ELSEVIER

Crop Protection 20 (2001) 779–799

Crop Protection

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Review article

Biological control of *Bemisia tabaci* using predators and parasitoids ☆

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Received 28 November 2000; received in revised form 9 July 2001; accepted 20 July 2001

Abstract

Bemisia tabaci is an extremely polyphagous pest that causes direct damage and can act as a vector of viral plant diseases. The activity of natural enemies can be exploited by employing proper conservation and augmentation techniques. In addition to use of extant fauna, importation of parasitoids belonging to the genera *Encarsia* and/or *Eretmocerus* and of various predators has been successfully employed in greenhouses and out of doors. Biological control practice in greenhouses differs greatly in warmer climates, where interchanges of the pest and its enemies with the outdoor environment are possible, than in cold countries where the crop is more isolated. Recent successes in the biological control of *Trialeurodes vaporariorum* and *B. tabaci* in greenhouses and out of doors lead the way to a better understanding of the types of studies necessary for implementing future programs. Although certain natural enemy species have proven effective components in *B. tabaci* control, there are still unexplored, potentially valuable species in many areas of the world. This paper reviews the identity and biological attributes of known natural enemies, summarizes the studies conducted on them during the last decade, reviews current efforts in biological control of *B. tabaci* in greenhouse and field crops, and highlights research gaps and directions deserving further development. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: *Bemisia tabaci*; *Bemisia argentifolii*; Classical biological control; Augmentation; Conservation

Contents

☆ 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.

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PII: S0261-2194(01)00111-9

1. Introduction

Bemisia tabaci has been spreading into new territories and causing extensive damage for almost a century and continues to be a severe pest mainly of field crops and vegetables in many parts of the world. There is growing interest in finding control methods for *B. tabaci* other than the use of insecticides, particularly in regions unable or unwilling to sustain heavy pesticide usage. In addition, the rapid build-up of insecticide resistance in this pest calls for alternative management solutions for dealing with pest outbreaks.

Biological control of whiteflies in general has an interesting history. Many attempts at controlling whitefly pests using natural enemies have ended in complete success (e.g. Onillon, 1990). Biological control in one case, that of the greenhouse whitefly, *Trialeurodes vaporariorum,* resulted in a new technique and an associated new term ("seasonal inoculative release") (van Lenteren, 1986). *B. tabaci,* however, has defied most attempts of control using natural enemies and is problematic in much of the world (Oliveira et al., 2001). Predators and parasitoids of *B. tabaci* have been described and studied for many years, but the most intensive efforts to use them in biological control programs have been undertaken following recent severe outbreaks (ca. 1987 to the present). In this review, we will describe the natural enemies that are presently available for the biological control of *B. tabaci*. The first section updates biological information published in the last decade and supplements previous work (e.g. van Lenteren, 1986; Gerling, 1990a; Cock, 1993; Gerling and Mayer, 1996). We then discuss current approaches and case histories of biological control of *B. tabaci*. To a limited degree we also examine biological control of *T. vaporariorum*, which is often a contemporaneous pest. Based on experiences with both whitefly species, we conclude by presenting a list of points for further research that may help in the planning and implementation of future biological control programs. Faria and Wraight (2001) discuss fungal pathogens as biological control agents of *B. tabaci*, and Naranjo (2001) focuses more specifically on the conservation and evaluation of predators and parasitoids in IPM systems for this pest.

2. Predators

2.1. Identity

The contribution of indigenous predators in delaying pest density increases has not been fully addressed. Understanding how predators influence whitefly densities in the field has been rudimentary, and their contribution has often been undervalued (see Naranjo, 2001). One problem is the difficulty of identifying predators of *B. tabaci*, especially in crops that harbor numerous predator and prey species. Another factor is that the potential of many predator species in reducing the pest is only recognized following the establishment and outbreak of *B. tabaci* populations in new areas. Consequently, the inventory of *B. tabaci* predators is continuously changing both as to the number of included species and their utility as biological control agents. *B. tabaci* predators include arthropods belonging to 9 orders and 31 families. This compilation (Table 1) is based on an update of previous lists (Gerling, 1986; López-Avila, 1986; Cock, 1993; Nordlund and Legaspi, 1996) and accounts for synonymies of major predator groups. Most *B. tabaci* predators are beetles (Coccinellidae), true bugs (Miridae, Anthocoridae), lacewings (Chrysopidae, Coniopterygidae), mites (Phytoseiidae) and spiders (Araneae). Only few natural enemy species have been studied in detail, and for many, records are limited to laboratory observations or qualitative field records. Biological control potential has been examined in only a few species (e.g., *Delphastus catalinae* and *Serangium parcesetosum* [Coccinellidae], *Macrolophus caliginosus* [Miridae], *Chrysoperla carnea* and *C. rufilabris* [Chrysopidae]). Presently, some predators are commercially available for *B. tabaci* or other pests (Table 1).

2.2. Biology

The host range of *B. tabaci* predators may be affected by the nutritional qualities of the host. Cohen and Brummett (1997) reported that the relative lack of methionine makes *B. tabaci* a less suitable prey for the development and reproduction of many predator species in comparison with aphids. Thus, predators range from

Table 1
Predators recorded for *B. tabaci*

Taxa	References[a]	Remarks[b]
ACARI		
Phytoseidae		
Amblydromella sudanica (= *Typhlodromus sudanicus*)	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R
Amblyseius olivi	Abou-Awad et al. (1998)	S
Amblyseius sp.	Cock (1993)	R
Cydnoseius medanicus (= *Typhlodromus medanicus*)	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R
Cydnoseius negevi	El-Banhawy et al. (1999)	S
Euseius aleyrodis (= *Amblyseius aleyrodis*)	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	S
Euseius gossipi	Cock (1993)	R
Euseius hibisci	López-Avila (1986), Nordlund and Legaspi (1996)	S
Euseius scutalis (= *Amblyseius deliensis*), (= *A. gossipi*), (= *A. rubini*)	Gerling (1986), López-Avila (1986), Cock (1993), Nordlund and Legaspi (1996)	S
Galendromus occidentalis (= *Typhlodromus occi dentalis*)	López-Avila (1986), Nordlund and Legaspi (1996)	R, C
Neoseiulus californicus (= *Amblyseius chilenensis*)	López-Avila (1986), Nordlund and Legaspi (1996)	R, C
Neoseiulus cucumeris	Nawar and El-Sherif (1993)	S, C
Neoseiulus cydnodactylon (= *Amblyseius cydnodac tylon*)	El-Banhawy et al. (2000)	S
Typhlodromus athiasae	López-Avila (1986), Nordlund and Legaspi (1996)	R
Typhlodromalus limonicus (= *Amblyseius limonicus*)	López-Avila (1986), Nordlund and Legaspi (1996)	R
Typhlodromips swirskii (= *Amblyseius swirskii*)	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R
Stigmaeidae		
Agistemus exsertus	López-Avila (1986)	S
ARANEAE		
Araneidae		
Neoscona arabesca	Nordlund and Legaspi (1996)	R
Clubionidae		
Undetermined sp.	Nordlund and Legaspi (1996)	R
Dictynidae		
Dictyna annexa	Nordlund and Legaspi (1996)	R
Dictyna bellans	Nordlund and Legaspi (1996)	R
Phantyna segregata	Nordlund and Legaspi (1996)	R
Linyphiidae		
Undetermined sp.	Nordlund and Legaspi (1996)	R
Tetragnathidae		
Tetragnatha sp.	Nordlund and Legaspi (1996)	R
Theridiidae		
Achaearanea sp.	Nordlund and Legaspi (1996)	R
Dipoena abdita	Nordlund and Legaspi (1996)	R
Latrodectus sp.	Nordlund and Legaspi (1996)	R
Theridion australe	Nordlund and Legaspi (1996)	R
Theridula gonygaster	Castiñeiras (1995)	R
Theridula opulenta	Dean (1994)	R
Theridula sp.	Castiñeiras (1995)	R
Thomisidae		
Misumenops sp.	Nordlund and Legaspi (1996)	R
Uloboridae		
Philoponella sp.	Nordlund and Legaspi (1996)	R
Uloborus sp.	Nordlund and Legaspi (1996)	R

