabaci* (MEAM1) is mainly influenced by predators. Plant effects on herbivore mortality are often associated with antibiosis, which is usually expressed as a reduction in survival, longer development times and feeding failure (Cornell & Hawkins, 1995; Walker & Jones, 2001). Using differential irrigation regimes, we were able to significantly manipulate plant quality, as evidenced by differences in height and canopy temperature, which have been shown to affect abundance and performance of *B. tabaci* and its natural enemies on cotton (Gerling *et al.*, 1986; Skinner, 1996b; Hilje *et al.*, 2001; Chilcutt *et al.*, 2005; Asiimwe *et al.*, 2013). Here, the only change in survival rates of *B. tabaci* (MEAM1) due to plant quality was observed for eggs, where survival was greater in deficit irrigation treatments. This was consistent with our population data, which showed higher egg densities with increasing deficits in irrigation in some years (Asiimwe *et al.*, 2013). Antibiosis or other plant-based effects did not appear to influence developmental rate. Nymphal cohorts were typically completed in about 2 weeks with no clear effects of irrigation treatments (data not shown). However, our findings on plant quality could have been confounded by outbreaks of spider mites and whiteflies when natural enemy densities were reduced and in the deficit-irrigated plants (Asiimwe *et al.*, 2013). These outbreaks resulted in premature defoliation and possible negative feedback effects on plant qualities that were not directly quantified. In addition, the presence of *L. hesperus* could have affected fruiting patterns, and resource partitioning potentially affected the quality of the plants for whiteflies. Overall, these factors, individually or collectively, could have influenced our findings by affecting plant quality in unintended ways. Nonetheless, our findings are consistent with Walker & Jones (2001) and Cornell & Hawkins (1995), showing that plant effects are rarely the primary source of mortality during immature stages.

Despite evidence from our study that the top-down influences of natural enemies are dominant in this system, we did not explicitly measure fecundity and thus might have underestimated the bottom-up effects of plant quality. We also did not measure mortality in the adult stage. Denno & Peterson (2000) argued that mobile and highly fecund phytophagous insects, such as adults of *B. tabaci* (MEAM1), are more likely to benefit from improved plant quality through rapid population growth and consequent escape from natural enemies. However, *B. tabaci* (MEAM1) is a multi-voltine insect with overlapping generations, and mortality of immature stages ultimately impacts within-season adult abundance during a large portion of the season when emigration and immigration are minimal (Naranjo & Ellsworth, 2005). The patterns of mortality and survival observed here were consistently reflected in densities of all stages, with significantly higher egg, nymph and adult densities when natural enemy densities were reduced (Asiimwe *et al.*, 2013).

Conclusion

Agro-ecosystems are highly managed systems characterised by a narrow range of genotypes or phenotypes, specific and targeted application of production inputs such as water, fertilisers and pesticides, and defined growing periods. These factors interact to determine pest densities and, subsequently, damage incurred from pests. In the cotton system, natural enemies have a major impact on the mortality of immature *B. tabaci* and are contributing to biological control and management of this key pest (Naranjo *et al.*, 2004a; Naranjo & Ellsworth, 2005; 2009a,2009b). We extended these findings by investigating the dual role that plant quality, as a result of irrigation, could potentially have on survival of *B. tabaci* (MEAM1), directly and indirectly, by mediating the effects of natural enemies in the field. Our results show that top-down effects of natural enemies, particularly generalist predators, dominate mortality of *B. tabaci* (MEAM1) and their impact is not influenced by the bottom-up effects of plant quality, thus validating the importance of conservation biological control for the management of populations of *B. tabaci* (MEAM1) in cotton.

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References

Abrahamson, W.G. & Weis, A.E. (1997) *Evolutionary Ecology across Three Trophic Levels: Goldenrods, Gallmakers, and Natural Enemies*. *Monographs in Population Biology,* Vol. 29. Princeton University Press, Princeton, New Jersey.

Asiimwe, P., Ecaat, J.S., Otim, M., Gerling, D., Kyamanywa, S. & Legg, J.P. (2007) Life-table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda. *Entomologia Experimentalis et Applicata*, **122**, 37–44.

Asiimwe, P., Naranjo, S.E. & Ellsworth, P.C. (2013) Relative influence of plant quality and natural enemies on the seasonal dynamics of *Bemisia tabaci* in cotton. *Journal of Economic Entomology*, **106**, 1260–1273.

