Journal of Pest Science (2020) 93:893–910
https://doi.org/10.1007/s10340-020-01210-0

REVIEW

Insecticide resistance and its management in *Bemisia tabaci* species

A. Rami Horowitz[1,2] · **Murad Ghanim**[1] · **Emmanouil Roditakis**[3] · **Ralf Nauen**[4] · **Isaac Ishaaya**[5]

Received: 14 October 2019 / Revised: 12 January 2020 / Accepted: 9 February 2020 / Published online: 17 February 2020

Abstract

The sweet potato (cotton) whitefly *Bemisia tabaci* is a major agricultural pest in various fields and vegetable crops worldwide. It causes extensive damage by direct feeding on plants, reducing quality, secreting honeydew and transmitting plant viruses. *B. tabaci* is known for its genetic diversity and considered a complex of biotypes or, as suggested, a complex of distinct cryptic species. Management of whiteflies relies mainly on the use of insecticides; however, its ability to develop resistance to major insecticide classes creates a serious challenge to farmers and pest control specialists. Among the cryptic species of *B. tabaci*, MED is considered more resistant than the MEAM1 to insecticides such as pyriproxyfen and neonicotinoids; however, in recent years there are other species of *B. tabaci* including MEAM1, Asia I and Asia II-1 that have developed high resistance to various groups of insecticides. Advanced methods based on molecular and gene sequence data obtained from resistant and susceptible field-collected *B. tabaci* populations resulted in a better understanding of resistance mechanisms in this pest. Several components of IPM-IRM (Integrated Pest Management-Insecticide Resistance Management) programs such as selective and biorational insecticides, insecticide rotation with different modes of action and nonchemical control methods are among the countermeasures of insecticide resistance management for this pest. In the current review, we concentrate on insecticide resistance and resistance management of *B. tabaci,* focusing on reports published mainly over the past 10 years.

Keywords *Bemisia tabaci* biotype/species: insecticide resistance · IPM·IRM strategies

Key message

- *Bemisia tabaci* is globally considered one of the top agricultural pests.
- Tremendous efforts are invested in developing new insecticides which are highly target-specific in *B. tabaci.*
- *Bemisia tabaci* has evolved resistance to insecticides from most chemical classes including novel insecticides.
- Advanced methods based on molecular and gene sequence data obtained from resistant and susceptible field-collected *B. tabaci* populations resulted in better understanding of resistance mechanisms in this pest.
- There are several components of IPM-IRM programs such as selective and biorational insecticides, insecticide rotation with different modes of action and nonchemical control methods.

Introduction—the whitefly *Bemisia tabaci*

The sweet potato (cotton) whitefly, *Bemisia tabaci* (Gennadius, 1889) (Hemiptera: Aleyrodidae) is a global, serious pest of vegetable, field and ornamental crops (Byrne and Bellows 1991; Oliveira et al. 2001; Stansly and Naranjo 2010). This pest directly harms plants by feeding on phloem sap and excretes honeydew on leaves and fruits, which forms

Communicated by N. Desneux.

A. Rami Horowitz
hrami@volcani.agri.gov.il

[1] Department of Entomology, Agricultural Research Organization (ARO), Gilat Research Center for Arid & Semi-Arid Agricultural Research, 85280 Rishon LeZion, Israel

[2] Katif Research Center, Sedot Negev; the Ministry of Science, Technology & Space, 85200 Netivot, Israel

[3] Institute of Olive Tree, Subtropical Crops and Viticulture, Hellenic Agricultural Organization – Demeter, 71307 Heraklion, Greece

[4] Crop Science Division R &D - Pest Control, Bayer AG, 40789 Monheim, Germany

[5] Department of Entomology, ARO, The Volcani Center, 7505101 Rishon LeZion, Israel

a substrate for the growth of black sooty mold that stains the leaves, impairs photosynthesis and reduces fruit quality. In cotton, the honeydew may cause fiber stickiness that interferes with the spinning process in the textile mills and greatly reduces the product's value (Ellsworth et al. 1999; Hequet et al. 2007). *Bemisia tabaci* is a vector of more than 100 plant viruses (Jones 2003; Hogenhout et al. 2008), and in some cases, viral diseases are limiting growth factors and may cause total crop loss. Cotton leaf curl Virus (CLCV), which is transmitted by *B. tabaci*, is a major disease of cotton in Asia and Africa, and tomato yellow leaf curl virus (TYLCV) is among the most damaging viruses that harms tomato crops worldwide.

