Mortality Factors Affecting Whitefly Populations in Arizona Cotton Management Systems: Life Table Analysis

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Abstract

Direct-observation studies were conducted in replicated experimental plots to identify causes and estimate rates of mortality of whiteflies in cotton over the course of six generations from late June through late October. In plots receiving no whitefly or Lygus *insecticides, predation and dislodgment were major sources of egg and nymphal mortality, and overall survival from egg to adult ranged from 0-18.2%. Similar patterns were observed in plots treated with the insect growth regulator (IGR) Knack. Applications of the IGR Applaud or a mixture of endosulfan and Ovasyn caused high levels of small nymph mortality and reduced rates of predation on nymphs during the generation immediately following single applications of these materials in early August. Whitefly populations declined to very low levels by mid-August in all plots, and few differences were observed in patterns of whitefly mortality among treated and control plots 4-6 weeks after application. The population crash was associated with an unknown nymphal mortality factor which reduced immature survivorship during this first post-treatment generation to zero. The application of insecticides for control of* Lygus *in subplots modified patterns of mortality in all whitefly treatments by generally reducing mortality from predation during generations observed from mid-July through August. Parasitism was a very minor source of mortality throughout and was unaffected by whitefly or* Lygus *insecticides.*

Introduction

Many biotic and abiotic mortality factors impact the population dynamics of *Bemisia tabaci* (Biotype B) in agricultural ecosystems, yet we have a poor understanding of the rates of these mortality factors and how they may be involved in overall population regulation. For a multivoltine and multi-crop pest like *B. tabaci* estimating rates of mortality in the field is extremely complex and difficult. The effects of various conventional insecticides are generally well known; however, studying the effects of such factors as predation and parasitism, or even insect growth regulator insecticides, is much more difficult. This task is made even harder because of overlapping generations of whiteflies in the field and because pest management activities provide further sources of mortality that may enhance or disrupt natural enemies. Life table analysis (Deevey 1947) is the most direct and robust method for estimating the sources and rates of mortality affecting a population. Life table studies categorize the sources of mortality and provide a means to quantify rates of death from various factors over the course of a generation.

Over the past three years we have been conducting studies to demonstrate and evaluate different strategies for whitefly management in Arizona cotton (Ellsworth et al. 1998, Ellsworth and Naranjo 1999, Naranjo and Hagler 1997, Naranjo et al. 1998a,b). These multi-component, commercial and quasi-commercial scale experiments have evaluated sampling methodologies, thresholds for insecticide application, methods of application, insecticide resistance, and natural enemy conservation. An integral part of these studies has also been the development of life tables which have allowed us to

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categorize and quantify sources and rates of whitefly mortality relative to different management systems. Our previous results suggest that the use of the insect growth regulators (IGR) Applaud_? (buprofezin) and Knack_? (pyriproxyfen) for whitefly control helps conserve native predators and whitefly parasitoids (Naranjo and Hagler 1997, Naranjo et al. 1998a, b). Here we present preliminary results of a second year of replicated life table studies.

Materials and Methods

Studies were conducted at the University of Arizona, Maricopa Agricultural Center in Maricopa, AZ. The study was conducted using NuCOTN 33B and contrasted four whitefly control regimes; Applaud used first, Knack used first, a rotation of conventional insecticides (1995-IRM), and an untreated control. The threshold for use of IGR treatment was 1 large nymph/disk plus 3-5 adults/leaf (Ellsworth et al. 1996). All conventional insecticide applications were made at 5 adults/leaf (Ellsworth et al. 1995). In addition to applications for whitefly, each treatment plot was split, and each half either received sprays for *Lygus hesperus* or were left untreated for *Lygus.* Insecticides for *Lygus* were applied as needed based on a threshold of 15-20 *Lygus* (adults + nymphs, with nymphs present) per 100 sweeps (Ellsworth 1998, Ellsworth and Diehl 1998). All applications were made by ground, and seasonal usage of insecticides for the studies described here is summarized in Table 1. Each insecticide regime was replicated 4 times using a randomized block, split-plot design in a total area of about 9 acres. Additional detail on the entire experiment is provided in Ellsworth and Naranjo (1999).

