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Review article

Conservation and evaluation of natural enemies in IPM systems for *Bemisia tabaci*[☆]

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Abstract

Conservation biological control emphasizes the preservation and enhancement of natural enemies and is the cornerstone of all approaches to biological control. This review critically examines recent and current research efforts in conservation biological control by predators and parasitoids of *Bemisia tabaci* worldwide. A large number of natural enemy species have been identified from many agricultural systems. Further research has demonstrated that these natural enemies may act along with other mortality agents to inflict high levels of mortality on populations of *B. tabaci*. Less effort has been placed on determining the factors constraining or potentially enhancing biological control. The widespread use of broad-spectrum insecticides in many crops has severely hampered the contribution of predators and parasitoids to pest suppression. However, the arsenal of selective insecticides has grown in the past decade and their increased usage may permit the true integration of biological control into IPM systems. The effects of species interactions (e.g., intraguild predation) and host-plant attributes on disruption of biological control are poorly understood in most systems. Research in the area of habitat manipulation and enhancement is minimal. Very little research has addressed the evaluation of natural enemy effects on *B. tabaci* population dynamics in any system. As a result our ability to predict and exploit these effects for pest suppression are limited. Problems in estimating and interpreting parasitism are highlighted. Recent life table studies of *B. tabaci* in Arizona cotton are summarized to demonstrate how integration of natural enemies with use of selective insecticides resulted in the development of an efficient pest management system. Avenues for future research are discussed that may enhance the use of conservation biological control as a key tactic in IPM of *B. tabaci*. Published by Elsevier Science Ltd.

Keywords: *Bemisia tabaci*; *B. argentifolii*; Conservation biological control; Arthropod predators; Parasitoids; Selective insecticides; Habitat manipulation; Parasitism; Life table analysis

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[☆]Recent evidence suggests that *B. tabaci* represents a species complex with numerous biotypes and two described cryptic species. The binomial *B. tabaci* here is used in the broadest sense to include all members of the species complex unless a more specific designation is indicated. This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or a recommendation for its use by USDA.

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1. Introduction

Bemisia tabaci remains a key pest of many field and horticultural crops throughout subtropical and tropical regions of the world with significant problems also occurring in protected agricultural systems in temperate regions (Brown et al., 1995). Many biological characteristics, including multivoltinism, broad host-range, ability to migrate, high reproductive rate, tolerance for high temperatures, ability to vector a variety of devastating plant viruses, and a propensity to develop resistance to a wide class of insecticides underlie its pest potential and have contributed to the difficulty of developing robust and sustainable management systems. Significant advances have been made in understanding the biology, behavior, ecology and population dynamics of this pest, and in developing and implementing pest management systems (Gerling and Mayer, 1996). However, biological control of *B. tabaci* by parasitoids, predators and fungi represents a key strategy whose potential has gone largely unrealized in many affected cropping systems throughout the world. This is a function of many factors including heavy reliance on insecticides as the primary tactic of control, problems in overcoming some of the biological characteristics of the pest noted above, especially its role as a plant virus vector, and the relatively small amount of research effort devoted to the topic of biological control compared with other areas of investigation.

It is generally acknowledged that biological control alone is unlikely to provide adequate pest control, but through careful integration with other pest suppression tactics it could represent a significant source of sustainable control (Dowell, 1990; Gerling, 1992; Cock, 1994; Heinz, 1996). A paradigm for pest management of *B. tabaci* in many affected crops can be represented by the pyramid depicted in Fig. 1 (see also Ellsworth and Martinez-Carrillo, 2001). Current management systems for many crops are dominated by the use of insecticides that typically rely on sampling, threshold, and resistance information to optimize timing of applications and make best use of existing chemistry (Palumbo et al., 2001). A variety of avoidance strategies that form the underlying foundation of the management pyramid have been largely untapped, and are the subject of several articles in this Special Issue. Although some of these “avoidance” strategies might require elements from the upper portions of the pyramid, for example,

sampling for augmentative biological control and area wide survey, the overall effect of avoidance would be the lowering of pest density with a reduction in the need for prescriptive insecticidal control. The integration of “avoidance” strategies into overall management programs could significantly improve the efficiency and sustainability of integrated pest management (IPM) systems for this pest. In this context biological control represents a crucial strategy that needs to assume a more dominant role in research and implementation efforts.

1.1. Research effort in biological control

Given the worldwide distribution and the long standing history of the pest problem (Oliveira et al., 2001) there is a large, and exponentially expanding, literature base for *B. tabaci* (including *B. argentifolii*) with over 3500 citations (excluding abstracts) since 1894 (Cock, 1986, 1993; Naranjo et al., 2000). Published research in all areas of biological control has assumed a relatively small proportion of this literature, although there has been a steady increase in effort since the mid 1980s (Fig. 2). About 42% of all citations on biological control were published since 1996 indicating a growing interest in this pest control strategy. Considerable research has been conducted to examine and define the basic biology and behavior of natural enemies associated with *B. tabaci* (Table 1). Such laboratory and greenhouse studies have, and continue, to provide

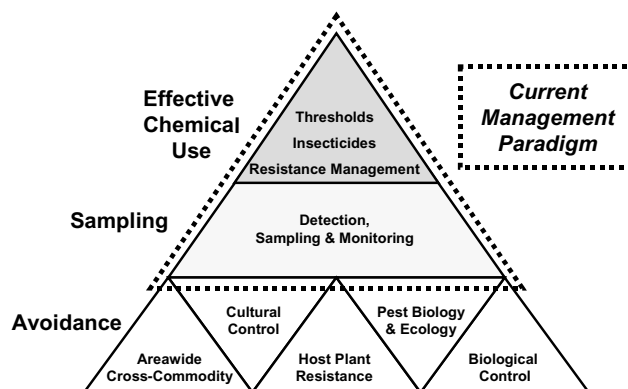


Fig. 1. Components of an IPM program emphasizing avoidance strategies such as biological control as the foundation of sustainable pest management systems. The elements delineated by the dotted line represent the current paradigm of insecticide-dominated management systems in most affected crops.

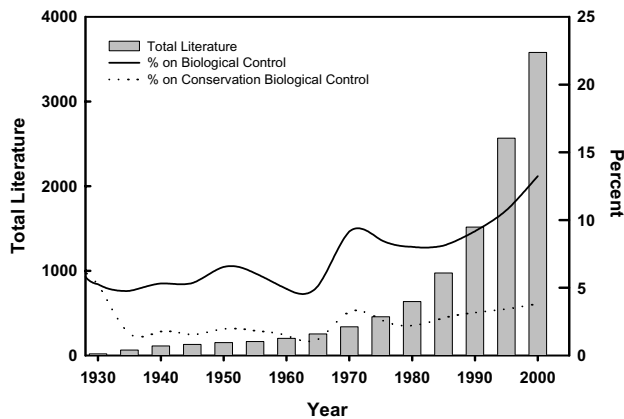


Fig. 2. Historical summary of research on *B. tabaci/argentinae* and the proportion of effort in the area of biological control as indicated by the published literature (3580 publications, excluding abstracts) as of August 2000 (Naranjo et al., 2000). The first report on this pest was published in 1889; for clarity the timeline is shown beginning around 1930.

Table 1
Summary of research literature on *B. tabaci/argentinae* in the area of biological control^a

Category	Publications	% of total ^b	% of conservation ^b
Biology/behavior	135	28.5	
Systematics	47	9.9	
Reviews	37	7.8	
Classical	11	2.3	
Augmentation	117	24.7	
Conservation	137	28.9	
Survey	75		54.7
Insecticide effects			
Laboratory	20		14.6
Field	31		22.6
Experimental	13		9.5
Efficacy	17		12.4
Parasitoids	310	65.4	
Predators	160	33.8	
Pathogens	59	12.4	

^a There were 474 total publications (excluding abstracts) in all areas of biological control as of August 2000 (Naranjo et al., 2000).