Asiimwe, P., Naranjo, S.E. & Ellsworth, P.C. (2014) Effects of irrigation levels on interactions among Lygus hesperus (Hemiptera: Miridae), insecticides, and predators in cotton. *Environmental Entomology*, **43**, 263–273.

Benrey, B. & Denno, R.F. (1997) The slow-growth-high-mortality hypothesis: a test using the cabbage butterfly. *Ecology*, **78**, 987–999.

Bentz, J.A., Reeves, J., Barbosa, P. & Francis, B. (1996) The effect of nitrogen fertilizer applied to *Euphorbia pulcherrima* on the parasitization of *Bemisia argentifolii* by the parasitoid *Encarsia formosa*. *Entomologia Experimentalis et Applicata*, **78**, 105–110.

Bi, J.L., Ballmer, G.R., Hendrix, D.L., Henneberry, T.J. & Toscano, N.C. (2001) Effect of cotton nitrogen fertilization on *Bemisia argentifolii* populations and honeydew production. *Entomologia Experimentalis et Applicata*, **99**, 25–36.

Bi, J.L., Toscano, N.C. & Madore, M.A. (2003) Effect of urea fertilizer application on soluble protein and free amino acid content of cotton petioles in relation to silverleaf whitefly (*Bemisia argentifolii*) populations. *Journal of Chemical Ecology*, **29**, 747–761.

Bi, J.L., Lin, D.M., Lii, K.S. & Toscano, N.C. (2005) Impact of cotton planting date and nitrogen fertilization on *Bemisia argentifolii* populations. *Insect Science*, **12**, 31–36.

Buonaccorsi, J.P. & Elkinton, J.S. (1990) Estimation of contemporaneous mortality factors. *Researches on Population Ecology*, **32**, 151–171.

Carey, J.R. (1989) The multiple decrement life table: a unifying framework for cause-of-death analysis in ecology. *Oecologia*, **78**, 131–137.

Chilcutt, C.F., Wilson, L.T., Lascano, R., Bronson, K.F. & Booker, J. (2005) Scaling and the effects of plant, soil and landscape characteristics on sap-feeding herbivores in cotton. *Environmental Entomology*, **34**, 75–86.

Clancy, K.M. & Price, P.W. (1987) Rapid herbivore growth enhances enemy attack – Sublethal plant defenses remain a paradox. *Ecology*, **68**, 733–737.

Cornell, H.V. (1990) Survivorship, life-history, and concealment-a comparison of leaf miners and gall formers. *American Naturalist*, **136**, 581–597.

Cornell, H.V. & Hawkins, B.A. (1995) Survival patterns and mortality sources of herbivorous insects – some demographic-trends. *American Naturalist*, **145**, 563–593.

Cornell, H.V., Hawkins, B.A. & Hochberg, M.E. (1998) Towards an empirically-based theory of herbivore demography. *Ecological Entomology*, **23**, 340–349.

Costamagna, A.C. & Landis, D.A. (2006) Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. *Ecological Applications*, **16**, 1619–1628.

Damman, H. (1987) Leaf quality and enemy avoidance by the larvae of a pyralid moth. *Ecology*, **68**, 88–97.

Daugherty, M.P., Briggs, C.J. & Welter, S.C. (2007) Bottom-up and top-down control of pear psylla (*Cacopsylla pyricolla*): fertilization, plant quality, and the efficacy of the predator *Anthocoris nemoralis*. *Biological Control*, **43**, 257–264.

Denno, R.F. & Peterson, M.A. (2000) Caught between the devil and the deep blue sea, mobile plant hoppers elude natural enemies and deteriorating host plants. *American Entomologist*, **46**, 95–109.

Denno, R.F., McClure, M.S. & Ott, J.R. (1995) Interspecific interactions in phytophagous insects: competition revisited and resurrected. *Annual Review of Entomology*, **40**, 297–331.

Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L. & Huberty, A.F. (2002) Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology*, **83**, 1443–1458.

Dinsdale, A., Cook, L., Riginos, C., Buckley, Y.M. & De Barro, P. (2010) Refined global analysis of *Bemisia tabaci* (Hemiptera: Sternorrhyncha: Aleyrodoidea: Aleyrodidae) mitochondrial cytochrome oxidase 1 to identify species level genetic boundaries. *Annals of the Entomological Society of America*, **103**, 196–208.

