Mortality factors affecting *Bemisia tabaci* populations on cotton in Turkey

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Keywords
Bemisia tabaci, key-factor, life-table, marginal mortality, parasitism, predation

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Received: June 25, 2008; accepted: November 13, 2008.

doi: 10.1111/j.1439-0418.2008.01369.x

Abstract

Cohort-based, partial life tables were constructed to determine the sources and rates of mortality factors affecting *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) on cotton in the eastern Mediterranean region of Turkey over a two year period. Mortality factors were recorded as due to predation, parasitism, dislodgement and unknown for five developmental stages. Across 10 independent cohorts, the highest median rate of marginal mortality pooled over all stages was attributed to parasitism (0.69) followed by predation (0.67). The key factor was hypothesized to be parasitism based on graphical and regression-based comparison of individual factor *k*-values to total generational mortality. The greatest amount of marginal immature mortality occurred during the fourth nymphal stadium (median = 0.77) and mortality during this stage was also most predictive of variation in total mortality. Pooled over all developmental stages, the highest rates of irreplaceable mortality were associated with parasitism (median: 0.112), followed by predation (0.088), dislodgement (0.020) and unknown (0.017). Although crawler mortality was not explicitly measured, sensitivity analyses indicated that mortality during this stage would have changed total mortality by only 0.45–1.21% and had no effect on identification of key factors. There was no significant effect of cotton cultivar on any mortality factor or total mortality over the two years of study. Results suggest that conservation of natural enemies, particularly parasitoids, may provide for more sustainable management of *B. tabaci* on cotton in Turkey.

Introduction

The Çukurova plain of Adana, located in eastern Mediterranean region of Turkey, is one of the largest cotton growing area of the country with approximately 126 000 ha devoted to irrigated and non-irrigated cotton cultivation (Anonymous 2004). Insect pest problems have increased steadily with the inception of irrigated cotton cultivation in this region (Şengonca 1982). Following outbreaks of *Bemisia tabaci* (Gennadius) (Hom.: Aleyrodidae) in 1974, this insect has became the most important pest in cotton under irrigated conditions (Şengonca 1975). Yield losses occur as a result of feeding injury and honeydew contamination of the cotton lint. Control of *B. tabaci* has most often relied upon insecticide applications that, in addition to disrupting potential biological control agents, also often leads to the development of resistance. Since 1974, numerous studies on population dynamics, population development and parasitism of *B. tabaci* have been conducted on cotton in the Çukurova plain. For example Özgur and Şekeroglu (1986) found that population development of *B. tabaci* on glabrous

cotton cultivars with either small or okra-leaf shapes or more open canopy structures were lower than on cultivars with large pubescent leaves and more closed canopy. Özgür et al. (1989) reported that the bulk of the *B. tabaci* population overwinters in the foothills outside the Çukurova plain mainly on *Cistus* spp. and then migrate in the spring into cultivated areas. Karut and Akdağcık (2006) found that although percent parasitism rates varied among sampled fields and sites, *Eretmocerus mundus* Mercet and *Encarsia lutea* (Masi) (Hymenoptera: Aphelinidae) are the most abundant parasitoids of *B. tabaci* in Turkish cotton fields with percent parasitism reaching 71.4% and 77.6% in sprayed and un-sprayed fields respectively.

As part of the development of sustainable pest management, biological control has been studied as an alternative method for *B. tabaci* control in Turkey since 1976 (Kaygısız 1976). Biological control of *B. tabaci* has been investigated as a management component in other parts of the world since the early 1900's, although a steady increase in effort has only been realized since the 1980's (Naranjo 2001). Considerable research has focused on understanding population dynamics and biological control of *B. tabaci* and in developing pest management systems mainly in the USA and Israel (Riley et al. 1996; Ellsworth and Martinez-Carrillo 2001; Gerling et al. 2001; Naranjo 2001), but there is a need to better understand the mortality factors affecting *B. tabaci* populations on cotton in Turkey. The construction of life tables is vital to the description and understanding of the mortality factors in a population. Such analyses are not only of considerable theoretical interest, but also may eventually provide a rational and predictive basis for pest control (Southwood 1978).