^b Percentages may not sum to 100 within a section due to overlap in categories, and/or overlap in coverage within individual citations.

important information bearing on the potential of particular natural enemies being considered for introductory, augmentative or conservation biological control applications. This literature was not further partitioned because of the difficulty of categorizing many of the studies by biological control approach. Comparing the three main approaches to biological control, the greatest amount of effort has been placed in the area of conservation, followed closely by augmentation (Table 1). Introduction, or classical, biological control has received the least attention, although there has been considerable research in this area, particularly

in the United States (Lacey and Kirk, 1993; Kirk and Lacey, 1996). The progress of these efforts have been primarily reported through published abstracts of symposia, conferences, and workshops (Naranjo et al., 2000). Efforts in augmentation have primarily focused on protected agricultural systems (e.g., van Lenteren et al., 1997; Hoddle et al., 1998; Gerling et al., 2001), although some research has examined the potential utility and efficacy of augmentation in field crops (e.g., Heinz et al., 1999; Simmons and Minkenberg, 1994; Joyce and Bellows, 2000). Biological control with parasitoids has received the most attention, followed by use of arthropod predators and fungal pathogens. These patterns derive from a combination of factors, including pest distributions centered in semi-arid regions of the world, differences in faunal compositions in specific crops, and the difficulty of directly measuring predation.

1.2. Scope of this review

Gerling et al. (2001) and Faria and Wraight (2001) provide general discussions of recent efforts in biological control of *B. tabaci* with parasitoids, predators and fungi. These reviews include descriptions of known agents, examination of various aspects of natural enemy biology and ecology, introduction and augmentation biological control, and application in various pest management programs. This article will focus more specifically on a critical examination of research on conservation of existing predators and parasitoids as an approach for integrating biological control into current and developing IPM systems. Conservation of fungi will not be explicitly covered because these agents are used mostly as inundative agents in biological control of this pest (Faria and Wraight, 2001). Emphasis is placed on research efforts during the past 5–10 years as there have been many prior review articles addressing issues of conservation, and general biological control. This review will focus primarily on unprotected agricultural systems. However, many of the principles discussed would be applicable to conservation of augmented agents in protected systems as well. Examples and research in field crops, especially cotton, will be frequently highlighted as this reflects my own research and experience, and also the bias in the published literature on this pest. Suggested avenues for further research are highlighted in the final section.

2. Conservation biological control

Conservation of natural enemies is often credited with being the oldest form of biological control. However, compared with classical and augmentation biological control it has received relatively little attention as a

method of arthropod pest suppression (Ehler, 1998; Landis et al., 2000). DeBach (1974) defines conservation biological control as “...manipulation of the environment to favor natural enemies, either by removing or mitigating adverse factors or by providing lacking requisites”. This broad definition emphasizes the fundamental importance of conservation to all approaches of biological control. The efficacy of imported or mass-reared natural enemies in many systems will likely depend on attention to conservation measures that improve the suitability of the environment into which they are released (van den Bosch and Telford, 1964; Gurr and Wratten, 1999).

Conservation biological control can be broadly categorized into three overlapping components which encompass survey and potential of extant natural enemies, elucidation and manipulation of factors constraining or enhancing natural enemy abundance and activity, and evaluation of biological control efficacy (Fig. 3). Published research in conservation biological control represents about one-third of all the biological control literature on *B. tabaci*, and this pattern has been relatively consistent over time (see Fig. 2). Further partitioning of this biological control literature indicates that survey and identification of potential natural enemies comprises the bulk of research efforts in conservation (Table 1). Considerable research also has been conducted to examine the factors constraining or enhancing biological control. The vast majority of this research has focused on the effects of insecticides on predators and parasitoids. Very little research has addressed biological control efficacy, and many of these studies provide only preliminary or inconclusive results (see Section 2.4). These three components, and their associated approaches and methodologies (Rabb et al., 1976; Luck et al., 1988) will now serve as a template for assessing research effort and progress in conservation biological control of *B. tabaci*.

2.1. Survey: is there potential for biological control?

The interest in and use of conservation as a biological control approach is predicated on the assumption that

there is some potential for pest suppression from either extant natural enemies, or agents added through introduction or augmentation. Thus, surveys to determine the identity and potential of candidate natural enemies are a crucial first step. Natural enemies of *B. tabaci* have been surveyed in a number of affected cropping systems. One of the earliest reports was provided by Berger (1921) who described various parasitoids, predators and fungi associated with *Bemisia* spp., other whiteflies, and scale insects in Florida. Overall, surveys for natural enemies of *B. tabaci*, primarily parasitoids and arthropod predators, have been conducted in at least 26 countries over the past eight decades. Much of this survey work has been summarized in several reviews (Greathead and Bennett, 1981; Lopez-Avila, 1986; Cock, 1994; Nordlund and Legaspi, 1996; Gerling et al., 2001; Faria and Wraight, 2001).

A large number of natural enemy species are found associated with or attacking *B. tabaci* worldwide. Based on published lists, Gerling et al. (2001) cataloged 114 arthropod predators of *B. tabaci* belonging to 9 orders and 31 families. This list is likely to change as research progresses. Many predators are generalist feeders, and predation is extremely difficult to positively assess in the field. Using immunologically based gut assays, Hagler and Naranjo (1994a, b) definitively identified 9 predators feeding on *B. tabaci* in Arizona cotton and have since positively identified another 9 species (unpublished) not appearing on the Gerling et al. (2001) list. Parasitoids attacking *B. tabaci* are much easier to assess, but taxonomic problems make it difficult to positively enumerate the species involved. Based on various published sources, Gerling et al. (2001) estimates 34 species of *Encarsia*, 14 species of *Eretmocerus*, and several species belonging to the genera *Amitus* and *Metaphycus* attacking *B. tabaci* worldwide. This list, too, is certain to change with further progress in the systematics of these groups. Faria and Wraight (2001) catalog 9 described and 2 undescribed species of fungi that have been shown to occur naturally in *Bemisia* populations worldwide. Although the exact numbers of species attacking *B. tabaci* may never be known

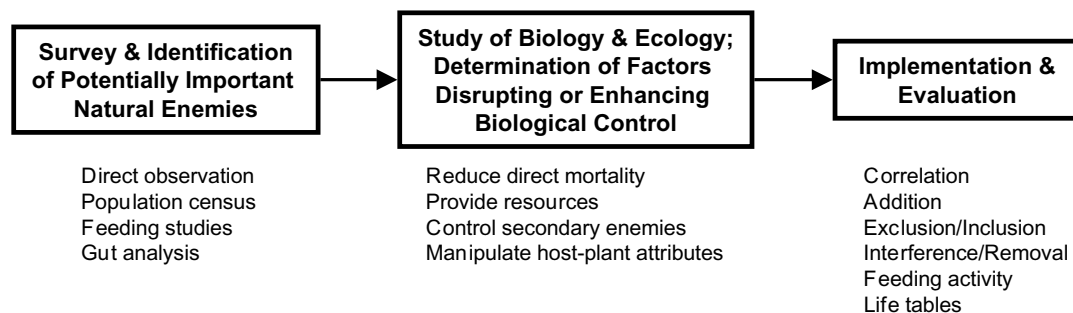


Fig. 3. Components and approaches of conservation biological control.

completely, these faunal lists suggest a significant potential for biological control in many affected cropping systems.

This potential is exemplified by recent findings in the Arizona cotton system. Field-based life table studies in unsprayed cotton demonstrate that the immature stages of *B. tabaci* are subject to high levels of mortality from a number of different sources (Fig. 4) (Naranjo and Ellsworth, unpublished). Based on 14 cohorts examined over a three year period, median survivorship to adulthood was 6.4% (range 0–27.1%). Predation by sucking predators (primarily Heteroptera) was responsible for nearly 36% of all immature mortality and about 31% of mortality was attributed to dislodgement, a portion of which probably represents mortality from predators with chewing mouthparts (primarily beetles). Parasitism by *Eretmocerus eremicus* and two species of *Encarsia* contributed another 4%. Although these levels of immature mortality are generally insufficient to suppress populations of *B. tabaci* below economic levels in this system, these mortality sources contribute significant irreplaceable mortality that permit efficient management of this pest in Arizona cotton with selective insecticides (see Section 2.4.2).