Dyer, L.A. & Letourneau, D.K. (1999) Relative strengths of top-down and bottom-up forces in a tropical forest community. *Oecologia*, **119**, 265–274.

Dyer, L.A. & Stireman, J.O. (2003) Community-wide trophic cascades and other indirect interactions in an agricultural community. *Basic and Applied Ecology*, **4**, 423–432.

Elkinton, J.S., Buonaccorsi, J.P., Bellows, T.S. & Vandriesche, R.G. (1992) Marginal attack rate, k-values and density dependence in the analysis of contemporaneous mortality factors. *Researches on Population Ecology*, **34**, 29–44.

Ellsworth, P.C., Bradley, J.R., Kennedy, G.G., Patterson, R.P. & Stiner, R.E. (1992) Irrigation effects on European corn borer-maize water relations. *Entomologia Experimentalis et Applicata*, **64**, 11–21.

Ellsworth, P.C., Naranjo, S.E., Castle, S.J., Hagler, J.R. & Henneberry, T.J. (1998) Whitefly management in Arizona: looking at the whole system. *Cotton, A College of Agriculture Report*, Series P112, pp. 311–318. University of Arizona, Tucson, Arizona.

Finke, D.L. & Denno, R.F. (2002) Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology*, **83**, 643–652.

Flint, H.M., Wilson, F.D., Hendrix, D., Leggett, J., Naranjo, S.E., Henneberry, T.J. *et al.* (1994) The effect of plant water-stress on beneficial and pest insects including the pink-bollworm and the sweet-potato whitefly in 2 short-season cultivars of cotton. *Southwestern Entomologist*, **19**, 11–22.

Flint, H.M., Naranjo, S.E., Leggett, J.E. & Henneberry, T.J. (1996) Cotton water stress, arthropod dynamics, and management of *Bemisia tabaci* (Homoptera: Aleyrodidae). *Journal of Economic Entomology*, **89**, 1288–1300.

Forkner, R.E. & Hunter, M.D. (2000) What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology*, **81**, 1588–1600.

Gerling, D., Horowitz, A.R. & Baumgaertner, J. (1986) Autecology of *Bemisia tabaci*. *Agriculture, Ecosystems and Environment*, **17**, 5–19.

Giles, K.L., Madden, R.D., Stockland, R., Payton, M.E. & Dillwith, J.W. (2002) Host plants affect predator fitness via the nutritional value of herbivore prey: investigation of a plant-aphid-lady-beetle system. *Biocontrol*, **47**, 1–21.

Gillespie, D.R. & McGregor, R.R. (2000) The functions of plant feeding in the omnivorous predator *Dicyphus hesperus*: water places limits on predation. *Ecological Entomology*, **25**, 380–386.

Gratton, C. & Denno, R.F. (2003) Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. *Oecologia*, **134**, 487–495.

Gripenberg, S. & Roslin, T. (2007) Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. *Oikos*, **116**, 181–188.

Harcourt, D.G. (1966) Major factors in survival of immature stages of *Pieris rapae* (L). *Canadian Entomologist*, **98**, 653–662.

Harvey, J.A., Harvey, I.F. & Thompson, D.J. (1995) The effect of host nutrition on growth and development of the parasitoid wasp *Venturia canescens*. *Entomologia Experimentalis et Applicata*, **75**, 213–220.

Harvey, J.A., van Dam, N.M. & Gols, R. (2003) Interactions over four trophic levels: food plant quality affects the development of a hyper-parasitoid as mediated through a herbivore and its primary parasitoid. *Journal of Animal Ecology*, **72**, 520–531.

Hassell, M.D. & Southwood, T.R.E. (1978) Foraging strategies of insects. *Annual Review of Ecology and Systematics*, **9**, 75–98.

Havill, N.P. & Raffa, K.F. (2000) Compound effects of induced plant responses on insect herbivores and parasitoids: implications for tri-trophic interactions. *Ecological Entomology*, **25**, 171–179.

Hilje, L., Costa, H.S. & Stansly, P.A. (2001) Cultural practices for managing *Bemisia tabaci* and associated viral diseases. *Crop Protection*, **20**, 801–812.

Huberty, A.F. & Denno, R.F. (2004) Plant water stress and its consequences for herbivorous insects: a new synthesis. *Ecology*, **85**, 1383–1398.

Hunter, M.D. (2001) Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: experiments, life tables, and time-series analysis. *Basic and Applied Ecology*, **2**, 295–309.