The aim of the this study was to construct partial, cohort-based life tables for *B. tabaci* in order to understand specific mortality factors affecting each immature stage in a major cotton production region of Turkey and to compare and contrast results with other cotton production regions of the world. This information will provide essential background for developing effective and more sustainable pest managenet systems to control *B. tabaci* populations.

Materials and Methods

Study sites

Studies were conducted in 2002 and 2003 in cotton plots in Balcalı, [Çukurova University, Agricultural Faculty Research Farm, Adana (37.00°N, 35.18°E)] and in Hacıali [Çukurova Agricultural Research Institute, Adana (36.79°N, 35.29°E)]. At the Balcalı site studies were conducted as part of an on-going experiment arranged in a randomized complete block with three treatments and four replicates. The treatments were the cotton varieties 'Lachata', 'Sg125' and 'Ç-1518'. Plots were 10 rows wide and 10 m long with 2 m spacing between plots. Cotton was planted on 5 May in 2002. The same design and cultivars were established on 5 April at this site in 2003.

At the Hacıali site, studies were carried out in a single 3 ha and 0.5 ha cotton field in 2002 and 2003, respectively. Seeds of a single variety 'Sg125' were planted in 80 cm rows in early May in both years. No insecticides were applied to cotton in either year at either site. Irrigation, fertilization and other cultural practices were done according to standard local practices.

Cohort establishment

The methods described by Naranjo and Ellsworth (2005) were used to establish cohorts of immature *B. tabaci* in the field. Briefly, for each replicate plot in Balcali 10–19 newly laid eggs (<1 day old) were identified on the underside of leaves and a small circle was drawn around the insect using a non-toxic, ultra-fine- point black permanent pen (Sanford, Bellwood, IL, USA) with the aid of a 10× hand lens (Ward's Natural Science, Rochester, NY, USA). At the Haciali site 30–46 eggs were marked per field. No more than five eggs were marked per leaf and no more than one leaf was marked per plant. A small numbered tag was placed around the petiole of the marked leaf, and another larger tag was tied to the top of the mainstem of the plant to facilitate relocation. Newly laid eggs were identified by their creamy-white colour and their location on leaves near the terminal or other new growth of the cotton plant (Naranjo and Ellsworth 2005).

A similar method was used to establish cohorts of settled 1st instar nymphs. At the Balcali site 10–22 nymphs were marked in each replicate plot; in Haciali 24–47 nymphs were marked per field. No more than four nymphs were marked on any one leaf and only a single leaf was used per plant. To verify that settled nymphs and not crawlers were marked, leaves were re-examined 1–2 h later (Naranjo and Ellsworth 2005). At the Balcali site, cohorts were established on 26 July and 15 August in 2002 and 11 June, 5 July and 1 August in 2003. At this site, separate cohorts were established in each of the four

replicate plots of each of the three varieties. At the Hacıali site cohorts were established in a single field on 8 July and 23 August in 2002 and on 9 June, 1 July and 5 August in 2003.

Mortality factors

After cohort establishment, nymphs and eggs were examined every 2–3 days in the field with aid of a 30× stereomicroscope (SD30; Olympus, Center Valley, PA, USA) until eggs enclosed or nymphs died or emerged as adults. At each examination, the instar of each live and dead nymph was recorded and the cause of death was determined for dead nymphs. Mortality was recorded as due to predation, parasitism, dislodgement and unknown. Predation was mainly due to predators with sucking mouthparts that emptied the contents of the prey leaving behind an empty nymphal cuticle or egg chorion (Naranjo and Ellsworth 2005). Parasitism was due to various aphelinid parasitoids (*Eretmocerus* and *Encarsia* spp.). These parasitoids may attack all nymphal stages (Foltyn and Gerling 1985; Headrick et al. 1995; Liu and Stansly 1996) but outward signs of parasitism in the field can only be detected in the 4th nymphal stadium through the presence of displaced host mycetomes, or parasitoid larvae or pupae within the host. The unknown category covers mortality that could not be attributed to one of the other obvious causes of death, including egg inviability, parasitoid host-feeding, insect pathogens or physiological mortality. Dislodgement represents mortality associated with weather, chewing predator or other factors. The mortality of the early first instar stage known as the crawler, a semi-mobile stage, was not examined. The crawler stage is very short in duration (Price and Taborsky 1992) and is likely subjected to very low levels of mortality (Naranjo 2007). However, sensitivity analyses were conducted to evaluate the potential effect of crawler mortality on total generational mortality and key factor determination (see Sensitivity to crawler mortality section below).