Cohorts of newly laid eggs and settled 1st instar nymphs were established over the course of 2 pre-spray and 4 post-spray generations from late June through late October in the replicated experimental plots described above. Cohorts consisted of at least 50 individuals of each stage in each plot. The location of each individual was marked on leaves with a non-toxic felt-tip pen. Each stage was then examined every 2-3 days directly in the field with the aid of a 15x hand lens. Mortality was recorded as due to insecticides, predators, parasitoids, inviability (eggs only), unknown and missing. The unknown category simply catalogs mortality that could not be attributed to one of the other causes of death and probably reflects physiological or natural mortality. The missing category represents mortality associated with weather (wind and/or rain) or chewing predation. In this preliminary report we present only apparent rates of mortality observed for each source. Future analyses will involve the estimation of marginal rates of mortality which corrects for the effects of contemporaneous mortality by multiple factors (e.g. predation, parasitism and insecticides) and allows for more robust statistical comparisons among treatments.

The particular treatments in which life table studies were conducted varied over the season. The first cohorts were established in control plots prior to the use of any whitefly or *Lygus* insecticides when whitefly abundance was extremely low. The second, fourth and sixth sets of cohorts contrasted control plots that were sprayed or not sprayed with *Lygus* insecticides. The third cohort contrasted the effects of whitefly insecticides and their interaction with *Lygus* sprays, and the fifth cohort contrasted the effects of whitefly insecticides alone.

Results

Egg Mortality: In the first generation, prior to any insecticide sprays, the major sources of mortality were predation (17%) and missing (18%) (Table 2). A very small fraction of the eggs were inviable (0.5%) and nearly 65% of the eggs hatched.

In the second generation, initiated 1 day after the first spray for *Lygus,* the largest source of mortality was dislodgment (28-29%) (Table 3). The rate of predation in *Lygus*-treated plots declined by about 50% compared with the control (from 12 to 6%), and rates of inviability increased over the first generation (2.5%). Rates of egg hatch averaged about 59% in control plots and 63% in *Lygus*-treated plots.

In the third generation, 0-1 day following the first application of insecticides for whitefly suppression, inviability was the largest source of mortality in all treatment plots (65-77%) (Table 4). Inviability was highest in the Knack regime reflecting one of the main modes of action of this insecticide (interference with embryogenesis, Ishaaya and Horowitz [1992]). Overall levels of egg predation were low and similar across all plots (1-7%). Contrary to the previous generation, predation was not depressed by *Lygus* insecticides despite a second application a week before the initiation of these cohorts. From 20-28% of the eggs were killed by dislodgment. Rates of egg hatch were extremely low in this generation (0.5-3.2%) and whitefly populations declined dramatically within our experimental area and on the MAC farm in general (see further discussion under Nymph Mortality).

Three weeks after the first application of whitefly insecticides, population densities of whitefly remained very low inhibiting the establish of cohorts in all treatment plots. Cohorts established in both subplots of the control plots revealed that *Lygus* insecticides did not alter the already low rates of egg predation (6%) (Table 5). From 13-17% of the eggs were inviable, and rates of hatch varied from 50-55%.

A final set of cohorts was established in the non-*Lygus* treated splits of the whitefly treatment plots about 4 weeks following whitefly insecticide application (Table 6). Rates of egg predation remained low in control and IGR plots (4-6%) and was very low in the 95-IRM plots (0.4%). On average 4-9% of eggs were inviable, and a large fraction of eggs were killed by dislodgment (25-38%). Overall rates of hatch were high (53-65%).

A final set of cohorts was established in both splits of the control plots in late September. As in the fourth generation, rates of egg predation were low and unaffected by *Lygus* insecticides applied > 6 weeks prior (Table 7). A large fraction of the eggs were inviable (27-32%) and rates of hatch were around 48%.

Nymph Mortality: Similar to that observed for eggs, the major sources of nymphal mortality were predation (39%) and missing (34%) in the first generation prior to any insecticide sprays (Table 2). A very small fraction of the nymphs were parasitized (2.1%) and the rate of emergence averaged 21%.

In the second generation, initiated 1 day after the first spray for *Lygus*, the largest source of mortality was dislodgment (ca. 27%) (Table 3). The rate of nymphal predation in *Lygus*-treated plots declined to 8% compared with the control at 24% (67% decline) and although the rate of parasitism was very low (1-2%), it too declined in *Lygus*-treated plots. The *Lygus* insecticide Vydate was responsible for killing about 16% of the whitefly nymphs. About 14% died from unknown causes and rates of emergence averaged 31% in control plots and 33% in *Lygus*-treated plots.