Economic losses due to *B. tabaci* are enormous; Henneberry and Faust (2008) summarized some reports related to economic losses, which estimated approximately 10 billion US dollars (USD) during the years 1980 to 2000. Perring et al. (1993) estimated the direct losses due to whiteflies outbreaks over a half billion USD in the USA during 1991, and in India they estimated the losses in 1991 to various bean crops to be approximately 300 USD (Henneberry and Faust 2008). In Arizona, California and Texas, cotton growers spent 154 million USD during 1994–1998 to control the whitefly and prevent cotton lint stickiness (Ellsworth et al. 1999). However, losses due to virus diseases transmitted by *B. tabaci* were considered the most damaging: Briddon (2003) reported that cotton leaf curl virus (CLCV) caused 5 billion USD losses to cotton in Pakistan from 1992 to 1997, and Legg et al. (2014) estimated that cassava mosaic disease (CMD) and cassava brown streak disease (CBSD) caused annual production losses of more than 1 billion USD in Africa.

Bemisia tabaci is known for its genetic diversity and is considered a complex of biotypes (Brown et al. 1995; Perring 2001; Xu et al. 2010) or, as suggested, a complex of distinct cryptic species (De Barro et al. 2011; Boykin et al. 2012; Liu et al. 2012; Boykin and De Barro 2014). The biotypes/species are largely differentiated based on biochemical or molecular polymorphism markers and differ in their biological characteristics such as host plant range, the capacity to cause plant disorders, attraction by natural enemies, expression of resistance and plant virus-transmission capabilities (e.g., Bedford et al. 1994; Sanchez-Campos et al. 1999; Horowitz et al. 2005; Kontsedalov et al. 2008; Watanabe et al. 2019). The B biotype is the most widespread biotype on a worldwide scale (belongs to the Middle East Asia Minor 1—MEAM1 group) and is proposed to be originated from the Middle East–Asia Minor region (De Barro et al. 2011). This biotype was identified in the late 1980s (Costa et al. 1993), following extensive outbreaks of *B. tabaci* in the southwest USA. An additional common biotype Q (belongs to the Mediterranean—MED group), which possibly originated in the Iberian Peninsula, has since spread globally (Horowitz et al. 2003; Boykin et al. 2007; Chu et al. 2010). So far, the genetic groups of *B. tabaci* are composed of at least 40 morphologically indistinguishable species (Dinsdale et al. 2010; De Barro et al. 2011; Boykin and De Barro 2014; Hu et al. 2017). In the current review, we will use both terminologies (biotype/species), depending on the cited literature.

Bemisia tabaci has evolved resistance to insecticides from most chemical classes; among the common cryptic species, MED (biotype Q) is considered more resistant than the MEAM1 (biotype B) to insecticides such as pyriproxyfen and neonicotinoids (e.g., Horowitz et al. 2005); however, in recent years, there are other species of *Bemisia* including MEAM1, Asia I and Asia II-1 that have developed high resistance levels to various groups of insecticides (e.g., Naveen et al. 2017; Dângelo et al. 2018).

The dynamics of *B. tabaci* species and their association with insecticide resistance

MEAM1 (B) is considered the most common *B. tabaci* species, and it has probably been dispersed throughout the world by international trade mainly with ornamentals. Early reports have indicated that an invasion of a new biotype resulted in the displacement of indigenous biotypes as a result of competition or possibly other reasons (B biotype displaced A biotype in the USA, Brown et al. 1995; the displacement of B by non-B populations such as Q, Guirao et al. 1997; Q biotype displaced B when insecticide selection occurred, Horowitz et al. 2005). Since then, many reports have shown similar changes in biotypes/species of *B. tabaci* elsewhere, apparently due to frequent use of insecticides and development of insecticide resistance. Since 2005, a shift of biotype B to Q occurred in many locations of China (e.g., Teng et al. 2010; Li et al. 2017). An opposite process has been observed in Israel, where since 2009, a significant shift in the biotype ratios has been observed: the B biotype replaced the Q biotype in most crops. At the same time, resistance to pyriproxyfen was reduced considerably. The reason for this phenomenon is not clear, but it may relate to using less pyriproxyfen and neonicotinoids (Crowder et al. 2011; Horowitz and Ishaaya 2014). In addition, biotype Q prefers protected crops (Kontsedalov et al. 2012) as also reported from the USA and Italy (Mckenzie et al. 2012; Parrella et al. 2012).

This paper reviews insecticide resistance and management issues among *B. tabaci* species with a focus on studies published mainly within the past decade.