Table 1 (*continued*)

Taxa	References[a]	Remarks[b]
COLEOPTERA		
Coccinellidae		
Brumoides suturalis	Gerling (1986), López-Avila (1986), Cock (1993), Nordlund and Legaspi (1996)	R
Brumus sp.	López-Avila (1986)	R
Cheilomenes sexmaculata (= *Menochilus sexmaculata*)	López-Avila (1986), Cock (1993)	R
Clitostethus arcuatus	Osborne et al. (1990)	S
Coccinella septempunctata	Gerling (1986), López-Avila (1986), Cock (1993), Nordlund and Legaspi (1996)	R, C
Coccinella undecimpunctata	Cock (1993)	R
Coleomegilla maculata	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R, C
Coleomegilla maculata cubensis	Alvarez and Abad-Antún (1995)	R
Cryptolaemus montrouzieri	Nordlund and Legaspi (1996)	R, C
Cycloneda sanguinea	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R
Delphastus pallidus	Castiñeiras (1995)	R
Delphastus pusillus	Nordlund and Legaspi (1996)	R, C
Eriopis connexa	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R
Hippodamia convergens	Nordlund and Legaspi (1996)	R, C
Harmonia dimidiata (= *Leis dimidiata*)	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R
Micraspis inops (= *Micraspis vincta*)	Cock (1993)	R
Nephaspis oculatus	Hoelmer et al. (1994)	S
Nephaspis gemini	Oliveira, personal communication	R
Nephaspis maesi	Cock (1993)	R
Scymnus sp.	López-Avila (1986)	R
Scymnus syriacus	Gerling (1986), Nordlund and Legaspi (1996)	R
Serangium n. sp.	Hoelmer and Kirk (1999)	R
Serangium cinctum	Gerling (1986), Nordlund and Legaspi (1996)	R
Serangium parcesetosum (= *Catana parcesetosa*)	Gerling (1986), López-Avila (1986), Cock (1993), Nordlund and Legaspi (1996)	S
Melyridae		
Collops vittatus	Nordlund and Legaspi (1996)	R
Nitidulidae		
Cybocephalus sp.	Nordlund and Legaspi (1996)	R
Cybocephalus binotatus	Nordlund and Legaspi (1996)	R
Staphylinidae		
Paederus fuscipes	Cock (1993)	R
DIPTERA		
Cecidomyiidae		
Aphidoletes aphidimyza	Cock (1993)	R, C
Muscidae		
Coenosia attenuata	Cock (1993)	R
Dolichopodidae		
Condylostillus sp.	Alvarez and Abad-Antún (1995)	R
Drosophilidae		
Acletoxenus formosus	Hoelmer and Kirk (1999)	R
Syrphidae		
Allograpta obliqua	Nordlund and Legaspi (1996)	R
Empididae		
Drapetis subaenescens	Nordlund and Legaspi (1996)	R
Tachidronia annulata	Nordlund and Legaspi (1996)	R

Table 1 (*continued*)

Taxa	References[a]	Remarks[b]
HEMIPTERA		
Anthocoridae		
Cardiastethus assimilis	Dean (1994)	R
Orius albidipennis	López-Avila (1986), Cock (1993)	R, C
Orius insidiosus	Dean (1994)	R, C
Orius strigicollis	Wang (1998)	R
Orius tantillus	Wang (1998)	R
Orius tristicolor	Nordlund and Legaspi (1996)	R, C
Orius spp.	Gerling (1986), Cock (1993), Nordlund and Legaspi (1996)	R
Lygaeidae		
Geocoris ochropterus	Nordlund and Legaspi (1996)	R
Geocoris punctipes	Nordlund and Legaspi (1996)	R, C
Geocoris pallens	Nordlund and Legaspi (1996)	R
Miridae		
Campylomma verbasci (= *C. nicolasi*)	Nordlund and Legaspi (1996)	R
Engytatus varians (= *Cyrtopeltis varians*)	Castiñeiras (1995)	R
Engytatus modestus (= *Cyrtopeltis modestus*)	Vázquez, personal communication	R
Deraeocoris sp.	Nordlund and Legaspi (1996)	R
Deraeocoris annulipes (= *D. nebulosus*)	Jones and Snodgrass (1998)	S
Deraeocoris indianus	Cock (1993)	R
Deraeocoris pallens	Cock (1993), Nordlund and Legaspi (1996)	S
Dicyphus hyalinipennis	Ceglarska (1999)	S
Dicyphus tamaninii	Albajes et al. (1996), Barnadas et al. (1998)	S
Lygus hesperus	Nordlund and Legaspi (1996)	R
Macrolophus caliginosus[c]	Nordlund and Legaspi (1996)	R, C
Nesidiocoris tenuis	Vacante et al. (1994)	S
Nabidae		
Nabis spp.	Nordlund and Legaspi (1996)	R
Reduviidae		
Sinea confusa	Nordlund and Legaspi (1996)	R
Zelus spp.	Nordlund and Legaspi (1996)	R
HYMENOPTERA		
Ceraphronidae		
Aphanogmus fumipennis	Gerling (1986), Nordlund and Legaspi (1996)	R
NEUROPTERA		
Chrysopidae		
Brinckochrysa scelestes	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	S
Ceraeochrysa cubana	Dean and Schuster (1995)	S, C
Ceraeochrysa cincta	Auad, personal communication	S
Chrysopa cymbele	Gerling (1986), López-Avila (1986)	R
Chrysopa exterior	Castiñeiras (1995)	R
Chrysopa formosa	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R, C
Chrysoperla carnea	Gerling (1986), López-Avila (1986), Cock (1993), Nordlund and Legaspi (1996)	S, C
Chrysoperla externa	Dean (1994)	S
Chrysoperla rufilabris	Nordlund and Legaspi (1996)	R, C
Mallada boninensis	Cock (1993), Nordlund and Legaspi (1996)	S
Mallada flavifrons (= *Anisochrysa flavifrons*) (= *Chrysopa flavifrons*)	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R
Nineta flava (= *Chrysopa flava*)	Gerling (1986), López-Avila (1986), Nordlund and Legaspi (1996)	R
Leucochrysa (*Nodita*) *firmini*	Vázquez, personal communication	R
Plesiochrysa lacciperda	Nordlund and Legaspi (1996)	R
Coniopterygidae		
Semidalis flinti	Hoelmer and Kirk (1999)	S
Conwenzia africana	Legg and Gerling (personal observations)	R

Table 1 (*continued*)

Taxa	References[a]	Remarks[b]
ODONATA		
Coenagrionidae		
Enallagma civile	Schaefer et al., (1996)	R
THYSANOPTERA		
Aeolothripidae		
Franklinothrips vespiformis	Arakaki and Okajima (1998)	R, C
Phalaeothripidae		
Undetermined sp.	Nordlund and Legaspi (1996)	R

[a] Gerling (1986); López-Avila (1987); Cock (1993); Nordlund and Legaspi (1996) are prior review articles listing known predator species of *B. tabaci* from the primary literature.
[b] R: field reports and laboratory tests on predation; S: any biology study with *B. tabaci* as prey; C: commercially available (not necessarily for *B. tabaci*).
[c] *Macrolophus melanotoma* according to Carapezza (1995).

generalists that require additional, methionine rich, foods to specialists whose metabolism is adjusted to the specific biochemical composition of whiteflies. Generalist predators often exhibit behavioral plasticity and are able to feed on several prey species shifting from one to the next as availability changes. Such feeding on mixed diets may improve predator performance as compared to feeding on single-prey diets (Dean and Schuster, 1995). This behavioral plasticity may also enable predators to exploit alternative prey when *B. tabaci* populations are low or temporarily absent. For example, warm climate greenhouse systems are often plagued by a sequential appearance of *T. vaporariorum*, and *B. tabaci*, and the behavioral plasticity of predators assures their long-term residence, facilitating predation on both pest species.