In the third generation immediately following the first application of insecticides for whitefly suppression, predation was highest in the control and Knack plots (24-33%) and lowest in plots receiving Applaud or endosulfan + Ovasyn [95-IRM] (10-14%) (Table 4). There also was a small reduction in predation in the control and Knack plots due to the application of Orthene for *Lygus* suppression one week before the initiation of the cohorts. Insecticide mortality was greatest for Applaud and 95-IRM treatments (46-69%). This is a reflection of the temporal similarity of insecticidal action in these two regimes. Applaud, a molting inhibitor, killed most of the insects in the first and second instars, and conventional insecticides were most effective against smaller instars when residues were highest. A smaller amount of mortality was attributed to Knack (21-25%) and a small amount of insecticidal mortality was observed in *Lygus* and non-*Lygus* treated control plots (5-9%). Dislodgment and unknown factors were significant sources of mortality in most treatments. Overall, the rates of mortality factors that affected large nymphs were diminished on a generational basis in 95-IRM, and especially Applaud plots, because very few nymphs survived past the 2nd instar in these treatments. Rates of parasitism were extremely low throughout (< 2%). An unusual source of mortality affected 4th instar nymphs during this generation and contributed to 0% survivorship across all treatment plots. The posterior sections of affected nymphs were severely sunken and necrotic areas were sometime visible at the tips of developing wingbuds. The apparent rate of mortality from this factor varied from 20% in control plots to < 4% in Applaud plots (Table 4). As noted, this low rate in the Applaud plots reflects the high level of small nymph mortality. However, the stage-specific rate of "sunken" mortality within the 4th instar was consistently 35-40% irregardless of treatment (not shown). These "sunken" nymphs were prevalent throughout the MAC farm irrespective of insecticide applications and no doubt contributed to the decline in whitefly populations throughout the area. Investigations are still underway to define the agent of this mortality.

As noted above, cohorts were established only in control plots 3 weeks after the first application of whitefly insecticides. The rate of predation remained relatively high in completely untreated plots (37%) compared with 30% in plots receiving *Lygus* insecticides (Table 5). This decline in predation was essentially offset by an increase in insecticide mortality in sprayed plots (7% compared with 1% in unsprayed plots). Dislodgment and unknown mortality factors were again significant in both treatments (16-22%). No "sunken" mortality was observed, and rates of emergence were 21-23%, substantially higher than the previous generation.

In the second post-treatment cohorts observed in whitefly treatment plots, predation was similar among IGR and conventional insecticide plots (21-23%) and only slightly lower than that observed in control plots (27%) (Table 6). Rates of parasitism were the highest observed all season and were greatest in control and Applaud plots (5%). Rates of mortality due to dislodgment and unknown causes were relatively high across treatments (14-33%) and a small amount of insecticidal mortality was observed in all plots (< 6%). Again, no "sunken" mortality was observed, and rates of emergence varied from 17.4% in control plots to around 30% in treated plots.

Low rates of emergence (5-8%) were observed in the final cohorts established in both splits of the control plots in late September (Table 7). No *Lygus* insecticide effects were apparent, and rates of predation averaged 21-22%. Parasitism declined from the previous generation to typical levels of 1-2%. A large fraction of the nymphs died from unknown causes that may have been associated with declining host quality after irrigation termination and defoliation, and declining temperatures.

Total Survivorship: We estimated total survivorship from egg to adult by assuming complete survival of first instar crawlers, the one immature stage we did not observe (Table 8). Survivorship was low overall, ranging from 0% for all treatments in the 3rd generation to 21% in *Lygus*-treated control plots in the 2nd generation. During the fifth generation observed (4-6 weeks after application of whitefly insecticides) survivorship was lowest in the control plots (11.3%) compared with treated plots (18-20%).

Discussion

For the second year, we identified and quantitatively measured mortality factors in natural populations of immature whitefly subject to different commercial management practices at MAC. Results differed somewhat between 1997 and this year. The 1998 season was peculiar in several regards. A cool and moist spring prevented timely planting and the early crop was further subjected to sand-blasting and thrips damage (Ellsworth and Naranjo 1999). Despite this, whitefly populations exceeded treatment thresholds during the first week in August, a pattern typical of central Arizona over the past several years. Natural enemies were abundant in the early season, but repeated, farm-wide insecticide applications for *Lygus* and other factors caused populations to decline significantly from mid-season onward. As a result we observed lower rates of predation on whitefly nymphs and especially eggs in 1998 compared with 1997. In 1997 we measured significant insecticide effects on predation in the first, and especially the second, post-treatment generations. In general, the use of IGRs preserved natural enemies, consequently contributing to the extended "residual" of suppression in these regimes by providing for high levels of predation (Naranjo et al. 1998a,b). In contrast, the use of conventional, broad-spectrum insecticides in the 95-IRM regime in 1997 reduced natural enemy populations and thus their contribution to whitefly control. Treatment differences due to whitefly control practices were less definitive in 1998 due in part to the factors discussed above. Natural enemy abundance was low throughout all treatments. Thus, the effects of conservation through the use of selective insecticides were more subtle. Also, the natural decline in whitefly populations in mid-August eliminated the need for additional insecticides and thus, diminished any further delineation of treatment effects that were so pronounced in 1997 (Naranjo et al. 1998b). We observed declines in levels of predation in the 95-IRM and Applaud plots compared with the control during the first post-spray generation (see Table 4) but we observed no treatment differences in a subsequent generation in the same plots 4-6 weeks later.