Data analyses

Determination of marginal rates of mortality

Marginal rates of mortality were estimated for each mortality factor using the methods outlined by Buonaccorsi and Elkinton (1990) and Elkinton et al. (1992). Due to the nature of the interacting mortality forces in this system (Naranjo and Ellsworth 2005), the estimation of marginal rates of death, M_B, were simplified to the general equation

$$M_B = d_B/(1 - d_A).$$

Where A and B denote competing contemporaneous mortality factors, d_B is the apparent rate of mortality from B, and d_A is the sum of apparent mortalities from all other relevant, competing contemporaneous factors. Marginal rates of unknown mortality can be obscured by predation and dislodgement, and marginal rates of predation can be obscured by dislodgement. Marginal rates were calculated separately for each developmental stage to arrive at stage-specific rates. In the case of dislodgement, apparent and marginal rates of mortality are the same as nothing can obscure dislodgement. As noted above, parasitoids can attack all nymphal stages of *B. tabaci* but can only be detected in the field during the 4th stadium. Thus, in order to account for the obscuring effects of competing mortality factors on parasitism, the apparent rate d_A was estimated as the sum of predation and dislodgement over all nymphal stages combined.

Analysis of cultivar effects

As noted above, life table data at the Balcalı site were collected in replicate plots of three different cultivars using a randomized block design. A mixed-model ANOVA was conducted to examine the potential effects of cotton cultivar on total mortality and on mortality associated with each of the four mortality factors identified. Block (replicate) was entered as a random variable and cohort was nested within the cultivar for these analyses. Separate analyses were conducted for 2002 and 2003 and marginal mortality rates were transformed by arcsine√marginal mortality to meet the assumptions of normality and variance homogeneity. Analyses were conducted using JMP v.5 (SAS Institute, Cary, NC, USA).

Results of these analyses for the Balcali site showed no differences among cultivars and so to improve sample size the data were pooled across replicate plots and cultivar on each date (five total cohorts over 2 years). In Hacıali, five independent cohorts were established over the 2 years. All subsequent analyses were based on these 10 independent cohorts.

Determination of key factor

To determine the relative contribution made by individual mortality factors to the population dynamics of *B. tabaci*, key factor analyses was conducted using the Varley and Gradwell (1960) method, which compares patterns of the total mortality (total $K = \Sigma k$) to that of individual k-values where

$k = -\ln(1-M_B)$. To further quantify key factors, individual k-values were regressed against total K. The individual k- value that results in the largest slope value denotes the key factor (Podoler and Rogers 1975). Data over 10 cohorts were used to estimate the key factor.

Irreplaceable mortality

Irreplaceable mortality is that part of total generational mortality that would not occur if a given mortality factor was eliminated (Southwood 1978; Naranjo and Ellsworth 2005). Following the methods of Carey (1989) and Naranjo and Ellsworth (2005), irreplaceable mortality was estimated for each mortality factor and each development stage. The general equation for its calculation is:

$$\left(1-\prod_{1}^{j}[1-M_i]\right)-\left(1-\prod_{1}^{j-1}[1-M_i]\right)$$

where M_i is the marginal mortality rate for factor or stage i, and j is the total number of all mortality factors or development stages.