2.2.1. Coccinellidae

B. tabaci are preyed upon by many species of Coccinellidae, which are considered important natural enemies of whiteflies in general and may exhibit various degrees of oligophagy (Obrycki and Kring, 1998). *Serangium parcesetosum* feeds on various whitefly species (Abboud and Ahmad, 1998) including *Dialeurodes citri* on citrus (Uygun et al., 1997) and *B. tabaci* on cotton. Its preference for whiteflies has been demonstrated in choice tests where it rejected eggs of Lepidoptera in favor of eggs and nymphs of *B. tabaci* (Legaspi et al., 1996b). *Clitostethus arcuatus*, another predator of several whitefly species (Booth and Polaszek, 1996), preys more on *B. tabaci* than on aphids (Kirk and Thistlewood, 1999). *Delphastus catalinae* (previously misidentified as *D. pusillus*) feeds on immature whitefly, but there are conflicting reports on prey consumption rates and whether oviposition is affected by the whitefly stage consumed (Hoelmer et al., 1993; Heinz and Parrella, 1994a). This species' reproduction requirements underlie its association with high whitefly densities (Gerling and Stern, 1993; Hoelmer et al., 1993; Heinz and Parrella, 1994a). Thus, *D. catalinae* would probably not persist with low whitefly populations, and its capacity to feed on alternative foods like spider mites (Hoelmer et al., 1993) may be crucial for its survival. Another coccinellid predator of whitefly, *Nephaspis oculatus* consumes fewer whiteflies and has a more efficient searching behavior than *D. catalinae*. Therefore, it may survive and reproduce under conditions of relatively low whitefly densities (Liu et al., 1997; Liu and Stansly, 1999).

2.2.2. Heteroptera

Heteroptera are usually polyphagous and prey specificity is rare (Riudavets, 1995; Fauvel, 1999). *Macrolophus caliginosus*, *Dicyphus tamaninii* and *D. hyalinipennis* (Miridae), and species of *Orius* (Anthocoridae) are predators of aphids (Alvarado et al., 1997; Ceglarska, 1999) and thrips (Riudavets and Castañé, 1998) in addition to feeding on *B. tabaci* and on *T. vaporariorum*. The two former species show some preference for the greenhouse whitefly when presented with mixed populations (Arnó, 1997; Barnadas et al., 1998). Several Heteroptera (*Geocoris* spp., *Orius tristicolor* and *Lygus hesperus*) are frequent predators of both *B. tabaci* and *Pectinophora gossypiella* on cotton (Hagler and Naranjo, 1994a). The Old World species *Deraeocoris pallens* preys on *B. tabaci* and on several other cotton pests (Gerling and Kravchenko, 1996; Ghavami et al., 1998), whereas in the New World, *D. nebulosus* can develop and reproduce using *B. tabaci* and other Homoptera as prey (Jones and Snodgrass, 1998).

2.2.3. Neuroptera

Chrysopids prey on whiteflies (Nordlund and Legaspi, 1996), but are mainly aphid predators (Tauber et al., 2000). In laboratory experiments both *Chrysoperla rufilabris* and *Ceraeochrysa cubana* were able to complete development on immature *B. tabaci* alone, but developmental periods were shortest on a mixed diet of whitefly and *Macrosiphum euphorbiae*. Moreover, *C. cubana* preferred whiteflies to aphids, but *C. rufilabris* did not (Dean and Schuster, 1995). Variable reports exist regarding development and maturation of *C. carnea* when feeding on whiteflies. Senior and McEwen (1998) reported that *C. carnea* failed to complete development on *T. vaporariorum*, and Lazare (1994) found that it preferred *Aphis gossypii* to *B. tabaci*. However, Balasubramani and Swamiappan (1994) reported that the development of *C. carnea* was faster on *B. tabaci* than on *A. gossypii* or moth eggs. Unfortunately, no comparisons were performed among the *C. carnea* populations originating in the different geographical regions in order to determine the presence of intraspecific differences.

Recently, at least two species of Coniopterygids were found feeding on *B. tabaci*. Hoelmer and Kirk (1999) reported preliminary studies with *Semidalis flinti*, and Legg and Gerling (unpublished) observed *Conwentzia africana* preying on all immature stages of *B. tabaci* on cassava in several African countries. In addition, Gerling (unpublished) observed an unidentified Coniopterygid larva feeding on whitefly nymphs in pepper greenhouses in Spain.

2.2.4. Phytoseiidae

The diet of Phytoseiid mites may include several whitefly and mite species as well as pollen (Nawar and El-Sheriff, 1993; McMurtry and Croft, 1997; Abou-Awad et al., 1998; El-Banhawy et al., 2000). The presence of *B. tabaci* on the host plant reduced predation of two-spotted spider mites by *Cydnoseius negevi* while increasing the predator's reproduction, suggesting higher quality of a mixed diet over two-spotted spider mites alone (El-Banhawy et al., 1999). *Typhlodromus swirskii* and *Euseius scutalis* appear to be promising biological control agents against *B. tabaci* based on their high intrinsic rates of increase in the laboratory (Nomikou et al., 2001) and their ability to suppress whitefly populations on isolated plants in a greenhouse (Nomikou, personal communication).

2.2.5. Host plant effects

Predator survival, behavior and control efficacy may be affected by plant characteristics directly or indirectly through their effect on the prey. The plant species may determine the success of a natural enemy. Legaspi et al. (1996b) reported higher survival of the coccinellid *S. parcesetosum* on hibiscus than on tomato, cantaloupe or cucumber, but whitefly predation rates were higher on cucumber than the other plant species. Legaspi et al. (1994, 1996c) reported that *C. rufilabris* feeding on *B. tabaci* successfully developed on cantaloupe and cucumber, but was unable to reach adulthood on a diet of *B. tabaci* when the whitefly was reared on poinsettia or lima beans despite feeding voraciously on *B. tabaci* eggs and nymphs. Whiteflies reared on these plants may have been nutritionally inadequate, although some direct effects via plant feeding was also assumed when larvae had no prey available (Legaspi et al., 1994, 1996c). Dean and Schuster (1995) reported 95% of *C. rufilabris* nymphs surviving to adulthood when *B. tabaci* were offered on *Hibiscus rosa-sinensis*.

Predatory Heteroptera have been shown to obtain extra benefit from plant feeding to various degrees and may use plant juices as a source of water and/or nutrients (Naranjo and Gibson, 1996; Coll, 1998). In addition, they depend on the host plants as oviposition substrates. Such dependence may mask the preference of predators for their prey (Riudavets and Castañé 1998).

Differences in *D. catalinae* behaviour on different plant cultivars have also been found. Heinz and Zalom (1996) reported that walking speed and lifetime fecundity were reduced on a pubescent compared to a glabrous cultivar of tomato, but residence times of the predator were longer on the pubescent plant. Together, a counterbalancing effect was produced and, as a result, predation efficiency of *B. tabaci* by *D. catalinae* on pubescent tomato leaves remained unaffected. Similarly, Guershon and Gerling (1999) reported no difference in prey consumption on smooth vs. pubescent cotton leaves, even though leaf hairiness modified the predator's behavior. In comparison, Heinz and Parrella (1994a) examined five natural enemy species and found an overall reduction in oviposition and prey consumption on poinsettia when trichome density increased.

2.3. Utility

Diverse methods have been employed to overcome the difficulty of evaluating the role of *B. tabaci* predators in the field (see also Naranjo, 2001). Hagler and Naranjo (1994a, b) used immunological methods to identify predators of *B. tabaci* in Arizona cotton through gut-content analysis. Naranjo and Ellsworth (1999) used an observational technique to develop life tables for *B. tabaci*. They found that predation was a major mortality factor in Arizona cotton. Various census and correlation methods have also been used. Based on sampling of *B. tabaci* and predators in Israeli cotton, Gerling (1996) reported that whitefly population declined during several years following high initial whitefly populations. These declines could not be explained by changes in the levels of parasitism and were not associated with the arrival of new species of natural enemies, therefore they were attributed to changes in the dietary preferences of native generalist predators. Gerling and Kravchenko (1996) showed a rise in *B. tabaci* and a decline in predator populations, especially for *Orius* spp. following the use of insecticides in cotton fields. Using a similar approach, *C. carnea*, another common predator, was determined to be an ineffective control agent of *B. tabaci* in cotton (Gerling et al., 1997). The polyphagous *Nesidiocoris tenuis* is considered a useful predator in the Canary Islands (Carnero et al., 2000), and augmentative releases of *D. pallens* in greenhouse eggplant provide effective control of *B. tabaci* (Ulubilir et al., 1997).