Despite the large number of natural enemy species that may attack *B. tabaci* and the high levels of mortality that can sometimes be attributed to natural enemy activity, there are few definitive examples of successful biological control (Gerling, 1996). The best examples of the putative suppressive role of extant natural enemies in the field come from studies demonstrating pest resurgence. Abdelrahman and Munir (1989) showed in commercial-scale, paired studies that applications of broad-spectrum insecticides for control

of *B. tabaci*, *Heliothis armigera*, *Aphis gossypii*, and *Empoasca lybica* in Sudan cotton caused reductions in parasitism and predator populations, and precipitated economic populations of *B. tabaci* in two of three field sites. Devine et al. (1998) demonstrated resurgence of *B. tabaci* in cotton treated with the pyrethroid cypermethrin in Israel. Similar comparative studies in Arizona cotton provided inconsistent results (Ellsworth and Naranjo, unpublished). Populations of *B. tabaci* were elevated on certain sampling dates in fields receiving applications of broad-spectrum insecticides for control of *Lygus hesperus* in one year, but differences were not significant in the second and third years. Although other factors, such as hormoligosis cannot be ruled out, these results generally suggest that natural enemies may play an important, but variable, role in pest suppression. Various studies have reported high levels of parasitism in *B. tabaci* nymphs (e.g. Gerling, 1966; Bellows and Arakawa, 1988; Kajita et al., 1992; McAuslane et al., 1993; Stansly et al., 1997), but these results have never been definitively associated with economic suppression of pest populations.

2.2. Manipulation: can disruption to biological control be minimized?

A number of factors may cause agricultural environments to be unsuitable for natural enemies, and thus, interfere with their ability to contribute to pest suppression. Such factors include adverse climate and microclimate, scarcity of water and supplemental foods like nectar and pollen, competition, intraguild predation, physical and chemical attributes of the crop plant, lack of sufficient shelter, adverse cultural practices, and use of insecticides (DeBach and Hagen, 1964; van den Bosch and Telford, 1964). These problems are further exacerbated in annually disturbed cropping systems (Ehler and Miller, 1978; Wiedenmann and Smith, 1997) where infestations of *B. tabaci* are typically most severe.

2.2.1. Insecticides

Clearly, the most significant factor disrupting biological control of arthropod pests in most cropping systems is the use of insecticides (Stern et al., 1959; Croft, 1990). This topic area has received considerable attention in the *Bemisia* literature with 51 citations reporting on effects of insecticides on natural enemies from field and laboratory studies, the majority published since 1990 (see Table 1). Results from both laboratory toxicology studies and field application studies of conventional, broad-spectrum insecticides are predictable; use of such materials typically leads to direct natural enemy mortality in the laboratory and reduced population densities and activity in the field (e.g., Natarajan, 1990; Stam and Elmosa, 1990; Jones et al., 1995; Attique and Ghaffar, 1996; Abou-Elhagag, 1998;

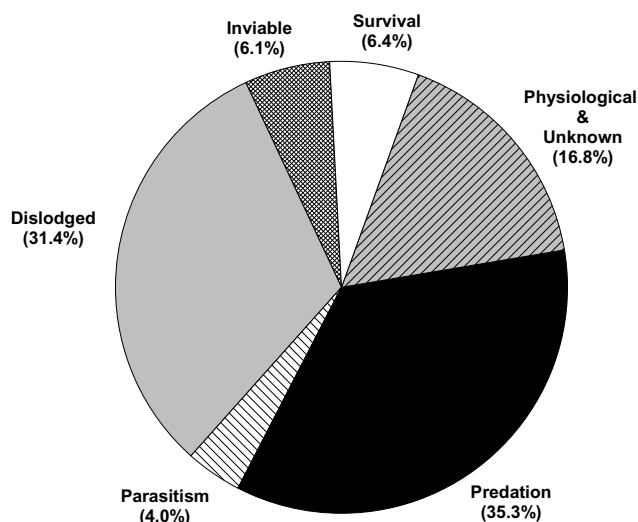


Fig. 4. Contribution of various factors to mortality of immature *B. tabaci* stages in cotton. Results summarized from 14 cohort-based, field life tables conducted in cotton in central Arizona, USA over a three year period (Naranjo and Ellsworth, unpublished).

Schuster and Stansly, 2000; Simmons and Jackson, 2000).

Because insecticides are likely to remain a major component of pest suppression for *B. tabaci*, minimizing the effects of these insecticides on natural enemies in cropping systems will require more selective approaches for use of broad-spectrum insecticide and/or more selective materials. Strategies that focus on the former, termed ecological selectivity, have been successful in other pest systems (Newsom et al., 1976; Johnson and Tabashnik, 1999). These approaches include reduced rates of application, use of less persistent materials, temporal and spatial changes in application methods, and changes in formulation and delivery (Croft, 1990). Ecologically selective approaches have received only minor attention in the management of *B. tabaci* (Ahmed and Muzaffar, 1977; El-Ghany et al., 1992). One notable exception may be use of systemic formulations of imidacloprid and other related compounds (see Palumbo et al., 2001) which appear to achieve selectivity by avoiding contamination of the plant surface (see Tables 2 and 3). In contrast, much research has been conducted to examine the effects of putatively selective and biorational materials which have both become more readily available worldwide in the last decade (Palumbo et al., 2001).

Laboratory evaluations of toxicity of two commonly used insect growth regulators, buprofezin and pyriproxy-

fen, along with imidacloprid and bifenthrin, a representative fourth generation synthetic pyrethroid, to aphelinid parasitoids attacking *B. tabaci* are summarized in Table 2. Research to date indicates that the effects of both the chitin-inhibitor buprofezin, and the juvenile-hormone analog pyriproxyfen are stage- and species-specific. Buprofezin has been shown to be moderately to highly toxic to early developmental stages of two species of *Eretmocer* and one species of *Encarsia*, but generally benign to pupal and adult stages of the *Eretmocer* species examined (Table 2). Effects on younger stages are likely manifested through effects on the host itself rather than the parasitoid directly (Gerling and Sinai, 1994). Pyriproxyfen has been evaluated on fewer species and results are less consistent (Table 2). This insecticide was found highly toxic to early immature stages of *Eretmocer* *eremicus*, but benign to young stages of three species of *Encarsia*. Effects on pupal stage parasitoids were equally mixed, even for the same species. For example, Hoddle et al. (2001) found pyriproxyfen harmless to *Eretmocer* *eremicus*, but Koppert's (1998) side-effects database rated this material moderately harmful to the same species. Pyriproxyfen was also found more harmful to *Encarsia formosa* compared with *Encarsia pergandiella* or *Encarsia transvena* (Table 2). This insecticide was found relatively benign to adult stages of either genus. Sublethal effects, summarized for the two insect growth

Table 2

Summary of laboratory evaluations of the toxicity of selected insecticides to aphelinid parasitoids attacking *B. tabaci*^a