Sensitivity to crawler mortality

Because of the mobility of the crawler stage and the experimental techniques used in this study, mortality of this short duration stage was not measured directly. In order to evaluate the potential effects of this mortality component a sensitivity analyses was conducted based on reasonable assumptions of expected mortality rates for this stage. First it was assumed that the overall mortality rate of the crawler stage was similar to that of settled first-instar nymphs. A normal random number generator (http://www.wessa.net/rwasp_rngnorm.wasp, accessed 01 December 2008) was used to estimate rates of mortality for the crawler stage for each of the 10 independent cohorts based on the mean and SD from the N1 stage (0.257 and 0.105). A second set of expected crawler mortality rates were similarly estimated from Naranjo (2007) (mean = 0.10, SD = 0.041). Total generational mortality and key factor regressions were re-estimated after adding these additional mortality components.

Results

No differences were found among the three cultivars in either total generational mortality (2002, $F = 0.43$, d.f. = 2,15, $P = 0.65$; 2003, $F = 0.16$, d.f. = 2,24, $P = 0.85$) or in marginal rates of the four mortality factors recognized (2002, $F < 2.71$, d.f. = 2,15, $P > 0.09$; 2003, $F < 0.68$, d.f. = 2,24, $P > 0.52$). As a result, all further analyses were done independent of cultivar.

Marginal rates of mortality for each factor pooled over all immature life stages were highly variable (fig. 1a). The median rates of mortality were: parasitism (0.692), predation (0.671), dislodgement (0.339) and unknown (0.309). Similarly, pooled over all mortality factors there was considerable variation in marginal rates of mortality in each development stage (fig. 1b). The highest median rate of mortality was associated with the fourth nymphal stage [N4] (0.774), followed by egg (0.550), N1 (0.247), N3 (0.172) and N2 (0.149). The marginal rates of mortality in N1 and N3 were similar and less variable. Predation was the largest mortality factors in all life stages except N4 where parasitism was the greatest (fig. 2). The median total generational mortality was 0.957 over 10 cohorts. The addition of 10 and 25.7% additional mortality for the crawler stage raised total mortality to 0.961 (0.45% change) and 0.969 (1.21% change).

The mortality curve for parasitism was most similar to the total mortality curve (fig. 3a) and parasitism resulted in the largest regression slope (table 1) suggesting that it is the key factor. Likewise, mortality during the fourth stadium was most similar to

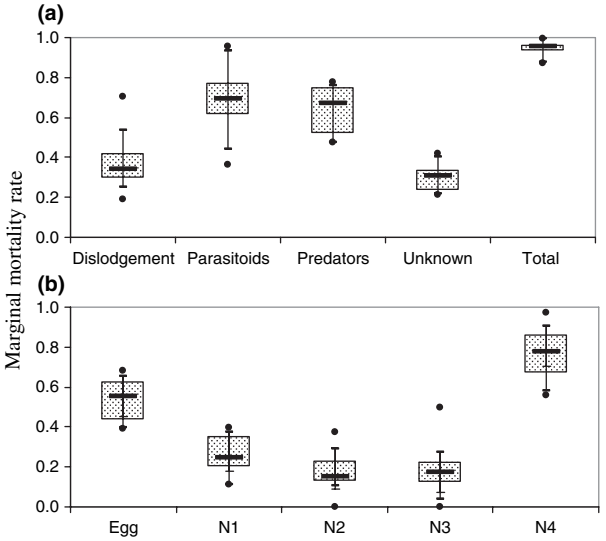

Fig. 1 (a) Box plots of marginal rates of mortality for *Bemisia tabaci* in cotton by mortality factors pooled over all stages; (b) box plots of marginal rates of mortality during each developmental period pooled over all mortality factors for 10 generations. Lines within boxes represent the median, the box bounds the 25th and 75th percentiles the whiskers denote the 10th and 90th percentiles, and points denote the range.

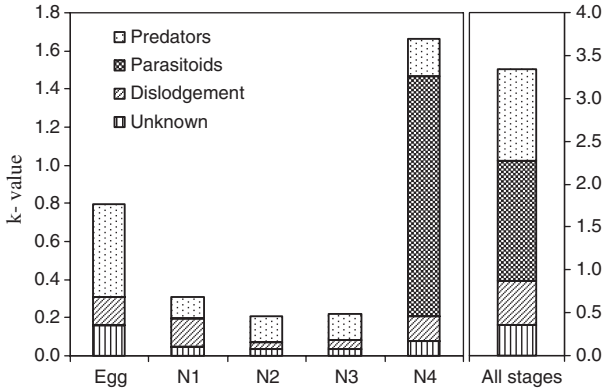

Fig. 2 Mean levels of mortality within each life stage and all immature stages combined expressed as *k*-values.