Zoophytophagy (feeding on plants in addition to prey) may increase predator utility. For example, several predatory Heteroptera in cotton (*Geocoris* spp., *Orius* spp., *Deraeocoris* spp.) or vegetables (*Macrolophus* spp.) may colonize plants and establish resident populations in the crop early in the season, a time of low prey densities, and help prevent later pest build-ups (Ehler and Miller, 1978; Alomar et al., 2001). Moreover, supplementing prey diet with plant material may accelerate nymphal development, increase nymphal and adult longevity and survival, and enhance fecundity (Naranjo and Gibson, 1996). However, plant feeding by some species of predatory Heteroptera may cause economic injury (Schaefer and Panizzi, 2000) making their use controversial. Risk to the crop is more acute when the predators switch to feed on plants due to prey depletion, especially late in the season when the fruits are ripening. Specific management practices, like the selective use of insecticides, must be adopted to avoid risk to the crop while still profiting from predation of the whitefly (Alomar and Albajes, 1996; Alomar, 2001).

3. Parasitoids

3.1. Identity

The listed fauna of *B. tabaci* parasitoids is extensive, but relatively few have been studied or are intentionally used for pest control (Table 2). This is partly due to poor knowledge of their taxonomy, biology and/or ecology. A complete listing of all parasitoid host ranges and regional affiliations is not possible at present because of the state of flux in ongoing importation and survey efforts. Noyes (1998) listed 23 species of *Encarsia* and 10 species of *Eretmocerus*. Goolsby et al. (2000) reported the importation and handling of 7 *Encarsia* and 9 *Eretmocerus* species, whereas Schuster et al. (1998) found 12 species of *Encarsia* in their survey of *B. tabaci* parasitoids in Florida, the Caribbean, and Central and South America. Together, these studies report 28 species of *Encarsia* and 12 species of *Eretmocerus* attacking *B. tabaci*. The reports also mention undetermined species attributed either to a known species complex (e.g. "*meritoria* complex" or "*strenua* complex" of Schuster et al. (1998)) or simply as *Eretmocerus* or *Encarsia* spp. Following recent taxonomic revisions and new findings, we list 34 species of *Encarsia* (including 3 records that require confirmation) that were reared from *B. tabaci* in the field, and one association, *Eretmocerus tricolor*, that was found during laboratory experiments. We found 11 recognized species of *Eretmocerus*, three additional taxonomic entities (*emiratus* from Ethiopia, uniparental *mundus* from Australia, and nr. *furuhashi*) and an undescribed *Eretmocerus* sp. Biological studies have been conducted on 11 *Encarsia* and 8 *Eretmocerus* spp. (Table 2).

Collection, identification and classification of *B. tabaci* parasitoids have been intensive during the last decade. Here we review the main results of these efforts. Primary parasitoids of *B. tabaci* are known from the genera *Encarsia*, *Eretmocerus* (Hymenoptera, Aphelinidae) (Gerling et al., 1980) and *Amitus* (Hymenoptera, Platygasteridae) (Joyce et al., 1999). In addition, a *Metaphycus* sp. (Hymenoptera, Encyrtidae) has been recorded (Polaszek et al., 1992) from *B. tabaci*. Hyperparsitic *Signiphora* spp. have also been recorded (Table 2).

3.1.1. Encarsia

The genus *Encarsia* includes more than 200 described species (Woolley and Heraty, 1998). Their females develop on whiteflies or armored scales. Males may develop on the same hosts as the females or be heteronomous, i.e., develop as secondary parasitoids on aphelinids (= autoparasitoids), the eggs of Lepidoptera or other hosts (Walter, 1983; Gerling, 1990b; Hunter et al., 1996b). *Encarsia* species are important for control of the greenhouse whitefly (*En. formosa*) (van Lenteren, 1986), ash whitefly (*En. inaron*) (Gould et al., 1992), and citrus whitefly (*En. lahorensis*) (Argov, 1986). Recently, additional *Encarsia* species have been included in biological control efforts in California using *En. protransvena* and *En. sophia* (= *transvena*) against *B. tabaci* and *En. variegata* against citrus whitefly (Pickett, personal communication). However, with the exception of *En. formosa* (van Lenteren and Martin, 1999) and despite the frequent use of *Encarsia* species, data on their biological and taxonomic characteristics remain deficient even for commonly used species.

Currently, *Encarsia* species are grouped arbitrarily on the basis of overall similarity. This can lead to misconceptions about behavior and host associations that are crucial for biological control programs (e.g. van Lenteren and Martin, 1999). Presently, efforts are being made to improve *Encarsia* identification. In addition to morphological characters, molecular systematics (comparing species based on their genetic similarities) is being used, offering a growing body of useful character systems (Heraty and Polaszek, 2000). For example, accurate separation of the species *En. formosa* and *En. luteola,* which is difficult using morphological characters

Table 2
Parasitoids recorded for *B. tabaci*

Taxa	Reference	Remarks[a]
Hymenoptera		
Fam: Aphelinidae		
Genus: *Encarsia*		
accenta	Schmidt et al. (2001)	R
acaudaleyrodis	Polaszek et al. (1999)	R
adusta	Schmidt et al. (2001)	R
azimi (= *adrianae*)	López-Avila (1987), Polaszek et al. (1992) (as *adrianae*)	R
bimaculata	Heraty and Polaszek (2000)	R
brevivena	Hayat (1989), Polaszek et al. (1992)	R
cibcensis	López-Avila (1987), Polaszek et al. (1992)	S
citrella	Evans and Polaszek (1997)	R
desantisi	Polaszek et al. (1992)	R
duorunga	Huang and Polaszek (1998)	R
formosa	Polaszek et al. (1992), Polaszek et al. (1999)	R, C
guadeloupae	Schmidt et al. (2001)	R
hamoni	Evans and Polaszek (1998)	R
hispida	Polaszek et al. (1992)	R
inaron	Polaszek et al. (1992	S (complex?)
japonica	Polaszek et al. (1992)	R record requires confirmation
lanceolata	Evans and Polaszek (1997)	R
longifasciata	Polaszek et al. (1992)	R
lutea	Gerling et al. (1980), Polaszek et al. (1992)	S
luteola	Polaszek et al. (1992)	S
meritoria	Schuster et al. (1998), Schmidt (2001)	S = *hispida*?
mineoi	Polaszek et al. (1992)	R
moyuddini	Shafee and Rizvi (1982)	R
nigricephala	Polaszek et al. (1992)	S
oakeyensis	Schmidt et al. (2001)	R
paracitrella	Evans and Polaszek (1997)	R
pergandiella	Polaszek et al. (1992)	S (complex)
polaszeki	Evans (1997)	R
protransvena	Heraty and Polaszek (2000)	R
porteri	Polaszek et al. (1992)	S
pseudocitrella	Evans and Polaszek (1997)	R
quaintancei	Polaszek et al. (1992)	R
reticulata	Rivnay and Gerling (1987)	R, ? synonym of *azimi*
sophia = *bemisiae, sublutea, transvena*	Ishii (1938), Polaszek et al. (1992) (as *transvena*), Heraty and Polaszek (2000) (*sophia*)	R, C
tricolor	Gerling, personal information	S, lab. record
Genus: *Eretmocerus*		
adustiscutum	Hayat (1998)	R
emiratus	Zolnerowich and Rose (1998)	R
emiratus (Ethiopia)	Goolsby et al. (2000)	R
eremicus	Rose and Zolnerowich (1997)	S
hayati	Zolnerowich and Rose (1998)	S
joeballi	Rose and Zolnerowich (1997)	R
melanoscutus	Zolnerowich and Rose (1998)	R
mundus	Gerling et al. (1980)	R, C
mundus-Australia	DeBarro et al. (2000b)	R, C uniparental
nr. *furuhashi*	Goolsby et al. (2000)	R
orientalis	Tzeng and Kao (1995)	R
queenslandensis	DeBarro et al. (2000b)	R, C
staufferi	Rose and Zolnerowich (1997)	S
tejanus	Rose and Zolnerowich (1997)	S
Eretmocerus sp.	Goolsby et al. (2000)	S
Fam: Signiphoridae		
Genus: *Signiphora*		
aleyrodis	Schuster et al. (1998), Viscarret et al. (2000)	Hyperparasitoid
sp.	Viscarret et al. (2000), Castiñeiras (1995)	Hyperparasitoid