Insecticide resistance in *Bemisia tabaci* species

Insecticide resistance in *B. tabaci* is widespread, and it has evolved to most of the insecticides used (Basit 2019). According to Mota-Sanchez and Wise (2019) (Arthropod

Pesticide Resistance Database, Michigan State University), there are so far approximately 650 reported cases of insecticide resistance in the genus *Bemisia,* and resistance was detected to more than 60 active ingredients.

The mechanisms of resistance in *B. tabaci* are similar to those described for other pest species, i.e., metabolically driven by elevated levels of detoxification enzymes or by point mutations resulting in target-site resistance.

Table 1 summarizes the global distribution of resistance to insecticides in species/biotypes of *B. tabaci* according to recent reports from various countries. Both MED (Q) and MEAM1 (B) species have developed resistance to most insecticide classes; however, where both species are available side by side, MED has developed higher resistance to many insecticides than MEAM1 (e.g., Yao et al. 2017; Luo et al. 2010 in China; Kontsedalov et al. 2012; Horowitz and Ishaaya 2014 in Israel). In India, the species Asia I and Asia II-1 were found more resistant to insecticides than Asia II-7 (Naveen et al. 2017).

Resistance to different chemical classes of insecticides

Organophosphates (OPs) and carbamates

Resistance to organophosphates (OPs) is well established in *B. tabaci* in many countries (Horowitz et al. 2007; Ahmad et al. 2010; Naveen et al. 2017). In some cases, levels of resistance to OPs and carbamates were unstable and fluctuated from very low to high (Ahmad et al. 2010). In Turkey, resistance in biotype B (MEAM1) to OPs ranged between 20- and 310-fold (Erdogan et al. 2008). In Greece, the resistance level to pirimiphos-methyl was reported to be higher in greenhouses compared with open fields (Roditakis et al. 2009). High resistance to OPs such as acephate and triazophos was detected in Asia 1 whiteflies from India (Roy et al. 2019). In China, relatively low level of resistance to an OP (chlorpyrifos) was detected; however, initial baseline-level toxicity was rather high (Wang et al. 2017). Similarly, in the Q biotype of *B. tabaci*, from eastern China, low resistance to another OP (dichlorvos) as well as to the carbamate carbosulfan was exhibited (Yuan et al. 2012).

Resistance levels to methomyl (a carbamate) were shown to be low to moderate in MED strains from Spain, probably due to less frequent use and the adoption of IPM strategies (Fernandez et al. 2009).

The mechanisms of resistance to OPs and carbamates in *B. tabaci* are known for many years and have been studied since the 1980s; however, no substantially new results have been published over the past decade. Altered sensitivity alleles of acetylcholinesterase, the target site for OPs, have been described, and several levels of resistance are attributed to varying numbers of such alleles (Byrne and Devonshire 1993, 1997; Byrne et al. 1994). The insensitivity to OPs has also been linked to additional mechanisms of resistance such as increased esterase activities (Byrne and Devonshire 1991; Denholm et al. 1998) and was correlated with the levels of resistance (Dittrich et al. 1990). Alon et al. (2008) have shown that altered AChE sensitivity to OPs is linked to a F392W mutation in acetylcholinesterase 1 of *B. tabaci.* However, in the same study, overexpression of the carboxylesterase 1 gene was also correlated with chlorpyrifos resistance, suggesting that both mechanisms are involved in resistance to OPs (Alon et al. 2008).

Pyrethroids

Pyrethroid resistance in whiteflies is widespread although the magnitude and pattern of resistance and cross-resistance vary considerably among countries and cropping systems (Cahill et al. 1995, 1996; Denholm et al. 1996; Erdogan et al. 2008; Roditakis et al. 2009; Naveen et al. 2017). In some cases, very high resistance was detected to pyrethroids such as cypermethrin and bifenthrin in populations of B biotype from northwestern China (Ma et al. 2007) and Cyprus (Vassiliou et al. 2011). In other regions of China, resistance levels to pyrethroids, e.g., *lambda*-cyhalothrin and cypermethrin, have been declined also in Biotype Q (Yuan et al. 2012; Yao et al. 2017).