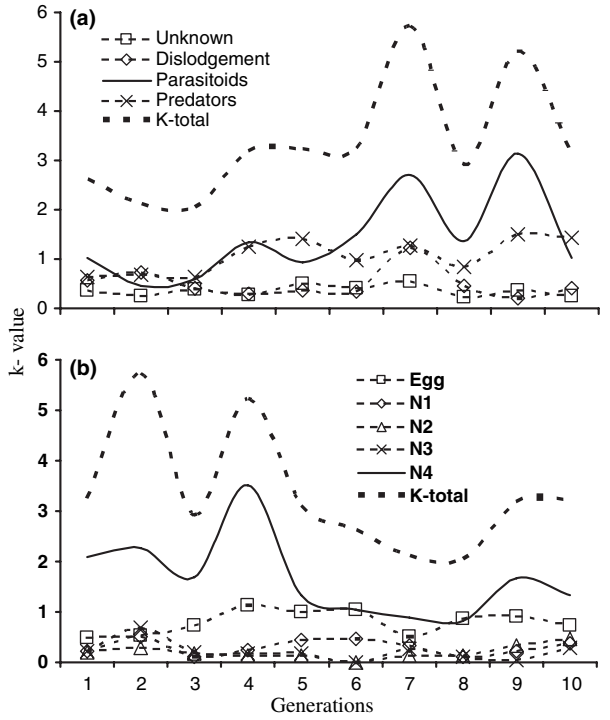

Fig. 3 Key factor analysis of *Bemisia tabaci* over 10 generations by (a) factor and (b) stage, based on the methods of Varley and Gradwell (1960).

total mortality and had the largest slope (fig. 3b) indicating that mortality during this stage was the key factor. The addition of 10 or 25.7% mortality for the crawler stage altered some regression coefficients slightly, but did not alter the determination of parasitism as the key factor.

Pooled over all developmental stages, the highest rates of irreplaceable mortality were associated with parasitism (median: 0.112), followed by the predation (0.088), dislodgement (0.020) and unknown

Table 1 Key factor analysis of *Bemisia tabaci* over 10 generations in cotton, based on methods of Podoler and Rogers (1975)

Crawler mortality[1]	Mortality factors			
	Unknown	Dislodgement	Parasitism	Predator
0	0.047	0.079	0.681	0.192
0.10	0.048	0.080	0.681	0.191
0.257	0.049	0.066	0.667	0.185
	Stages			
	Egg	N1	N2	N3	N4
0	0.006	0.036	0.029	0.102	0.566
0.10	0.007	0.035	0.027	0.101	0.568
0.256	0.011	0.037	0.028	0.097	0.599

Figures represent the slope of the regression coefficient estimated by regressing factor or stage *k*-values on total *K* from the entire generation. [1]Rates of 0.1 and 0.257 are based on estimates from Naranjo (2007) and mean rate of N1 mortality, respectively, that were added to total *K*. The regression coefficients do not sum to unity due to the extra mortality in total *K* for rates >0.