Table 2 (*continued*)

Taxa	Reference	Remarks[a]
Fam: Encyrtidae		
Genus: *Metaphycus* sp.	Polaszek et al. (1992)	
Fam: Platygasteridae		
Genus: *Amitus*	Polaszek et al. (1992), Viggiani and Evans (1992)	R
Amitus sp.	Bográn et al. (1998)	R
bennetti	Drost et al. (1999), Joyce et al. (1999)	S
funscipennis	Manzano (personal communication)	S lab record

[a] R = Reported, S = biology studied (in the past or at present), C = commercially applied, ? = taxonomy in question.

alone, can be facilitated with restriction site analysis (Babcock and Heraty, 2000). Although severely limited by the number of taxa that can be sampled, the analysis of nucleotide sequences can be used to test the relationships of existing groups and, perhaps more importantly, evaluate the morphological characters used to define those groups. The latter point may be the most relevant for sorting field-collected material in biological control programs for which host associations and specific identifications are essential (Heraty, personal communication). Further information on taxonomy and specific interrelationships of *Encarsia* species is available in recently published keys and descriptions (Schauff et al., 1996; Evans, 1997; Evans and Polaszek, 1997; Evans and Castillo, 1998; Hayat, 1998; Huang and Polaszek, 1998; Woolley and Heraty, 1998; Heraty and Polaszek, 2000).

3.1.2. Eretmocerus

The genus *Eretmocerus* comprises only parasitoids of whitefly (Gerling, 1990b), and like *Encarsia* species, they have been used for biological control (Goolsby et al., 2000). *Eretmocerus* spp. occur worldwide and are distinct from *Encarsia* both biologically and taxonomically. They oviposit under the host and develop in a vital capsule within the host (Gerling et al., 1991), and have a large-clubbed, 3-segmented antenna that sets them apart from confamilial species (Rose et al., 1996). Recent contributions added to our understanding of *Eretmocerus* through morphological analyses of North American species, and by examining courtship behavior, reproductive relationships and allozyme patterns (Hunter et al., 1996a; Rose et al., 1996; Rose and Zolnerowich, 1997). One species, *Eretmocerus mundus*, was the subject of intraspecific behavioral and biological analyses, which indicated significant differences in geographical populations (Heinz and Parrella, 1998). In Australia, two new *Eretmocerus* (*Er. mundus* (parthenogenetic strain) and *Er. queenslandensis*) parasitoids of *B. tabaci* were recently described in a study that included both morphological and molecular systematic approaches using mitochondrial and ribosomal gene regions (DeBarro et al., 2000b). Additional species will probably be identified from the ongoing South American studies (e.g., in Brazil and Colombia), where extensive *B. tabaci* outbreaks have occurred during the last 5–10 years (e.g. Anderson and Oliveira, personal communication).

3.1.3. Amitus and additional genera

Until about 15 years ago, the genus *Amitus* had been recorded from many whitefly species (e.g., Viggiani and Evans, 1992), but not from *B. tabaci*. Thus it is possible that *Amitus bennetti,* found in Puerto Rico by Dr. F. Bennett in 1986 had moved to *B. tabaci* from other, local whitefly species. *Amitus bennetti* has been introduced for experimental control and study purposes to the US (Joyce et al., 1999), to the Netherlands (Drost et al., 1999) and to Israel (Gerling, unpublished). Presently it is not used for biological control. A second species, *A. fuscipennis*, naturally parasitizing *T. vaporariorum* in Colombia, readily develops on *B. tabaci* under laboratory conditions (Manzano, personal communication).

The genus *Signiphora* includes several hyperparasitic species known from *B. tabaci* including one described species, *S. aleyrodis* (Schuster et al., 1998; Viscarret and Polaszek, 2000) and two generic records of *Signiphora* sp., from Cuba (Castiñeiras, 1995) and Argentina (Viscarret et al., 2000).

3.2. Biology

Encarsia, *Eretmocerus* and *Amitus* are solitary, and with the exception of first instar *Eretmocerus*, develop internally. All parasitize whitefly nymphs and emerge from the dead fourth instar host. *Encarsia* and *Eretmocerus* attack mainly the second to fourth host instars with the latter preferring to oviposit under younger whitefly nymphs. They are synovigenic (require a protein meal) and often host-feed in order to mature a full complement of eggs (Gerling, 1990b). *Amitus* prefers to oviposit in first instar whitefly nymphs. It is proovigenic, emerging from its pupal case with a full egg complement, which it lays during approximately 3 days (Joyce et al., 1999). Although developmental durations and fecundity vary among species and environmental conditions, some general patterns can be noted. *Amitus* has the longest development of about 3–4 weeks and lays the largest number of eggs (over 60 eggs/female) (Drost et al., 1999; Joyce et al., 1999). *Eretmocerus* and *Encarsia* have a developmental period of ca. 12–25 days and may develop somewhat faster, or slower than their unparasitized host. *Eretmocerus* is usually more fecund than *Encarsia* but neither reaches the levels of *Amitus* except under extremely favorable laboratory conditions (e.g. Arakawa, 1982). All three genera contain both uniparental and biparental species.

3.2.1. Host location

Experiments have shown that parasitoids cannot identify whitefly infested plants when presented in a mixture of infested and uninfested ones. Host-finding is achieved following a random search on the leaf and visual location of hosts from a very short (about 1 mm.) distance (van Lenteren and Martin, 1999; Rapid and Gerling, personal observations). Olfaction plays a role in host finding and parasitoid females show arrestment responses once they encounter honeydew contaminated leaves (Shimron et al., 1992). The time spent searching upon a leaf is also dependent upon previous searching results and is greatly extended once hosts are found and successfully parasitized (Shimron et al., 1992; van Lenteren and Martin, 1999).

3.3. Host range and utility

With the exception of some *Eretmocerus* species, many whitefly parasitoids are oligophagous, facilitating exploitation of new, introduced whitefly species by indigenous parasitoids. This has caused the establishment of new faunal complexes of *B. tabaci* parasitoids following the pest's spread into new regions, resulting in the extensive list of parasitoids (Table 2). However, oligophagy is usually coupled with differential host preferences that affect their efficacy as biological control agents (e.g. DeBach and Rosen, 1991). For instance, *En. formosa,* well known as a parasitoid of *T. vaporariorum*, was more efficient controlling this species than *B. tabaci* (Brasch et al., 1994). In contrast, other parasitoid species that were discovered following *B. tabaci* invasions into new regions have proven useful. *Er. emiratus* originating in the Arabian Peninsula, *Er. mundus* from the Mediterranean and *En. sophia* from Australia are presently used in Texas and California (Goolsby and Ciomperlik, 1999; Goolsby et al., 2000; Pickett, personal communication). Likewise, the local uniparental Australian *E. mundus* is used against *B. tabaci* on tomato, okra and squash (DeBarro, personal communication). Thus, as noted by Gerling (1996), the classical concept pointing to the "original home country" of the pest as the source for its most effective natural enemies may not hold for *B. tabaci*, and its natural enemies should be sought throughout the range of the pest's occurrence. Kirk et al. (2000) contributed a novel approach to the study of the relationships between the region of search for the natural enemy and its ultimate effectiveness. Following the introduction of *B. tabaci* parasitoids from Thailand and Spain into Texas and observations of the former's failure and the latter's success in becoming established and helping to control the host, they conducted a mitochondrial cytochrome oxidase I gene (mt COI, $\sim$720 bp) analysis of the whitefly in all three localities. From these, they concluded that the effectiveness of the Spanish *Er. mundus* in Texas might be correlated with the similarity between the Texas whiteflies to those in Spain and the dissimilarity to those in Thailand (99.4–99.6% vs. 85% sequence identity, respectively). They suggested "that specific co-evolved parasitoid genotypes and/or strains may be required to achieve optimal matches for biological control of whiteflies in each distinct clade".