	Stage tested												Sublethal effects		References
	Egg/larva			Pupa				Adult							
	Bup	Pyr	Bif	Bup	Pyr	Imid	Bif	Bup	Pyr	Imid	Bif	Bup	Pyr		
<i>Eretmocer</i>															
<i>eremicus</i>	4	—	—	1	—	—	—	—	—	—	—	0	—	Gerling and Sinai (1994)	
	—	—	—	1	3	1	4	1	2	1	4	—	—	Koppert (1998)	
	4	4	—	1	1	—	—	1	1	—	—	0	—	Hoddle et al. (2001)	
<i>mundus</i>	—	—	4	1	—	—	4	1	—	—	4	0	—	Jones et al. (1995, 1998)	
	—	—	—	1	—	4 ^b	2	—	—	—	—	—	—	Gonzalez-Zamora et al. (1997)	
<i>orientalis</i>	—	—	—	—	—	—	—	2	—	4 ^b	4	—	—	Tzeng and Kao (1999)	
<i>tejanus</i>	3	—	4	1	—	—	4	1	—	—	4	—	—	Jones et al. (1995, 1998)	
<i>Encarsia</i>															
<i>formosa</i>	—	—	—	—	—	—	—	1	—	—	4	—	—	Jones et al. (1995)	
	—	1	—	—	3	—	—	—	1	—	—	—	—	Liu and Stansly (1997)	
	—	—	—	2	4	1, 4 ^b	4	1	1	1, 4 ^b	4	—	—	Koppert (1998)	
<i>luteola</i>	3	—	—	4	—	—	—	—	—	—	—	0	—	Gerling and Sinai (1994)	
<i>pergandiella</i>	—	—	—	—	—	—	—	1	—	—	4	—	—	Jones et al. (1995)	
	—	1	—	—	1	—	—	—	—	—	—	—	—	Liu and Stansly (1997)	
<i>transvena</i>	—	1	—	—	1	—	—	—	1	—	—	—	—	Liu and Stansly (1997)	

^a Bup = buprofezin, Pyr = pyriproxyfen, Bif = bifenthrin, Imid = imidacloprid (systemic). Values denote IOBC ratings (Hassan, 1992) based on control-corrected mortalities: 1 = <25% mortality; 2 = 26–50% mortality; 3 = 51–75% mortality; 4 = >75% mortality. Bioassays included both topical and contact exposure, depending on stage.

Sublethal effects evaluated include repellency from treated hosts, adult longevity, progeny production, and development time and emergence rates of progeny; 0 denotes no effect; — denotes a measurable negative effect in one or more attribute.

^b Imidacloprid applied as a foliar spray.

Table 3
Summary of laboratory evaluations of the toxicity of selected insecticides to predators known to attack *B. tabaci*^a

	Stage tested								Sublethal effects		References
	Nymph/larva				Adult						
	Bup	Pyr	Imid	Pyret	Bup	Pyr	Imid	Pyret	Bup	Pyr	
<i>Geocoris punctipes</i>	—	—	—	—	—	—	1 ^c	3	—	—	Boyd and Boethel (1998)
	—	—	—	—	—	—	1 ^c	1	—	—	Elzen et al. (1998)
	1	2	—	—	1	1	—	—	0	0	Naranjo and Prabhaker, unpublished
<i>Orius insidiosus</i> ^b	—	—	—	—	—	—	1 ^c	3	—	—	Elzen et al. (1998)
	1	1	4, 4 ^c	4	1	1	4, 4 ^c	4	—	—	Koppert (1998)
	1	1	—	—	1	1	—	—	0	0	Naranjo and Prabhaker, unpublished
<i>Dicyphus tamaninii</i>	1	1	2 ^c	3	—	—	—	—	—	—	Castane et al. (1996)
	—	—	2	—	—	—	—	—	—	—	Figuls et al. (1999)
<i>Macrolophus caliginosus</i>	1	1	4, 4 ^c	4	1	1	3, 4 ^c	4	—	—	Koppert (1998)
	—	—	1 ^c	—	—	—	—	—	—	—	Figuls et al. (1999)
<i>Collops vittatus</i>	—	—	—	—	1	1	—	—	0	—	Naranjo and Prabhaker, unpublished
<i>Delphastus pusillus</i>	—	—	—	—	1	1	4 ^c	4	—	—	Koppert (1998)
<i>Hippodamia convergens</i>	—	—	—	—	—	—	2 ^c	4	—	—	Elzen et al. (1998)
	—	—	—	—	—	4	—	—	—	—	Koppert (1998)
<i>Chrysoperla carnea</i>	1 ^d	—	—	—	—	—	—	—	0	—	Balasubramani and Regupathy (1994)
	1	—	—	—	—	—	—	—	—	—	Bigler and Waldburger (1994)
	—	—	—	—	—	—	4 ^c	2	—	—	Elzen et al. (1998)
	—	—	—	3	—	—	—	—	—	—	Kapadia and Puri (1991)
	—	1	1, 4 ^c	4	—	1	1	4	—	—	Koppert (1998)
<i>Chrysoperla rufilabris</i>	3 ^e	—	—	—	—	—	—	—	—	—	Liu and Chen (2000)
	—	—	—	4	—	—	—	4	—	—	Schuster and Stansly (2000)

^aBup = buprofezin, Pyr = pyriproxyfen, Imid = imidacloprid (soil drench), Pyret = pyrethroids (bifenthrin, fenpropathrin, permethrin or cyfluthrin). Values denote IOBC ratings (Hassan, 1992) based on control-corrected mortalities: 1 = <25% mortality; 2 = 26–50% mortality; 3 = 51–75% mortality; 4 = >75% mortality. Bioassays tested contact exposure.

Sublethal effects evaluated include, progeny production and developmental time; 0 denotes no effect; — denotes a measurable negative effect in one or more attribute.

^bsimilar results for *O. laevigatus* and *O. majusculus* reported by Koppert, 1998; Delbeke et al., 1997; van de Veire et al., 1996.

^cImidacloprid applied as a foliar spray.

^dTopical bioassays

^eResults from treatment of 1st instars, all other immature stages tested had a rating of 1.

regulators only, indicate that buprofezin is generally benign, but that pyriproxyfen had negative effects on several species (Table 2). Imidacloprid has been examined for few species of *B. tabaci* parasitoids. Results suggest that while systemic applications are generally harmless, foliar applications can be highly toxic. Bifenthrin, a broad-spectrum pyrethroid, was highly toxic to all stages of all species examined. Thus, from a comparative perspective, it appears that several of the more widely used insecticides are relatively selective and that selectivity could be further enhanced by better timing of applications relative to parasitoid development.

With one minor exception, buprofezin has been found benign to immature and/or adult stages of seven predator species that attack *B. tabaci* (Table 3). Liu and Chen (2000) reported moderate toxicity to 1st instar *Chrysoperla rufilabris*, but no toxicity to any other developmental stage. Pyriproxyfen was likewise reported to be relatively benign to a number of predator species. Naranjo and Prabhaker (unpublished) found some wing deformities in *Geocoris punctipes* adults

treated as final-stage nymphs, and Koppert (1998) reported high levels of mortality to the adults of the coccinellid *Hippodamia convergens*. Pyriproxyfen has been reported as toxic to other species of Coleoptera in laboratory bioassays (Hattingh and Tate, 1995; Smith et al., 1999). The few studies examining sublethal effects from these two insect growth regulators show no or only minor effects (Table 3). Reports of toxicity from imidacloprid to several species are mixed due to different avenues of exposure (systemic or foliar), predator feeding behaviors, and susceptibility. Systemic exposure was found moderately to highly toxic for several heteropteran species including *Orius insidiosus*, *Dicyphus tamaninii*, and *Macrolophus caliginosus* (Table 3). Foliar formulations of imidacloprid were reported to be harmful to *O. insidiosus* and *M. caliginosus* by Koppert (1998), but Elzen et al. (1998) found that foliar applications were harmless to *O. insidiosus* and *G. punctipes*. Sensitivities to systemic modes of exposure are not unexpected as many predaceous Heteroptera are facultative herbivores (Naranjo and Gibson, 1996) and would be affected if underlying susceptibilities exist.

Foliar applications were moderately to highly toxic to adult stages of several beetles and *C. carnea*. Larval stages of *C. carnea* showed differential susceptibility depending on the mode of exposure (Table 3). Exposures to third and fourth generation pyrethroids were largely detrimental, although it appears that some populations of *G. punctipes* and *C. carnea* may have reduced susceptibility to cyfluthrin. Similar to the parasitoids, it appears that several commonly used insecticides, especially the insect growth regulators, are relatively selective based on laboratory bioassays.