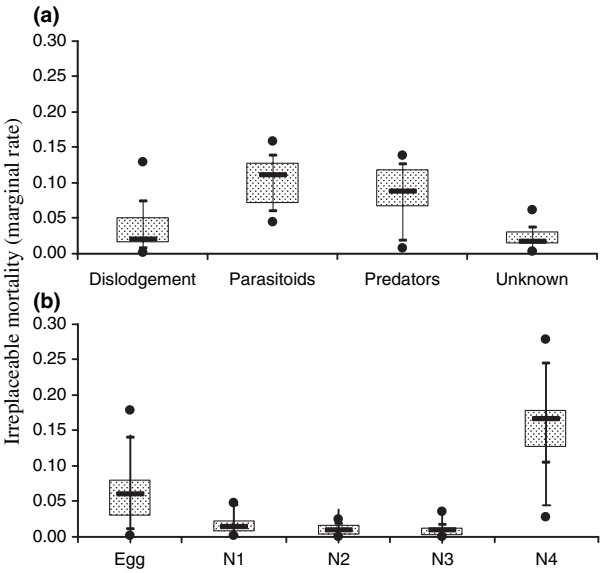

Fig. 4 (a) Box plots of marginal rates of irreplaceable mortality for *Bemisia tabaci* in cotton by mortality factors pooled over all stages; (b) box plots of marginal rates irreplaceable of mortality during each developmental period pooled over all mortality factors for 10 generations. Lines within boxes represent the median the box bounds the 25th and 75th percentiles the whiskers denote the 10th and 90th percentiles, and points denote the range.

(0.017) (fig. 4a). Across all developmental stages the highest rates of irreplaceable mortality were associated with 4th instar nymphs (median: 0.166) and the egg (0.060). Median rates of irreplaceable mortality of N1, N2 and N3 were low and varied between 0.009 and 0.013 (fig. 4b).

Discussion

Efficient pest control depends on knowledge of the biological and ecological factors affecting pest survival. Here we characterized and quantified the mortality factors affecting populations of immature *B. tabaci* in the Turkish cotton system over a two year period at two sites, measured the key factors most associated with variation in total mortality, and assessed the relative importance of each mortality factor.

Based on marginal mortality, parasitism and predation were found to be the largest components of overall immature *B. tabaci* mortality followed by dislodgement and unknown factors. The high level of predation may be attributed to the large number of predator species that feed on *B. tabaci* in cotton in the Çukurova plain. Species such as *Euseius scutalis* (Acarina: Phytoseiidae), *Orius* spp. (Hemiptera: Anthocoridae), *Geocoris* spp. (Hemiptera: Lygaeidae), *Piocoris* spp. (Hemiptera: Lygaeidae), *Deraeocoris* spp. (Hemiptera: Miridae), *Macrolophus caliginosus* Wgn. (Hemiptera: Miridae), have been reported as predators of *B. tabaci* in Turkish cotton (Ghavami 1999). Naranjo and Ellsworth (2005) found predation to be the largest mortality factor affecting populations of *B. tabaci* in cotton in Arizona, USA. In contrast, Asiimwe et al. (2007) reported that parasitism provided the highest mean rate of marginal mortality within a generation followed by dislodgement and predation on cassava in Uganda. No mortality due to insect pathogens was specifically identified in this study despite the fact that several fungal pathogens are known from many parts of the world where this pest occurs (Lacey et al. 1996). It is possible that insects where affected by fungal pathogens but did not present outward signs of infection in the field. In any case, such mortality would have been lumped into the unknown category which overall had only low to moderate rates of mortality.

The highest level of mortality was associated with the fourth nymphal stage followed by the egg stage. This same pattern was described by Naranjo and Ellsworth (2005), and these authors also determined that predation during the last nymphal instar was the primary key factor affecting *B. tabaci* on cotton in Arizona. In contrast, Horowitz et al. (1984) reported that mortality of eggs and crawlers usually contributed most to total mortality. Similarly, Gerling et al. (2004) reported that unassigned mortality in the egg to second nymphal instars was the key factor for *Siphoninus phillyreae* (Haliday) (Homoptera: Aleyrodidae) on pomegranate. Based on the methodology employed in our study, crawler mortality was not directly estimated. However, based on reasonable assumptions of expected rates of mortality during this short life stage, total generational mortality was altered only slightly and it had no affect on the determination of key factors. Because median estimates of total of mortality were already very high (0.957), the addition of small or even moderate rates of additional mortality changed total mortality very little. Naranjo (2007) estimated that crawler mortality was about 10% in an Arizona, USA cotton system but whether this rate is reflective of the Turkish system is unknown. Future studies should include crawler mortality.