Several parasitoid species became established or are being released against *B. tabaci*. The best known is *En. formosa*, which is routinely used against the greenhouse whitefly in greenhouses (van Lenteren and Martin, 1999). Other species that have been released for *B. tabaci* control include *En. nigricephala, En. pergandiella*, and *En. sophia*, *Er. mundus* (both, the Australian uniparental, and the Old World biparental strains), *Er. emiratus*, *Er. eremicus* and *Er. hayati* (see "Case history studies") (Hoelmer, 1996; DeBarro et al., 2000b; Goolsby et al., 2000; Hoelmer, Onillon, and van der Blom, personal communications).

4. Case history studies

Biological control of *B. tabaci* through the release of natural enemies has been attempted for at least 30 years. However, only recently, following extensive efforts including worldwide natural enemy collection and large scale laboratory and field testing (e.g., Goolsby et al., 2000), have some programs been thoroughly monitored. Some biological control projects have only recently begun (e.g. in Spain (van der Blom, and García) and Australia, (DeBarro), personal communications) or are still ongoing (e.g. in California, Pickett, personal communication). Therefore, no full conclusions as to the principles governing the potential success or failure of *B. tabaci* biological control can be drawn.

Here we present current developments in the biological control of *B. tabaci* in greenhouse and field crops. The boundaries between these two modes of plant production become blurred as we move from temperate to warmer climates. In the warm climate greenhouses, *B. tabaci* often penetrate from outside, and if permitted to develop unabated may later leave the greenhouse and re-infest the environment. Therefore, the information presented in the following examples may be useful for a variety of cropping conditions. Finally, *B. tabaci* and the greenhouse whitefly may co-occur, and their behavior and damage in greenhouse and outdoor cropping systems may be similar (Albajes and Alomar, 1999). Thus, the conditions under which biological control of *B. tabaci* might be practiced should also be examined in light of experiences with well-studied *T. vaporariorum* systems (Gabarra and Besri, 1999; van Lenteren and Martin, 1999). Moreover, strategies developed for *T. vaporariorum* control may prove effective against *B. tabaci* and may require consideration of both pest species jointly (Avilla et al., 2001).

4.1. Greenhouse crops

Greenhouses can be divided into two groups; sealed enclosures largely isolated from the outside, and partially closed structures, allowing an interchange of organisms with the environment (Avilla et al., 2001). The former are used in cold climate countries and support a unique "greenhouse fauna". The latter occur in countries with warm and Mediterranean-type climates allowing natural re-colonization by pests and natural enemies from the outdoors with a resulting similarity between the fauna that occurs in the open field and under cover (Albajes and Alomar, 1999). Approaches to pest control differ with emphasis on the release of natural enemies in cold climates (van Lenteren and Martin, 1999) and release of natural enemies in addition to conservation of local nature enemies in the warmer climates (e.g. Gabarra and Besri, 1999; Avilla et al., 2001).

4.1.1. Parasitoids

Early attempts to find an efficient parasitoid for *B. tabaci* focused on *En. formosa*, available worldwide and commonly used for greenhouse whitefly control (Brasch et al., 1994; Heinz, 1996). Recent studies in poinsettia-growing greenhouses have shown that *Er. eremicus* was more effective than the Beltsville strain of *En. formosa* in reducing whitefly densities to a level acceptable to consumers (Hoddle et al., 1997, 1998; Hoddle and van Driesche, 1999a, b; van Driesche et al., 1999). However, the required releases of *Er. eremicus* were 27-fold more expensive than the use of insecticides (van Driesche et al., 1999). Additional problems occur wherever *B. tabaci* coexists with *T. vaporariorum*. For example, in southern Spain where *B. tabaci* populations invade greenhouses in the early autumn, but decline during the cold season, *T. vaporariorum* populations continue to increase in the winter and dominate the greenhouses in the spring (Arnó and Gabarra, 1994). Since *En. formosa* is unable to build-up populations on *B. tabaci* and its activity is reduced during winter, it does not become established in time to control *T. vaporariorum* in the spring (Arnó and Gabarra, 1996). Thus, biological control strategies must include the release of additional natural enemies.

The nearctic *Er. eremicus* and the palaearctic *Er. mundus* are used commercially for *B. tabaci* control particularly in Mediterranean-climate greenhouses. Both species are biparental, kill hosts through host feeding and oviposition, and perform well under high temperatures. *Er. eremicus* attacks both *B. tabaci* and *T. vaporariorum* and provides control for mixed host populations, whereas *Er. mundus*, a native to the Mediterranean and abundant even in treated fields (Rodríguez et al., 1994; Gerling and Fried, 2000; Kirk et al., 2000), does not attack *T. vaporariorum*. Therefore, a mixture of parasitoid species is recommended for release by commercial companies (e.g. Koppert, Biobest and Bioplanet) when mixed whitefly populations occur. Satisfactory results were obtained using *Er. eremicus* over 500 ha tomato and 1000 ha pepper in the southeast of Spain and the Canary Islands (García, Lacasa, and van der Blom, personal communications). The imported *Er. eremicus* is often replaced by naturally occurring *Er. mundus* and occasionally also by *En. sophia* (van der Blom, personal communication). Although *Er. mundus* is a promising candidate for deployment in commercial greenhouses, its production and availability are currently limited.

The parthenogenetic *En. hispida* has shown promise for the biological control of *B. tabaci* in tomato greenhouses (Onillon and Maignet, 2000). Whereas, releases of *En. pergandiella* has resulted in decreased parasitism of *B. tabaci* (Onillon et al., 1994). Similarly, Gabarra et al. (1999) noted that the effectiveness of *En. formosa* as a greenhouse whitefly parasitoid diminished once exotic *En. pergandiella* expanded into the Mediterranean basin. This phenomenon was attributed to autoparasitism (see above). In contrast, Heinz and Nelson (1996) suggested that interspecific interactions between *En. formosa* and *En. pergandiella* might facilitate biological control by providing a resource for parasitoids that may switch from one host to the other. Bográn et al. (2002) reported that releases of *En. formosa* together with *En. pergandiella* reduced the levels of host suppression. However, initial parasitoid population densities affected the outcome of competitive interactions between *En. pergandiella* and *Er. mundus*. Similar studies by Hunter et al. (2002) suggest that the dominance of the autoparasitoid *En. sophia* over *Er. eremicus* had little effect on *B. tabaci* control. It is noteworthy that theoretical work by Mills and Gutierrez (1996) suggests that under certain conditions, facultative autoparasitism could disrupt control by the primary parasitoid, leading these authors to discourage importation and release of autoparasitoids.

4.1.2. Predators and combined use of predators and parasitoids

Predators have been used for *B. tabaci* control in greenhouses with varying degrees of success. Releases of *M. caliginosus* in gerbera greenhouses gave acceptable whitefly control (Pasini et al., 1998). When *D. catalinae* was released on caged poinsettias in a greenhouse, the reduction of whitefly populations did not differ from that obtained by the parasitoids *En. luteola* or *En. pergandiella* (Heinz et al., 1994). Although whiteflies are not considered suitable prey for long-term lacewing development, they may be useful if immediate remedial action rather than maintenance of low whitefly populations is sought. Inundative releases of *C. rufilabris* on hibiscus proved successful for *B. tabaci* control (Breene et al., 1992).