Some research has been conducted to evaluate the effects of various biorational insecticides many of which are considered potentially selective. In laboratory bioassays, Stansly and Liu (1997) found that a neem-extract, an insecticidal soap, and two sugar esters derived from *Nicotiana glauca* had little or no effect on *E. pergandiella*. Use of an emulsified mineral oil caused high mortality to immature parasitoids and reduced parasitization by adults. Bentz and Neal (1995) tested similar materials and found that all caused some mortality of pupal and adult *E. formosa*, and reduced parasitism of greenhouse whitefly. The *N. glauca* extract was the least toxic and they concluded that it could be compatible with biological control in greenhouse systems. These sugar esters were also reported to be benign to all stages of *Nephaspis oculatus*, a coccinellid predator of *B. tabaci* (Liu and Stansly, 1996a). Although these biorationals and others are still experimental, or have seen limited usage, they could represent important insecticidal tools that would minimize disruption of natural enemies in some systems.

Laboratory bioassays provide valuable information regarding the potential for non-target effects of insecticides under ideal conditions of exposure. Although it is generally assumed that effects will be less severe in the field, the realized effects of these compounds can only be accurately assessed under more realistic conditions (Croft, 1990; Hassan, 1992; Wright and Verkerk, 1995; Johnson and Tabashnik, 1999). Field studies integrate a number of both direct and indirect factors, including weathering and persistence of residues, behavioral attributes of natural enemies that may increase or decrease exposure to residues, reductions in host and prey populations, and sublethal effects on development and reproduction. Evaluating these many factors and their interactions is a daunting challenge (Stark and Wennergren, 1995).

Very few studies have addressed the selectivity of the compounds discussed above in the field, and without exception, all have been limited to assessing effects on overall natural enemy abundance and/or activity. Devine et al. (1998) showed no effects on levels of parasitism of *B. tabaci* or populations densities of generalist predator with use of buprofezin alone or synergized with piperonyl butoxide. Compared to untreated

controls, Gerling and Naranjo (1998) found elevated levels of parasitism, but reduced densities of parasitoids on several dates in Israeli cotton fields treated with buprofezin. Darwish and Farghal (1990) reported that generalist predator populations were reduced more than 50% two days following application of buprofezin in Egyptian cotton after which populations rebounded. By comparison, use of broad-spectrum materials caused initial reductions of over 90% in this same study. Recent studies in Arizona cotton have examined the comparative effects of buprofezin, pyriproxyfen, and conventional, broad-spectrum insecticides on population dynamics of *B. tabaci* and associated parasitoids and generalist predators (Naranjo and Hagler, 1997; Naranjo et al., unpublished). Use of conventional insecticides, regardless of the number of applications, significantly reduced seasonal densities of all predator groups. Spiders, beetles and heteropteran predators were generally unchanged from the untreated control when fields were sprayed with either buprofezin or pyriproxyfen. In one year, both insect growth regulators caused reductions in population densities of *Drapetis* spp., a predatory fly. In the other two years, reductions in this species were found only for fields treated with pyriproxyfen. Overall, these results suggest that the insect growth regulators are much more selective than conventional insecticides and that buprofezin is more selective than pyriproxyfen. Field testing of non-target effects for other selective and biorational insecticides relative to *B. tabaci* has been very limited (Natarajan, 1990; Surulivelu, 1991; Simmons and Jackson, 2000).

Even with the availability of selective insecticides for management of *B. tabaci*, disruption of natural enemies through use of broad-spectrum materials is still likely in some agricultural systems. For example, cotton in most parts of the world is affected by multiple key pests for which selective options for control are unavailable. In Arizona cotton, the insect growth regulators buprofezin and pyriproxyfen are used for selective suppression of *B. tabaci*, and transgenic cotton is widely used for selective control of lepidopteran pests. However, fruit-feeding *Lygus hesperus* can be a severe pest, and their control requires the use of broad-spectrum insecticides. Economic considerations also are important. For example, the high cost of insect growth regulators in some areas may force growers to opt for cheaper, but more disruptive insecticides. These factors emphasize the challenges we face in integrating biological control into economically viable pest management strategies for multiple pest systems.

2.2.2. Other disruptive factors

A number of other factors may contribute to disruption of biological control; however, aside from insecticides, these factors have received comparatively

little attention in systems affected by *B. tabaci*. Intraguild predation, defined as trophic interaction (predation, parasitism) between natural enemies sharing a common prey or host, is well known in many crop systems (Rosenheim et al., 1995). *Chrysoperla carnea* larvae readily fed upon immature *E. transvena* within 4th instar *B. tabaci* in laboratory assays (Kapadia and Puri, 1990). Adult *Delphastus pusillus* did not differentiate between unparasitized *B. tabaci* and those parasitized with young *E. transvena*, but both adults and larvae avoided older larval and pupal stages in laboratory studies (Hoelmer et al., 1994). The impact of these examples of intraguild predation on biological control of *B. tabaci* in the field are largely unknown.

Perhaps the best known instances of intraguild predation are found in the aphelinid heteronomous hyperparasitoids attacking *B. tabaci* (Hunter and Kelly, 1998). These parasitoids produce females as primary parasitoids, but produce males as hyperparasitoids of their own or other primary parasitoids. Theory and models argue that such behaviors may be disruptive to biological control (Mills and Gutierrez, 1996). However, limited empirical data suggest that while interactions among *B. tabaci* parasitoids may occur, they do not necessarily interfere with suppression of pest populations in semi-field or greenhouse systems (Heinz and Nelson, 1996; Hunter et al., 2002). With the large diversity of natural enemies attacking *B. tabaci* in any given system (see Section 2.1), intraguild predation is probably common and may play an integral part in determining the role and impact of specific natural enemy species in affected crops.

Characteristics of the host plant also may affect the biology and behavior of natural enemies. Degree of host plant hairiness is often considered an important characteristic influencing colonization and subsequent infestation by *B. tabaci*. Preference is generally associated with more hirsute plants (Wilson and George, 1986). Similar, but generally opposite patterns have been shown with regard to parasitoid searching behaviors and parasitism on various host plants (Heinz and Parrella, 1994; Kapadia and Puri, 1994; McAuslane et al., 1995; Headrick et al., 1996, 1997; Gruenhagen and Perring, 1999). Additional factors such as degree of leaf glossiness or levels of nitrogen fertilization may also affect the abundance and biology of parasitoids (Bentz et al., 1996; Jackson et al. 2000). Very few studies have examined the effects of plant or plant-mediated characteristics on predators attacking *B. tabaci*. *Delphastus pusillus* performed better on poinsettia with fewer trichomes (Heinz and Parrella, 1994), but greater trichome density on tomato, although altering some searching behaviors, did not affect overall levels of biological control by this predator (Heinz and Zalom, 1996). Guershon and Gerling (1999) showed that the interaction between plant hirsuteness in cotton, and

plant-mediated differences in nymphal *B. tabaci* setosity, altered certain searching and handling behaviors, but not levels of predation by *D. pusillus*. Overall, the influence of host plant characteristics, and ultimately their impact on biological control of *B. tabaci*, are poorly understood.

2.3. Manipulation: can biological control be enhanced?

As shown, various factors may cause agricultural environments to be unsuitable for natural enemies, and manipulations that reduce or eliminate disruptive factors are critical. Equally important are manipulations that enhance the environment, making it more suitable for natural enemies, and thus, improving the probability of successful biological control (Rabb et al., 1976). Recent efforts have expanded research and utilization of habitat management techniques for conservation biological control of arthropods in various systems (Pickett and Bugg, 1998; Landis et al., 2000). However, efforts related to habitat management for conservation biological control of *B. tabaci* have been very limited.