Hunter, M.D. & Price, P.W. (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., Varley, G.C. & Gradwell, G.R. (1997) Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 9176–9181.

Karut, K. & Naranjo, S.E. (2009) Mortality factors affecting *Bemisia tabaci* populations on cotton in Turkey. *Journal of Applied Entomology*, **133**, 367–374.

King, B.H. (2002) Offspring sex ratio and number in response to proportion of host sizes and ages in the parasitoid wasp *Spalangia cameroni*. *Environmental Entomology*, **31**, 505–508.

Larsson, S. (1989) Stressful times for the plant stress: insect performance hypothesis. *Oikos*, **56**, 277–283.

Lill, J.T., Marquis, R.J. & Ricklefs, R.E. (2002) Host plants influence parasitism of forest caterpillars. *Nature*, **417**, 170–173.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute Inc., Cary, North Carolina.

Loader, C. & Damman, H. (1991) Nitrogen content of food plants and vulnerability of *Pieris rapae* to natural enemies. *Ecology*, **72**, 1586–1590.

Mattson, W.J. & Haack, R.A. (1987) The role of drought in outbreaks of plant-eating insects. *Bioscience*, **37**, 110–118.

McKenzie, S.W., Hentley, W.T., Hails, R.S., Jones, T.H., Vanbergen, A.J. & Johnson, S.N. (2013) Global climate change and above–belowground insect herbivore interactions. *Frontiers in Plant Science*, **4**, 412.

McMillin, J.D. & Wagner, M.R. (1998) Influence of host plant vs. natural enemies on the spatial distribution of a pine sawfly, *Neodiprion autumnalis*. *Ecological Entomology*, **23**, 397–408.

Moon, D.C. & Stiling, P. (2002) The effects of salinity and nutrients on a tritrophic salt-marsh system. *Ecology*, **83**, 2465–2476.

Naranjo, S.E. (2007) Survival and movement of *Bemisia tabaci* (Homoptera: Aleyrodidae) crawlers on cotton. *Southwestern Entomologist*, **32**, 17–23.

Naranjo, S.E. & Ellsworth, P.C. (2005) Mortality dynamics and population regulation in *Bemisia tabaci*. *Entomologia Experimentalis et Applicata*, **116**, 93–108.

Naranjo, S.E. & Ellsworth, P.C. (2009a) The contribution of conservation biological control to integrated control of *Bemisia tabaci* in cotton. *Biological Control*, **51**, 458–470.

Naranjo, S.E. & Ellsworth, P.C. (2009b) 50 Years of the integrated control concept: moving the model and implementation forward in Arizona. *Pest Management Science*, **65**, 1267–1286.

Naranjo, S.E., Cañas, L.A. & Ellsworth, P.C. (2004a) Mortalidad de *Bemisia tabaci* un sistema de cultivos multiples [Mortality of *Bemisia tabaci* in a multiple crop system]. *International Journal of Horticultural Science*, **43**, 14–21.

Naranjo, S.E., Ellsworth, P.C. & Hagler, J.R. (2004b) Conservation of natural enemies in cotton: role of insect growth regulators in management of *Bemisia tabaci*. *Biological Control*, **30**, 52–72.

Naranjo, S.E., Cañas, L.A. & Ellsworth, P.C. (2009) Mortality and population dynamics of *Bemisia tabaci* within a multi-crop system. *Proceedings of the Third International Symposium on Biological Control of Arthropods, Christchurch, New Zealand* (ed. by P. G. Mason, D. R. Gillespie and C. D. Vincent), Publication FHTET-2008-06, pp. 202–207. USDA Forest Service, Morgantown, West Virginia.

Pandey, S. & Singh, R. (1999) Host size induced variation in progeny sex ratio of an aphid parasitoid *Lysiphlebia mirzai*. *Entomologia Experimentalis et Applicata*, **90**, 61–67.

Podoler, H. & Rogers, D. (1975) A new method for the identification of key factors from life-table data. *Journal of Animal Ecology*, **44**, 85–114.

Preszler, R.W. & Price, P.W. (1988) Host quality and sawfly populations-A new approach to life table analysis. *Ecology*, **69**, 2012–2020.

Price, J.F. & Taborsky, D. (1992) Movement of immature *Bemisia tabaci* (Homoptera: Aleyrodidae) on poinsettia leaves. *Florida Entomologist*, **75**, 151–153.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weiss, A.E. (1980) Interaction among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecological Systems*, **11**, 41–65.