Joint releases of predators and parasitoids can prove useful, but may require consideration of intraguild predation. *Geocoris punctipes, Hippodamia convergens* and *O. insidiosus* all display a preference for *B. tabaci* parasitized by *Er. emiratus,* but the effects of this behavior on pest control have not been investigated (Naranjo, personal communication). Releases of *D. catalinae* together with *En. luteola* in poinsettia cultures controlled *B. tabaci* (Heinz and Parrella, 1994b). Releases of *D. catalinae* with other *Encarsia* species also reduced whitefly populations to lower levels than any of the studied combinations using parasitoids alone (Heinz and Nelson, 1996). Even though *D. catalinae* adults and larvae also may feed on whitefly nymphs that contain young stages of the parasitoids, they become more discriminating as the parasitoid develops and preferentially attack unparasitized whiteflies (see Heinz and Parrella, 1994a; Heinz et al., 1994; Hoelmer et al., 1994). This attribute may increase temporal separation, enhancing the integration of the two natural enemy types. In European greenhouses *M. caliginosus* is released widely, where it controls both *B. tabaci* and *T. vaporariorum*. However, because *M. caliginosus* often has an establishment time of more than 1 month, *En. formosa* is also released to provide more immediate whitefly suppression (Lenfant et al., 1998; Muhlberger and Maignet, 1999). *M. caliginosus* feeds on parasitized and unparasitized whitefly nymphs, but the complementary action of predation and parasitism is considered the key to maintaining low densities of *T. vaporariorum* (Castañé et al., 2000). This strategy reproduces the situation in the Mediterranean where predators enter greenhouses naturally following inoculative releases of parasitoids (Avilla et al., 2001). In Murcia and Almeroía (southern Spain) where both whitefly species occur, the releases of *Er. eremicus* with *O. laevigatus* have been integrated with the use of the fungus *Verticillium lecanii* in pepper. Crops also benefit from the natural colonization of the mirid *Nesidiocoris tenuis* (van der Blom, personal communication). Overall, biological control of *B. tabaci* in greenhouses, as compared to that of *T. vaporariorum*, remains problematic and may demand more supervision, increased releases of parasitoids, and/or the use of additional natural enemies (Gabarra and Besri, 1999; van Lenteren and Martin, 1999; Hoddle, 2001).

4.2. Field crops and outdoor vegetables

The utility of natural enemies in controlling *B. tabaci* has been examined in the field using various methods. Bográn et al. (1998) compared the mortality of whiteflies by parasitoids and predators on beans within completely closed vs. partially open-mesh field cages. Parasitism never exceeded 40%, and mortality attributed to unknown factors including predation varied from 3% to 13%. No density-dependent responses by the parasitoids were observed. Releases of *C. rufilabris* in caged watermelon contributed to a decrease in *B. tabaci* populations in Texas (Legaspi et al., 1996a). The predator *D. catalinae* was tested as a biological control agent of *B. tabaci* in the Imperial Valley of California, where the beetles were released in field cages and in the open field in cotton. *D. catalinae* survived, developed, reproduced, and decreased whitefly densities in the field by 55% and 67% in 1992 and 1993, respectively, but failed to suppress the pest below economic levels (Heinz et al., 1999). Releases of *Er. mundus* in caged cabbage resulted in 32% parasitism of *B. tabaci* (Zaki et al., 1999).

Several assessments of natural enemy activity in the open field have been conducted, but an apparent density-dependent reaction, i.e., an increase in mortality (as % parasitism) with the rise of *B. tabaci* populations, was only observed by Bellows and Arakawa (1988) and McAuslane et al. (1994). In other cases (e.g. Horowitz et al., 1984; Gerling and Kravchenko, 1996; Bográn et al., 1998; Naranjo, 2001; Hoelmer, personal communication), high rates of natural mortality have been observed in untreated plots, but density-dependent effects due to natural enemies have not been demonstrated. In contrast, there are several examples in which low whitefly populations and low damage levels have been coincidental with reduced insecticide treatment and/or the release of natural enemies.

For example, in Florida *B. tabaci* parasitism can reach high levels in organically grown crops and on moderately hirsute (as compared with heavily hirsute) plants. Weeds were also found to harbor a rich fauna of parasitoids that may contribute to the observed regulation of *B. tabaci* in unsprayed peanuts (Stansly et al., 1997). In Israel, Gerling (1996) observed lower *B. tabaci* populations in cotton fields following a reduction of insecticide use. Reduction of *B. tabaci* populations in Egyptian cotton fields was attributed to the importation and release of *En. formosa*, *Er. eremicus* (as *californicus*), *Er. mundus* and *D. catalinae* (Abd-Rabou, 1999), whereas field releases of *O. strigicollis* on eggplant were associated with reduced whitefly populations in Taiwan (Wang, personal communication). In the southeast of Spain, *E. eremicus* has been released in open air melon crops. Those fields were naturally colonised by *Orius* spp. and green lacewings, which contributed to the control of *B. tabaci* (García, personal communication).

Starting in 1992 following outbreaks of *B. tabaci* in the southern tier of the US, a major effort was undertaken to import, establish and augment natural enemies of *B. tabaci*. The USDA-APHIS-PPQ, Mission Plant Protection Center in Texas processed over 80 shipments of predators, parasitoids and pathogens between 1992 and 1998. Over 56 different populations of *Encarsia* and *Eretmocerus* were received, identified using morphological markers and RAPD-PCR, and cultured (Goolsby et al., 2000). A three-tiered evaluation method was used prior to parasitoid release. The introduced species were first released in laboratory cages onto whitefly infested cotton, melon and broccoli plants. Selected exotic parasitoids were then evaluated in field cages on melons, cotton and kale. Following these tests, 29 species or populations were released in garden plots to evaluate potential for establishment. From these studies, two species, *Er. hayati* and *Er. mundus,* were predicted to be the most likely to control *B. tabaci* populations. Using sentinel plants, rates of parasitism by these species were shown to increase from 1.5% in June of 1997 to 86.5% in October of the same year, suggesting the establishment of these exotics in Texas. These same two species were also used in Texas to successfully augment parasitism early in the season through the use of a banker plant system, a method where whiteflies and parasitoids were introduced on infested cole crop seedlings interplanted among clean seedlings (Goolsby and Ciomperlik, 1999). A similar method is presently used for control of *B. tabaci* on okra in Australia (Goolsby, personal communication).

From 1993 to 1999, parallel to the work conducted in Texas, intensive introduction efforts were made in Southern California and Arizona (Hoelmer, 1996). The efforts included rearing and release of over 50 million exotic parasitoids belonging to 13 species or populations, field cage studies to evaluate the most promising agents, studies of host plant suitability for different species of parasitoids, management of refuges of alternate host plants to preserve and aid establishment of parasitoid populations between crop cycles and over the winter, and follow-up evaluations of establishment (Hoelmer, 1996; Roltsch, Pickett and Corbett, unpublished). Additional studies examined the compatibility of different weed species as hosts of whitefly and their natural enemies with the goal of encouraging "positive" weeds and discouraging "negative" ones (Gruenhagen and Perring, 1999). By the end of the century, four species of *Eretmocerus* (*emiratus*, *hayati*, *mundus*, and nr. *emiratus* (Ethiopia)) have been recovered in California. The total number and proportion of exotic to native parasitoids have increased for 2 years following the cessation of releases, and exotic species were found in 74% of cotton fields surveyed during 1999 (Hoelmer and Roltsch, unpublished). *Er.* nr. *emiratus* were also recovered in the more northern San Joaquin Valley of California in areas where native parasitoids had been rare (Pickett, personal communication).

Overall, the introduction and augmentation of exotic parasitoids in California and Texas has brought about a change in the parasitoid complex attacking *B. tabaci*, but further work will be needed to quantify the impact and contribution of these biological control agents to suppression of *B. tabaci* (Goolsby et al., 2000, Hoelmer, personal communication).