Long-term studies to develop, evaluate, and implement annual and perennial plant refuge systems have been on-going in the Imperial Valley of California (Roltsch and Pickett, unpublished). This diverse agricultural region has suffered severe outbreaks of *B. tabaci* since the early 1990s. This region also is typical of the semi-arid areas of the world where infestations have been most problematic, and is characterized by spatially and temporally discontinuous habitat for support of natural enemy populations. Roltsch and colleagues are attempting to provide more continuous habitat for natural enemies adjacent to cultivated fields. These efforts include planting annual or perennial hosts that are tolerant of desert soils and climate, easy to maintain, host moderate populations of *B. tabaci*, and are attractive to natural enemies. The focus of their investigations is to provide suitable habitat for the establishment of exotic aphelinid parasitoids. However, the refuges have also been shown to harbor populations of generalist predators such as *Geocoris* spp. and *Orius* spp. The perennial chuparosa (*Justicia californica*) is considered promising because it hosts whiteflies over an extended period of the year and may facilitate overwintering of parasitoids. Annual refuge plants, including many cultivated species, have been found to be more practical for implementation into annual cropping systems. Elemental marking studies with collard and sunflower refuges bordering cotton and melon crops demonstrated that *Eretmocerus* spp. readily move from these refuge areas into the crops (Roltsch et al., unpublished). However, these refuge planting also are a significant source of *B. tabaci*. Overall, these studies demonstrate some promise for enhancing natural enemies of *B. tabaci* in agricultural systems. Consider-

able work remains in identifying plants that will provide a beneficial ratio of natural enemies to pest and that are cost-effective to cultivate within existing cropping systems. Further information on the extent and timing of natural enemy dispersal from the refuge to the crop also is needed.

2.4. Evaluation: how can efficacy and impact be measured?

The final component of conservation biological control to be considered is evaluation of efficacy and impact. A number of excellent reviews have addressed the general area of natural enemy evaluation for all approaches to biological control (Kiritani and Dempster, 1973; DeBach et al., 1976; Luck et al., 1988; Sunderland, 1988; Kidd and Jervis, 1996). Briefly, methods can be categorized as (1) addition of natural enemies to an area from which they are absent, (2) population census and correlation (3) exclusion or inclusion of natural enemies, usually using some sort of cage, (4) interference or removal of natural enemies by trapping, hand-picking, or more typically, use of insecticides, (5) a variety of methods that measure natural enemy feeding activity such as gut content analyses, and (6) life tables and other direct observation techniques that attempt to measure sources and rates of mortality. As emphasized by DeBach et al. (1976), most of these methods are most robust when employed in a comparative manner. Of all these methods, only the first, addition, is generally not useful in assessing natural enemies for conservation biological control.

In general, these methodologies have been vastly underutilized in assessing the impact of extant natural enemies of *B. tabaci* in the field. As a consequence, our understanding of the role of natural enemies in suppression of *B. tabaci*, and more importantly, our ability to exploit these effects have been very limited. Population census and correlation of pest and natural enemy densities is one of the most frequently used methods to evaluate impact (e.g. Kajita et al., 1992; McAuslane et al., 1995; Gerling et al. 1997; Stansly et al., 1997). This method is descriptive only and does not directly measure any cause and effect relationship. Thus, population census and correlation is very limited as a tool for generalizing and extrapolating results. Bogran et al. (1998) attempted to use exclusion and partial exclusion to measure the effects of parasitoids and predators on *B. tabaci* infesting beans in Honduras. Exclusion did not appear to affect rates of predation by sucking predators (<5%), rates of parasitism (\approx 30%) or densities of *B. tabaci* nymphs, pointing to methodological problems. Interference or disruption of natural enemies by insecticides was used in several studies as a means of demonstrating the overall potential of the entire natural enemy complex (see Section 2.1). Such

studies have not examined the effects of specific species or groups, or attempted to estimate quantitative rates of mortality by natural enemies. Based on gut-content results and predator population density, Naranjo and Hagler (1998) identified *O. tristicolor*, *L. hesperus*, and *G. punctipes* as the most prevalent predators of *B. tabaci* eggs. Unfortunately, because of limitations of the technique, it is not possible to estimate quantitative rates of predation by these species (Sunderland, 1988; Hagler and Naranjo, 1996). Life table analyses provide a detailed description of the mortality forces affecting a population and allow direct estimation of the probability of dying and the causes of death. Life tables and their associated analysis are a potentially robust methodology for assessing natural enemy effects (Bellows et al., 1992). They have not been widely applied to evaluation of biological control of *B. tabaci* in the field. Horowitz et al. (1984) constructed partial life tables for *B. tabaci* in Israeli cotton and used k-factor analysis to determine that mortality of eggs and first instar crawlers was most closely related to generational mortality. They did not attempt to estimate rates of mortality by specific causes, but did note that predation was probably responsible for some mortality to early stages. They also noted that parasitoids were a relatively minor source of mortality. Recently, life table studies conducted in Arizona cotton estimated sources and rates of mortality for immature stages of *B. tabaci* (see Section 2.1).

Many methodological and technical problems hamper our ability to accurately assess the population level effects of predators and parasitoids on *B. tabaci*. As noted, predation is notoriously difficult to study in the field, primarily because many predators are difficult to observe and often leave no evidence of attack. Such problems are obvious. Advances in understanding the role of predators in suppression of *B. tabaci* populations will require innovative application of existing methods and development of new techniques (Hagler and Naranjo, 1996). By comparison, assessing the activity of parasitoids is relatively simple, because they can be readily seen within the host and exuviae are distinctive. However, problems and limitations in extending these simple measurements of activity (i.e. percentage parasitism) to estimates of mortality and pest suppression are not sufficiently recognized by many researchers. Because of the prevalent use of percentage parasitism in the *B. tabaci* literature, it is worth examining this method in more detail.

2.4.1. Problems in estimating and interpreting parasitism

The general problems associated with measuring and interpreting percentage parasitism in insect population dynamic studies have been outlined and discussed in some detail (see Van Driesche, 1983; Van Driesche et al., 1991). The most common approach to estimating

parasitism of *B. tabaci* is to determine the percentage of obviously parasitized nymphs from leaf samples. The location of these leaves varies among host plants, but the leaves harboring the greatest number of 3rd and 4th instar nymphs are most often chosen. Even this simple methodology is problematic as pointed out by Hoelmer (1996, p. 456). Based on the same set of leaf samples from okra, he demonstrated that percentage parasitism varied from 16 to 81% depending on what stages of the parasitoid and host were used to calculate the percentage. Thus, it is important to maintain a consistent technique within a study and to clearly articulate the methodology so that different studies can be compared. Examination of the literature indicates that a clear description of methodology is frequently not provided. Percentage parasitism is useful for faunal surveys, where the goal is simply to determine species composition and relative abundance. Such estimates are also considered useful for comparing experimental treatments, but not for assessing the impact of parasitoids on host population dynamics (Van Driesche, 1983). I will argue below that use of percentage parasitism is also problematic in some experimental comparisons.