Richmond, D.S., Kunkel, B.A., Somasekhar, N. & Grewal, P.S. (2004) Top-down and bottom-up regulation of herbivores: *Spodoptera* *frugiperda* turns tables on endophyte-mediated plant defense and virulence of an entomopathogenic nematode. *Ecological Entomology*, **29**, 353–360.

Royama, T. (1981) Evaluation of mortality factors in insect life table analysis. *Ecological Monographs*, **51**, 495–505.

Ryalls, J.M.W., Moore, B.D., Riegler, R., Gherlenda, A.N. & Johnson, S.N. (2015) Amino acid-mediated impacts of elevated carbon dioxide and simulated root herbivory on aphids are neutralized by increased air temperatures. *Journal of Experimental Botany*, **66**, 613–623.

Seagraves, M.P., Riedell, W.E. & Lundgren, J.G. (2011) Oviposition preference for water stressed plants in *Orius insidiosus* (Hemiptera: Anthocoridae). *Journal of Insect Behavior*, **24**, 132–143.

Silvertooth, J. C. (2001) Determining height to node ratios in cotton. University of Arizona Cooperative Extension Bulletin No. AZ1210.

Simmons, A.M. (2002) Settling of crawlers of *Bemisia tabaci* (Homoptera: Aleyrodidae) on five vegetable hosts. *Annals of the Entomological Society of America*, **95**, 464–468.

Skinner, R.H. (1996a) Response of *Bemisia argentifolii* (Homptera: Aleyrodidae) to water and nutrient stressed cotton. *Environmental Entomology*, **25**, 401–406.

Skinner, R.H. (1996b) Leaf temperature effects on *Bemisia argentifolii* (Homoptera: Aleyrodidae) oviposition. *Environmental Entomology*, **25**, 1371–1375.

Smith, R.H. (1973) The analysis of intra-generation changes in animal populations. *Journal of Animal Ecology*, **42**, 611–622.

Southwood, T.R.E. (1978) *Ecological Methods*, 2nd edn. Chapman and Hall, London, U.K.

Stein, S.J. & Price, P.W. (1995) Relative effects of plant-resistance and natural enemies by plant developmental age on sawfly (Hymenoptera, Tenthredinidae) preference and performance. *Environmental Entomology*, **24**, 909–916.

Stiling, P. (1988) Density-dependent processes and key factors in insect populations. *Journal of Animal Ecology*, **57**, 581–593.

Stiling, P. & Rossi, A.M. (1997) Experimental manipulations of top-down and bottom-up factors in a tri-trophic system. *Ecology*, **78**, 1602–1606.

Turlings, T.C.J. & Wackers, F.L. (2004) Recruitment of predators and parasitoids by herbivore-injured plants. *Advances in Insect Chemical Ecology* (ed. by R. T. Carde and J. Millar), pp. 21–75. Cambridge University Press, Cambridge, U.K.

Varley, G.C. & Gradwell, G.R. (1960) Key factors in population studies. *Journal of Animal Ecology*, **29**, 399–401.

Walde, S.J. (1995) How quality of host plant affects a predator-prey interaction in biological control. *Ecology*, **76**, 1206–1219.

Walker, M. & Jones, T.H. (2001) Relative roles of top-down and bottom-up forces in terrestrial tritrophic plant-insect herbivore-natural enemy systems. *Oikos*, **93**, 177–187.

Walker, M., Hartley, S.E. & Jones, T.H. (2008) The relative importance of resources and natural enemies in determining herbivore abundance: thistles, tephritids and parasitoids. *Journal of Animal Ecology*, **77**, 1063–1071.

Waring, G.L. & Cobb, N.S. (1992) The impact of plant stress on herbivore population dynamics. *Insect Plant Interactions*, Vol. **4** (ed. by E. Bernays), pp. 167–187. CRC Press, Boca Raton, Florida.

West, S.A., Flanagan, K.E. & Godfray, H.C.J. (2001) Variable host quality, life-history invariants, and the reproductive strategy of a parasitoid that produces single sex clutches. *Behavioral Ecology*, **12**, 577–583.

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.

Williams, I.S. (1999) Slow-growth, high-mortality-a general hypothesis, or is it? *Ecological Entomology*, **24**, 490–495.

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