Parasitism was identified as the key mortality factor in our analyses here. *E. mundus* and *E. lutea* have been reported as the most important parasitoids of *B. tabaci* in cotton fields in the Çukurova plain (Ghavami 1999; Karut and Akdağcık 2006). Karut and Akdağcık (2006) reported high percent parasitism (77.6%), even in sprayed cotton plots in the region. Similar results were reported by Asiimwe et al. (2007) in their study on cassava where parasitism in the fourth instar was the most important factor driving total mortality. In contrast both Horowitz et al. (1984) and Naranjo and Ellsworth (2005) observed parasitism of *B. tabaci* in Israeli and Arizona cotton, respectively, but levels were generally low and it was not a decisive mortality factor. Naranjo and Ellsworth (2005) further found that most of the mortality provided by parasitism was replaceable by other factors, primarily predation and dislodgement. Results here show that parasitism is the key factor explaining the variability in total immature mortality rates of *B. tabaci* population on cotton in the Çukurova plain of Turkey.

Key factor analysis is a common component of most life table studies and natural enemies are frequently identified as key factors (Stiling 1988; Cornell and Hawkins 1995). Nonetheless, Royama (1996) argues that the determination of factors that truly drive the dynamics of populations must be based on multiple criteria that cannot be easily extracted from basic life table studies. Naranjo and Ellworth (2005) identified predation to be the key factor for *B. tabaci* in cotton in the southwestern USA and the weight of evidence, including the resurgence of pest populations with the use of broad spectrum insecticides that disrupts predator populations (S.E. Naranjo, unpublished data), suggests that predators (as the key factor) do play a vital role in the populations dynamics of *B. tabaci* in some parts of the world. Here, the marginal rate of parasitism was high and it contributed significant irreplaceable

mortality. Thus, it is reasonable to hypothesize that parasitism is a key factor but additional manipulative experiments and observations will be needed to test this hypothesis.

The overall greater level of parasitism in the cotton system here compared to other cotton production areas in, for example, the USA and Israel might be explained by several factors. Climatic differences could play a role. In the Çukurova plain, daily maximum temperature rarely exceeds 40°C and relative humidity generally varies between 60–75% during summer months. In contrast, relative humidities in cotton producing areas in Israel and the southwestern USA are typically very low during the summer and maximum temperature may reach near 50°C in these areas (Avidov 1956; AZMET 2008). Perhaps more importantly, the ecosystems in which cotton production is embedded is very different as well. Cotton is the dominant crop in the region of Arizona where the life table studies of Naranjo and Ellsworth (2005) were conducted and is primarily surrounded by native desert with very low crop diversity. Under these conditions, parasitism appears to be consistently low in cotton fields (Naranjo and Ellsworth 2005; Naranjo 2008). In contrast, rates of parasitism were consistently higher in cotton when measured in life table studies conducted within an artificial multi-crop system in this same region which provided close juxtaposition of cotton and other whitefly host crops and weeds on a season long basis (Naranjo et al. 2004). This suggests that parasitoids may be less able to track whitefly populations in low diversity systems were they may need to move relatively large distances to find host patches. This is supported by findings that aphelinid parasitoids are not strong dispersers (Hagler et al. 2002; Byrne and Bellamy 2003). In comparison, cotton in the Çukurova plain of Turkey is embedded in a relatively diverse cropping landscape that may more readily facilitate higher parasitoids populations that are able to better track host resources and thus contribute more to pest mortality.

Despite the high levels of natural mortality on *B. tabaci* populations demonstrated in this study, cotton in the region is typically sprayed with insecticide mixtures an average of four times during the season for whiteflies and other pests (Karut and Akdağcık 2006). The development of integrated pest management strategies focused on conservation of natural enemies, particularly parasitoids, may provide for more sustainable management of *B. tabaci* and other pests affecting cotton in the Çukurova plain of Turkey.

Acknowledgements

This work was funded by project TOGTAG-3037 from the TÜBITAK (The Scientific and Technological Research Council of Turkey). We thank Dan Gerling (Tel Aviv University), T-X Liu (Texas A&M University) and Cengiz Kazak (Çukurova University) for helpful comments on earlier draft of this manuscript.

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