There are at least four factors, aside from basic sampling error, that affect the validity and accuracy of estimates of percentage parasitism. The most obvious problem is that *B. tabaci* is multivoltine which leads to overlapping generations. Second, the development of parasitized and unparasitized *B. tabaci* is asynchronous, because the bulk of parasitoid development occurs, and is only apparent, in the final host stadium (Gerling, 1990). As a result, it takes longer for a 4th instar host to produce a parasitoid adult than a whitefly adult. The combination of these factors makes it difficult to estimate parasitism on a generational basis from the ratio of parasitized to unparasitized nymphs on the same leaf. The magnitude and direction of the bias depends in part on the pattern of growth of the host population. This is illustrated (Fig. 5) by comparing estimates of percentage parasitism based on leaf samples (ratio of obviously parasitized to unparasitized 4th instar host) and cohort-based life table studies that measured apparent parasitism of fourth stage *B. tabaci* directly (Naranjo and Ellsworth, unpublished). Percentage parasitism is underestimated with leaf samples when host populations are increasing and overestimated when host populations are declining (Fig. 5, insets). This occurs because the denominator term of percentage parasitism from leaf sample estimates is inflated or deflated, respectively. Both leaf sample and life table estimates conducted in this way yield only apparent (and irreplaceable) rates of mortality by parasitism, because the parasitoid must be sufficiently developed to be seen through the host cuticle. Earlier stages of parasitism (eggs, young larvae) may be obliterated by predation or other mortality events. The estimation of marginal rates

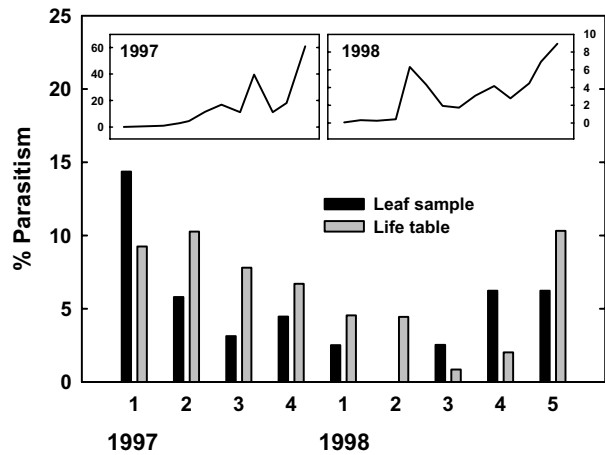


Fig. 5. Comparative estimates of *B. tabaci* parasitism by aphelinid wasps in cotton using leaf samples and field life tables, Arizona, USA. Inset panels show population density of nymphal stages over the corresponding period (Naranjo et al., unpublished).

of mortality can overcome this problem in life table analyses (Royama, 1981; Elkinton et al., 1992), but this method cannot be readily applied to leaf census data.

This leads to a third factor involving problems in detecting early stages of parasitism. Parasitoids may oviposit in, and even prefer, early nymphal stages (Liu and Stansly, 1996b; Jones and Greenberg, 1998), even though the bulk of development occurs in the final host stadium. In the Hoelmer (1996) example above, the highest level of parasitism was found when all 4th instar hosts were dissected to determine the presence or absence of parasitoid eggs and early instar larvae. This approach probably yields a more accurate estimate of parasitism, because it reduces the developmental asynchrony problem leading to a more realistic estimate of available hosts within the same generational cohort. Dissection also assesses some parasitoid-induced mortality before other factors such as predation can act. The approach is more costly, because of the extra time required for dissections. The recruitment method advocated by Van Driesche et al. (1991) in which the recruitment of both parasitoids and susceptible hosts are estimated over time, also could lead to more accurate estimates of generational parasitism, especially if early parasitoid stages are monitored.

A fourth factor, and one that is rarely acknowledged, involves the measurement of other sources of immature mortality acting on *B. tabaci* populations. As noted above, this factor may be important in estimating marginal rates of mortality associated with parasitism. It is also fundamental to interpreting the impact of parasitism on pest population suppression and regulation, and may even influence the validity of using simple measures of apparent parasitism to compare experimental treatments. A simple simulation model is

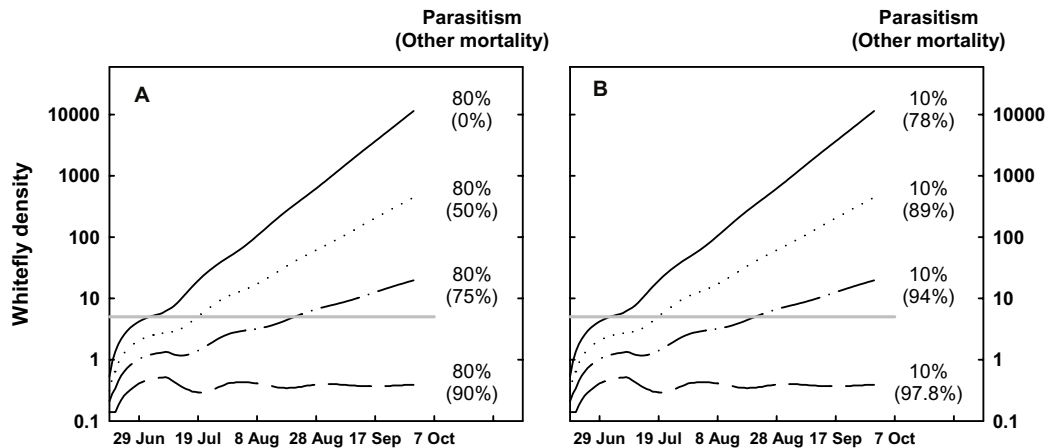


Fig. 6. Simulations of *B. tabaci* population dynamics in relation to specified generational rates of parasitism and other mortality factors (see text for details). (A) Parasitism held constant at 80% over all generations; (B) parasitism held constant at 10% over all generations. The gray horizontal line denotes the current action threshold for adult *B. tabaci*.

presented to illustrate this problem (Fig. 6). Constant levels of irreplaceable mortality were applied to a stage-structured population model of *B. tabaci* over a representative period of a cotton growing season in the southwestern USA. Simulations were initialized with one adult per unit density, used immature developmental rates typical of summer populations in Arizona cotton, and assumed that females laid 100 eggs (1:1 sex ratio) over a lifetime of 20 days. The four population trajectories in each panel display four outcomes based on constant levels of parasitism with changing levels of other immature mortality factors. Results clearly demonstrate the difficulty of equating levels of parasitism with potential pest suppression. Eighty percent parasitism of 4th instar nymphs (Fig. 6A) could be associated with exponentially increasing populations, populations displaying damped oscillations leading to regulation, or populations displaying exponential growth but where densities exceed the economic threshold at progressively later dates. These outcomes depend simply on the levels of other sources of mortality. Thus, high levels of parasitism, which are often reported in the literature, are not necessarily associated with control. Likewise, low levels of parasitism are not necessarily associated with lack of control potential. When accompanied with 97.8% mortality from other factors, 10% parasitism may supply a crucial level of irreplaceable mortality leading to population suppression below economic levels (Fig. 6B). The issue of density-dependence was not explicitly examined here, but it would not alter the fact that differential levels of other immature mortality can significantly alter population trajectories and confuse interpretation of parasitism levels.

These simulations also point out potential problems in using percentage parasitism as a measure of treatment effects in experimental studies. This is especially true if these measurements are being used to infer differential

impact of parasitoids. The use of apparent parasitism to compare experimental treatments relies on the important assumption that all else is equal. However, differential mortality from other sources among the treatments may obscure real generational effects of parasitoids that are not obvious from change, or lack of change, in simple percentage parasitism. For example, insect growth regulators such as buprofezin, and especially pyriproxyfen, can cause elevated levels of mortality in 1st instar nymphs and eggs compared with conventional or no insecticides. Comparison of rates of parasitism in 4th instar nymphs among these treatments must account for these differential mortalities early in the life cycle in order for the generational contribution of parasitism to be correctly interpreted for each experimental treatment. One can easily envision other treatment regimes that may alter patterns of age-specific mortality, and researchers need to be cognizant of these factors.

Overall, the reporting of percentage parasitism should be accompanied with information of host population density and whether pest populations are increasing or declining. This would provide some evidence of whether parasitism is contributing to suppression and could be used to design further, more definitive studies to test this hypothesis. Better yet would be information on other sources and rates of mortality. Such data could be crucial in assessing the effects of experimental treatments on parasitism as noted above, and in correctly estimating and interpreting the effects of a given level of parasitism on pest population dynamics.

2.4.2. Life table analyses

Because a large number of factors are likely to affect populations of *B. tabaci* in agricultural systems (see Section 2.1), life table studies are a potentially useful approach for structuring, quantifying, analyzing, and

interpreting mortality factors and interactions among mortality sources in pest management systems. With additional information on pest population densities and reproductive output, life tables also can provide an understanding of mechanisms underlying population dynamics and the contribution of natural enemies to these dynamics. To exemplify this approach, results from recent life table studies in Arizona cotton are summarized (also see Ellsworth and Martinez-Carrillo, 2001). These studies have focused on identifying and quantifying sources and rates of mortality affecting immature *B. tabaci*, and on understanding the interaction and contribution of natural enemy-induced mortality under different pest management strategies. Manuscripts detailing these studies are currently in preparation.