5. Conclusions—biological control of *B. tabaci*: problems and needs

Successful biological control requires sound definitions of the goals to be achieved and an intimate knowledge of the available organisms. For *B. tabaci*, the most striking characteristics of the pest include its extensive host range of over 500 known plant species (Cock, 1993), enabling it to be omnipresent on both agricultural and wild host plants, and its high reproductive rate that may exceed 300 eggs/female (Drost et al., 1998). These characteristics facilitate inter-crop movement (including movement into and out of greenhouses), rapid population increases, and highlight the difficulties of controlling *B. tabaci* using natural enemies (Gerling, 1996; Heinz and Zalom, 1996; Hoelmer, 1996). Several additional factors are worth consideration: (1) varying climatic conditions that may require the use of a variety of natural enemy species and control methods to be employed; (2) the lethal and sublethal effects of insecticides on natural enemies (see Naranjo, 2001); (3) selection of crop cultivars compatible with natural enemies; (4) large-scale monocultures allowing for massive migrations as host plant quality declines (e.g., Riley and Ciomperlik, 1997); (5) whitefly infestations associated with the practice of continuous crop production, (e.g., in northern Brazil melons are planted every 2 weeks in adjacent fields throughout the season (Oliveira, personal communication)); (6) the discontinuous nature of annual crops and wild host plants which do not provide stable environments for the establishment of natural enemies; (7) the presence of other pests (e.g., *T. vaporariorum*) that may introduce additional management considerations including the species-specificity of some natural enemies.

Under these circumstances, a reasonable approach might be to look for natural enemies that will become established and depress the pest population in the wild, but adapt to the environment of a particular crop. All three methods of natural enemy exploitation, introduction, augmentation and conservation should be developed. Overall strategies that will alleviate area-wide problems should be combined with those applicable to each particular crop (see Ellsworth and Martinez-Carrillo, 2001). A successful strategy will exploit extant natural enemies occurring in the production area (conservation), supplement these with additional species to meet specific needs (augmentation and introduction of exotics), and reduce pest movement among crops and non-crop sources. In addition, the nature of the plants in the environment and their availability and suitability as refuges to the pest and/or natural enemy are important factors that may be beneficially exploited (e.g., Gruenhagen and Perring, 1999).

As emphasized by Naranjo (2001), conservation should assume a central role in biological control strategies for this pest. Conserving natural enemies in surrounding areas (crops and non-crop vegetation) may enhance sources of predators and parasitoids that can aid reductions in overall whitefly densities. This strategy might make the difference between moderate pest influx into the crop vs. massive inundations; between the occasional need for insecticidal intervention vs. high populations requiring frequent treatments, and between a slow build-up of insecticide resistance vs. rapid development of resistance. Conservation also may provide the necessary stability for ephemeral, annual cropping systems that challenge the economic viability of seasonal inoculative releases. Finally, conservation can be made compatible with and complementary to the use of selective insecticides such as insect growth regulators (see Naranjo, 2001; Ellsworth and Martinez-Carrillo, 2001).

Although progress had been made, present knowledge of natural *B. tabaci* enemies, their value as biological control agents, the potential of natural vegetation as refugia, and methods of conservation are incomplete (see also Naranjo, 2001). Future emphasis is suggested in the following broad areas.

1. Identify and evaluate natural enemies. As reviewed by Naranjo (2001), existing experimental methods for evaluating the impact and efficacy of newly described and previously known natural enemies have been underutilized in both greenhouse and field environments. For example, life table studies offer a robust method for directly assessing rates of mortality by natural enemies (Hoddle and van Driesche, 1999a, b; Naranjo, 2001).
2. Identifying promising agents through the study of natural enemy biology and ecology. Determination of biological characteristics such as tritrophic relationships, and effects of climate on behavior and population dynamics of whitefly natural enemy interactions is needed. Based on the consideration of production system and the objectives of the biological control program, such information will help to identify promising natural enemies and develop methods for their use. For example, voraciousness of predators may be required to suppress outbreaks, but other traits are necessary for long-term maintenance. Special attention should be given to studies of nutritional preferences, the propensity of natural enemies to disperse, and searching behavior that permit subsistence at low whitefly densities. Short-term concerns that *B. tabaci* is not a preferred host for some predators should be balanced with long-term recognition of the benefits of mixed diets, especially when maintenance of resident populations of natural enemies is sought. Optimal exploitation of natural enemies must consider the fact that several species may be present contemporaneously and act in complementary ways. Thus, interspecific interactions should be considered.
3. Develop methodologies for using and maintaining natural enemies in and near the field. Refuges may enhance biological control. Dispersal from refuges into the crop plants is the key, and an understanding of feeding and movement behaviors is essential in order to achieve the desired benefit. Overall, conservation-oriented methodology should be developed to support a "holistic" pest control approach (Waage, 1990; Heinz, 1996) based on the long-term establishment of natural enemies in the environment. The success of natural enemies under these conditions could then provide suitable candidates for use in greenhouse environments (Nicoli and Burgio, 1997).
4. Adopt a conservative introduction policy for natural enemies. Special care should be taken during evaluation studies of exotic natural enemies to avoid the introduction of potentially damaging species. Since importations of autoparasitoids (against other Homoptera) have usually proven beneficial (DeBach and Rosen, 1991; Coulson, 2000), their introduction should continue provided their utility had been established. However, the negative effects of the introduced autoparasitic *En. pergandiella* in Europe on parasitism of the greenhouse whitefly (Gabarra et al., 1999) vs. the apparent benefits incurred from the introduced autoparasitic *En. sofia* in the US (Hoelmer, personal communication) point out questions that remain unanswered.
5. Evaluate the influence of biological control in the epidemiology of B. tabaci-transmitted viruses. The fact that *B. tabaci* transmits viruses in many crops and

causes significant losses (Duffus, 1996) has hampered the implementation of biological control and stimulated the need for insecticides. However, insecticides often fail to control viral transmission, especially in semiprotected crops typical of Mediterranean climates (Moriones and Luis-Arteaga, 1999). Under such conditions, biological control may contribute to reductions of *B. tabaci* populations, both in target crops and in inoculum reservoirs, reducing vector pressure and improving the prospects of virus control on susceptible hosts. Such reduction on virus tolerant plants may reduce the use of insecticides and the incidence of tolerance breakdown.

6. Integrate the biological control efforts with other control tactics. The prospects for successful reduction of the economic damage levels through the use of natural enemies are enhanced when the damage is light and natural enemy potential is optimized. Efforts should focus on an integrated approach which employs a variety of tactics to produce an environment favorable to natural enemies. For example, cultural methods for greenhouses include screening to avoid pests' entry, UV-absorbing covers and crop-free periods, whereas outdoor techniques in crop management include water stress management, fertilizer input, crop sequencing, and plant density manipulation (also see Ellsworth and Martinez-Carrillo, 2001). The influence of these methods, as well as of host plant resistance and selective insecticides, on natural enemies should be evaluated so that effects are complementary.

Acknowledgements

We are indebted to numerous colleagues for supplying information about the status of *B. tabaci* and the efforts involved in the various biological control projects. In particular, we wish to thank P. DeBarro (CSIRO, Australia), J. Goolsby and S. Naranjo (USDA, ARS, USA), M. Ciomperlik, J. Gould, K. Hoelmer and G. Simmons (USDA, APHIS, USA), C. Pickett and B. Roltsch (California Department of Agriculture, USA), A. Polaszek (Department of Entomology, The Natural History Museum and Imperial College of Science, Technology & Medicine, Great Britain), J. van der Blom (Koppert, BV, Spain), A. Lacasa (CIDA, Spain), E. Moriones (CSIC, Spain), and F. García (Syngenta Bioline, Spain). We also thank L. Vázquez (INSAV, Cuba), M. Goula (University of Barcelona, Spain), R.D. Gordon (Smithsonian Institution, USA), M. Nomikou (University of Amsterdam, The Netherlands), C.A. Tauber (Cornell University, USA), N. Vandenberg (USDA, ARS, USA), and V. Montserrat (Universidad Complutense de Madrid, Spain) for help on taxonomy and synonymies. Special thanks are due to D. Kopp (USDA/CSREES) and the anonymous reviewers for making many helpful suggestions. This work was supported by projects of INIA (SC00-008) and CICYT (AGF 1996-0483, 2FD 1997-1087) (Spain).

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