The addition of *Lygus*-treated plots to our life table studies in 1998, however, revealed interesting patterns related to overall cotton pest management strategies. During most of the generations examined we observed numerical declines in levels of predation associated with the application of broad-spectrum materials for *Lygus* suppression. This pattern was somewhat evident for egg predation, but most pronounced for nymphal predation. Across all generations and treatments in which *Lygus* suppression was contrasted, there was a decline in egg predation in half of the cases and a decline in nymphal predation 67% of the time. Thus, the gains in conservation afforded by the use of selective IGR for whitefly control may have been offset to some degree with non-selective *Lygus* insecticides. Nonetheless, *Lygus* insecticides had a decidedly different effect on whitefly dynamics, and by inference, natural enemies populations in the two years. In 1997 only a single spray was necessary for *Lygus* suppression, but this application lead to resurgence of whiteflies compared to plots not treated for *Lygus*, demonstrating the significant impact of this spray on the natural enemy complex (Ellsworth et al. 1998). *Lygus* was a severe problem in many cotton-producing areas in 1998 and required 3 sprays from mid-July through mid-August within our experimental arena at the MAC farm. However, we observed no resurgence in the whitefly population in *Lygus*-treated plots. We hypothesize that despite a pattern of reduced predation in *Lygus*-treated plots in 1998, the application of broad-spectrum insecticides in our plots had relatively little impact on the already low population densities of predators. Sweep net samples of predator abundance in the various treatment plots supports this argument (unpublished data). Regardless, with our arsenal of Bt cotton and IGRs, a selective control agent for *Lygus* is urgently needed in order for biological control to assume a significant and consistent role in Arizona cotton pest management.

The mortality factor that killed a large fraction of 4th instar nymphs and contributed to no immature survivorship during the 3rd generation remains a mystery. Associated with the death of 4th instars was a high level of egg inviability in the same generation. Whether the two phenomena are related is uncertain, but both are coincidental with the effect of Knack which disrupts embryogenesis in the egg and emergence in terminal stage nymphs. However, we did observe embryonic development in most eggs (at least to the point where eyes and mycetomes were visible) that failed to hatch, and the sunken appearance of 4th instar nymphs was inconsistent with the effects of Knack observed in the past. The spatial scale of the phenomenon also argues against Knack as a cause. Only a third of our plots received Knack, but the symptoms were found in all plots at about the same levels. In addition, preliminary residue analyses indicate that Knack was present only where it was purposely sprayed. Further, other non-Knack areas of the MAC farm contained sunken nymphs and accumulated inviable eggs. Overall, it seems very unlikely that Knack was involved, and further analyses are underway to define the cause or causes of this peculiar mortality, and to define its role in the area-wide whitefly population decline.

Finally, as in 1997, we found very low levels of parasitism in 1998. This was despite the continued releases of exotic parasitoids in the genus *Eretmocerus* into central Arizona (Gould 1999). We do know that predators such as *Geocoris* will readily feed on parasitized whiteflies (Naranjo 1999) and it is likely that many parasitized nymphs are lost to predation before the immature parasitoid is large enough to be detected by our observational methods. Nonetheless, even if we correct for predation and other contemporaneous mortality factors (unpublished data), rates of parasitism remain small in relation to the many other forces of mortality impacting whitefly populations in treated as well as untreated cotton.

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Table 1. Insecticide application history, MAC 1998

Applaud-L	Vydate	Orthene	Applaud		Vydate
Applaud			Applaud		
Knack-L	Vydate	Orthene	Knack		Vydate
Knack			Knack		
95-IRM-L (conventional)	Vydate	Orthene		endosulfan + Ovasyn	Vydate
95-IRM (conventional)				endosulfan + Ovasyn	
Control-L	Vydate	Orthene			Vydate
Control					

[a] Regimes followed by L were sprayed for *Lygus hesperus*

Table 2. Sources and observed mean (*n*=4) rates of whitefly mortality for cohorts initiated 29 June, 1998 (Generation 1)

Egg	Predation	0.169
	Inviable	0.005
	Missing	0.182
	Hatch	*0.644*
Nymph	Predation	0.387
	Parasitism	0.021
	Insecticide	0.000
	Missing	0.344
	Unknown	0.040
	Emergence	*0.208*