As discussed, immature stages of *B. tabaci* are subject to high levels of mortality from various sources in cotton (see Fig. 4). These levels of mortality are insufficient in most years to suppress pest populations, season-long, below economic levels. Thus, intervention with insecticides is typically necessary. During the early years of the whitefly outbreak in the southwestern USA, broad-spectrum insecticides were widely used. This practice largely precluded any biological control by indigenous natural enemies and was problematic to ongoing introductions of exotic parasitoids in the region (e.g., Hoelmer, 1996). Beginning in 1996, the insect growth regulators buprofezin and pyriproxyfen came into widespread use in Arizona under an USA–EPA emergency exemption. The selectivity of these materials to various natural enemies has been demonstrated in both laboratory and field evaluations (see Section 2.2.1), but the overall value of these materials in preserving natural enemy activity were unknown. To begin answering this question, life table studies were conducted in replicated cotton fields that received prescriptive applications of buprofezin, pyriproxyfen, or conventional insecticides. These treatments were contrasted with one another and with untreated fields over a three year period. The approach involved the establishment of natural cohorts of eggs and 1st instar nymphs from field populations that were observed every 2–3 days until adult emergence or death. Representative results from 1997 studies are highlighted below.

Partial results from two post-insecticide generations indicated that insecticides contributed substantial marginal rates of mortality to cohorts established immediately before sprays were applied (54.9–68.9%). As expected, this mortality component declined considerably in cohorts established two weeks after spraying (14.9–23.9%). Marginal rates of natural enemy mortality, especially that caused by sucking predators was substantial in untreated fields (74.1%), but significantly compromised in fields treated with conventional insecticides (37.1%). Mortality from predation was intermediate in fields treated with the insect growth regulators in

the first post-spray cohort (48.9–60.1%), but these levels rebounded and became indistinguishable from untreated fields within two weeks after application (65.5–72.9%). Marginal rates of parasitism were minor (0–8.1%) in all instances, and patterns were generally unaffected by insecticide treatment. Control of *B. tabaci* was achieved in all fields receiving insecticides (Fig. 7), but the manner in which control was attained differed among treatments. Survivorship curves for the various treatments (not shown) revealed that all insecticides functioned by contributing only a small amount (≈ 3 –4%) of irreplaceable mortality. However, while only a single spray of either of the insect growth regulators was required to maintain control, five applications of conventional insecticides were needed to achieve the same result. The insect growth regulators functioned by first replacing some mortality from predation and parasitism, and contributing an immediate, and essential, level of irreplaceable mortality. However, because these materials did not significantly disrupt the natural enemy complex, biological control was able to contribute to pest suppression for the remainder of the season. Thus, it was not the residual activity of the insecticides themselves that permitted long term control but the preservation of biological control activity (“bio-residual”). In contrast, repeated applications of conventional insecticides were required for control, because natural enemy populations (especially predators) were reduced and unable to contribute significant irreplaceable mortality. These studies demonstrate the role of multiple mortality factors in managing *B. tabaci* and provide a mechanistic understanding of the important contribution of conservation biological control.

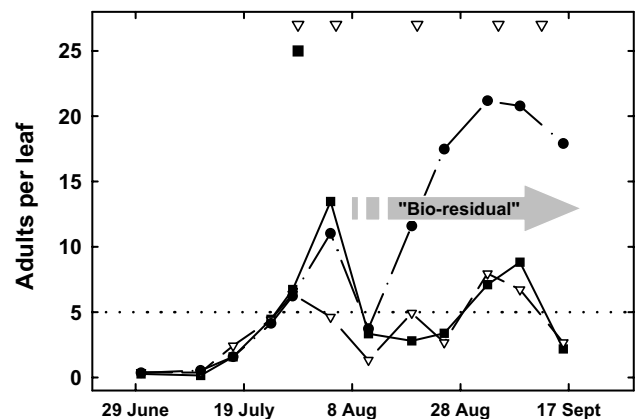


Fig. 7. Comparative population dynamics of *B. tabaci* under different pest management regimes, Arizona, USA, 1997. The dotted horizontal line denotes the current action threshold. Population trends in untreated control field (closed circles), and trends and application dates in fields receiving IGRs (closed squares) or a rotation of conventional insecticides (open triangles) are shown. Continued pest suppression in the IGR fields arises from the conservation of natural enemies and their subsequent activity, and highlights the “bio-residual” effect of these materials (Naranjo and Ellsworth, unpublished).

3. Conclusions and future research needs

The geographic expansion of *B. tabaci* over the last several decades has resulted in an exponentially increasing research effort into all aspects of pest biology, ecology, host–plant interactions, virus–vector relationships, biological control, and pest management. Although research in the area of biological control has assumed a relatively small proportion of the overall research effort, this area has been expanding since the mid 1980s. Large numbers of arthropod predator, parasitoid and fungal species are known to attack *B. tabaci* in a variety of agricultural systems worldwide. Some studies suggest that there is potential for these agents to exert biological control of this pest. However, much work will be required before biological control assumes a larger and more dominant role in pest management systems for *B. tabaci* in most affected crops. Conservation of natural enemies is a fundamental element in all biological control approaches and has probably been the most active area of research in biological control of *B. tabaci*. Unfortunately, progress in fully developing, evaluating and implementing conservation biological control has been slow. Most research to date is still descriptive with considerably less research addressing factors that may minimize disruption or enhance the abundance and activity of existing natural enemies. Even less research is devoted to determining the overall impact of conserved natural enemies on pest suppression. The following are suggested avenues of research that may advance our understanding and use of conservation biological control in pest management systems for *B. tabaci*.

1. Survey work should continue to refine the region- and crop-specific natural enemies of *B. tabaci*. Emphasis should be placed on definitive pest-natural enemy associations determined in the field, especially for predators. Many predators may simply be opportunists that feed only infrequently on *B. tabaci*. These species would be poor candidates for further study.
2. Criteria should be developed to help narrow these refined lists to only the most promising species. Such criteria are useful in defining target natural enemies for augmentation programs in protected agricultural systems (e.g., Drost et al., 1996; Heinz and Parrella, 1998). Obvious criteria might include consistent presence of the natural enemy in the affected crop, preference for *B. tabaci*, tolerance to commonly used insecticides, and ability to locate prey at low densities.
3. Because insecticides are likely to remain a major component of most systems, especially those with multiple pest species, the overall effects of both broad-spectrum and selective materials need to be

defined in the field. Laboratory studies provide valuable data on potential risk, but both lethal and sublethal effects need to be determined in the field. These effects need to be integrated to determine overall impacts on population dynamics and feeding activity. Ecological selectivity of insecticides should be more fully explored.

4. The effects of other potentially disruptive factors need to be better defined and studied. Intraguild predation is likely to be pervasive in many systems affected by *B. tabaci*. The population level effects of this and other species interactions, such as competition, require further study. The importance of the host plant in mediating predator-prey and host-parasitoid interactions has been demonstrated for some systems. Further investigation of these tri-trophic interactions could lead to strategies for minimizing disruption and well as enhancing the habitat for more effective biological control.
5. The development and use of refuges for habitat enhancement is in its infancy. Promising results from the southwestern USA suggest that such approaches should be pursued more vigorously. One of the major problems in most semi-arid regions is spatially and temporally discontinuous habitat for support of natural enemy populations.
6. Whitefly researchers have largely failed to take advantage of a number of well-defined experimental methods for determining the impact of natural enemies on pest population dynamics and control. These tools should be more widely utilized during all phases of the development of conservation biological control programs. I advocate the use of life tables as an underlying methodology for understanding and interpreting the contribution of natural enemies within the context of other mortality factors simultaneously affecting populations of *B. tabaci*.

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