Table 3. Sources and observed mean (*n*=4) rates of whitefly mortality for cohorts initiated 17 July, 1998 (Generation 2). Regime followed by L was sprayed for *Lygus hesperus*

Egg	Predation	0.116	0.059
	Inviable	0.024	0.025
	Missing	0.275	0.285
	Hatch	*0.585*	*0.631*
Nymph	Predation	0.239	0.080
	Parasitism	0.018	0.007
	Insecticide	0.027	0.160
	Missing	0.263	0.274
	Unknown	0.142	0.146
	Emergence	*0.311*	*0.333*

Table 4. Sources and observed mean (*n*=4) rates of whitefly mortality for cohorts initiated 6 August, 1998 (Generation 3). Regimes followed by L were sprayed for *Lygus hesperus*

Egg	Predation	0.060	0.063	0.036
	Inviable	0.682	0.653	0.690
	Missing	0.226	0.275	0.257
	Hatch	*0.032*	*0.009*	*0.017*
Nymph	Predation	0.329	0.105	0.255
	Parasitism	0.005	0.000	0.009
	Insecticide	0.047	0.687	0.210
	Missing	0.220	0.175	0.227

	Unknown	0.195	0.014	0.132	
	Sunken	0.204	0.019	0.167	
	Emergence	*0.000*	*0.000*	*0.000*	
Egg	Predation	0.066	0.073	0.009	0.057
	Inviable	0.731	0.667	0.768	0.663
	Missing	0.195	0.241	0.218	0.257
	Hatch	*0.008*	*0.019*	*0.005*	*0.023*
Nymph	Predation	0.233	0.136	0.243	0.139
	Parasitism	0.000	0.009	0.009	0.019
	Insecticide	0.086	0.612	0.250	0.463
	Missing	0.254	0.194	0.208	0.187
	Unknown	0.205	0.014	0.106	0.077
	Sunken	0.222	0.035	0.184	0.111
	Emergence	*0.000*	*0.000*	*0.000*	*0.004*

Table 5. Sources and observed mean (*n*=4) rates of whitefly mortality for cohorts initiated 25 August, 1998 (Generation 4). Regime followed by L was sprayed for *Lygus hesperus*

Egg	Predation	0.058	0.057
	Inviable	0.171	0.126
	Missing	0.267	0.263
	Hatch	*0.504*	*0.554*
Nymph	Predation	0.365	0.303
	Parasitism	0.009	0.024
	Insecticide	0.009	0.072
	Missing	0.222	0.209
	Unknown	0.187	0.162
	Emergence	*0.208*	*0.230*

Table 6. Sources and observed mean (*n*=4) rates of whitefly mortality for cohorts initiated 1 September, 1998 (Generation 5)

Egg	Predation	0.064	0.043	0.049	0.004
	Inviable	0.041	0.052	0.093	0.062
	Missing	0.248	0.378	0.262	0.297
	Hatch	*0.647*	*0.527*	*0.596*	*0.637*
Nymph	Predation	0.266	0.226	0.227	0.210
	Parasitism	0.055	0.05	0.024	0.014
	Insecticide	0.014	0.064	0.024	0.033
	Missing	0.158	0.136	0.189	0.234

Unknown	0.333	0.187	0.209	0.218
Emergence	*0.174*	*0.337*	*0.330*	*0.291*

Table 7. Sources and observed mean (*n*=4) rates of whitefly mortality for cohorts initiated 25 September, 1998 (Generation 6). Regime followed by L was sprayed for *Lygus hesperus*

Egg	Predation	0.061	0.075
	Inviable	0.316	0.273
	Missing	0.143	0.161
	Hatch	*0.480*	*0.491*
Nymph	Predation	0.210	0.220
	Parasitism	0.018	0.024
	Insecticide	0.026	0.050
	Missing	0.171	0.252
	Unknown	0.495	0.409
	Emergence	*0.080*	*0.045*

Table 8. Mean (*n*=4) survivorship from egg to adult over 6 generations, 1998. Regimes followed by L were sprayed for *Lygus hesperus*

1 (29 June)	0.134	-	-	-
2 (17 July)	0.182	-	-	-
3 (6 August)	0.000	0.000	0.000	-
4 (25 August	0.105	-	-	-
5 (1 Sept)	0.113	0.178	0.195	0.185
6 (25 Sept)	0.038	-	-	-
1 (29 June)	-	-	-	-
2 (17 July)	0.210	-	-	-

3 (6 August)	0.000	0.000	0.000	0.0001
4 (25 August	0.129	-	-	-
5 (1 Sept)	-	-	-	-
6 (25 Sept)	0.022	-	-	-