Pyrethroids target the para-type voltage-gated sodium channel (vgsc) in the central nervous system, leading to paralysis and rapid death. The two mutations L925I and T929V in the IIS4-5 linker of vgsc in *B. tabaci* were linked to pyrethroid resistance (Schuler et al. 1998; Lee et al. 2000; Morin et al. 2002; Bass et al. 2004; Roditakis et al. 2006; Alon et al. 2008; Farghaly 2010a). DNA microarrays were later used for resistance monitoring of field-collected populations based on the mutations in vgsc as well as acetylcholinesterase (Chung et al. 2011). In this study, high correlation was obtained between the microarray and direct sequencing, providing a large-scale tool for resistance monitoring in *B. tabaci.* Such molecular monitoring of resistance in *B. tabaci* has been used by others to detect resistance to pyrethroids, carbamates and OPs (Farghaly 2010b). Based on the molecular data obtained from resistant and susceptible populations, and the fact that the previously described mutations are stable in field populations, a simple PCR–agarose gel visualization-based assay was developed for reliably monitoring the frequency of the mutations known to confer resistance to pyrethroids and OPs. Results from larger monitoring campaigns revealed that this method is accurate and robust to reliably diagnose the spread of the respective resistance alleles (Tsagkarakou et al. 2009).

Table 1 Recent reports of resistance to insecticides in *Bemisia tabaci* species/biotypes

Country	Years of collection	Crop	Species/biotype	Resistance to insecticides (N = none; L = low; M = moderate; H = high; VH = very high)*	References
Brazil	2013–2014	Cotton, tobacco, soybean and various vegetables	MEAM1 (B)	Resistance levels to all insecticides tested were L to VH (azadirachtin, cartap, chlorantraniliprole, diafenthiuron, imidacloprid, lambda-cyhalothrin, spiromesifen)	Dângelo et al. (2018)
Burkina Faso	2014–2015	*Lantana camara*, tomato	MED-Q1, MED-Q3	For an OP (chlorpyrifos-ethyl); a pyrethroid (deltamethrin) and a neonicotinoid (acetamiprid)—MED-Q1 was more resistant than the MED-Q3	Drabo et al. (2017)
China NW	2004–2005	Poinsettia, cotton, grape and melon	B	Pyrethroids (cypermethrin and bifenthrin)—VH; imidacloprid—L to M; pyriproxyfen—M to H; abamectin—N	Ma et al. (2007)
China, SE	2005–2014	Various crops, but mostly vegetables	B and Q	Sulfoxaflor (B)—N to L, (B, dominant)—M; pymetrozine (B, Q)—L; neonicotinoids: imidacloprid, thiamethoxam (B, Q), nitenpyram (B, Q)—L; and cyantraniliprole (B, Q)—M to H	Yao et al. (2017)
China	2007–2008	Cotton, tomato and capsicum	B and Q	Neonicotinoids—(B)—L; (Q)-M to VH; abamectin (B, Q)—L; bifenthrin (B, Q)—L to H; cypermethrin (B, Q)—M to VH; and pyriproxyfen (B, Q)—L to M	Luo et al. (2010)
China, SE	2008–2009	Cotton, various vegetables, poinsettia, and grape	B and Q	Alpha-cypermethrin (B)—VH, (Q)—M to VH; neonicotinoids: imidacloprid, thiamethoxam (B, Q)—M to VH; Spinosad (B, Q)—N to L; abamectin—N; fipronil (B, Q)—L to M	Wang et al. (2010)
China, E	2010	Gerbera, cucumber, capsicum, cabbage	Q	Dichlorvos (OP)—L; carbosulfan (carbamate)—N; cypermethrin—L; neonicotinoids: imidacloprid, nitenpyram—L to H; abamectin—N	Yuan et al. (2012)

Table 1 (continued)

Country	Years of collection	Crop	Species/biotype	Resistance to insecticides (N = none; L = low; M = moderate; H = high; VH = very high)*	References
China	2011–2013	Tomato, pepper, cucumber	Q	Chlorpyrifos—L; bifenthrin—L to M; neonicotinoids: imidacloprid, thiamethoxam, acetamiprid—L to H, nitenpyram—L to VH; abamectin and spinetoram—N	Wang et al. (2017)
Greece, Crete	2005–2007	Various vegetables	Med (Q)	Pirimiphos-methyl (OP)—L to M; α-cypermethrin (pyrethroid)—M to VH; imidacloprid—L to VH	Roditakis et al. (2009)
Cyprus	2006–2007	Mostly various vegetables	B	Neonicotinoids: imidacloprid, thiamethoxam—H to VH, acetamiprid—L; bifenthrin—H to VH	Vassiliou et al. (2011)
India	2010–2013	Cotton, vegetables, maize, soybean and others	Asia I, Asia II-1, and Asia II-7	Asia II-7 (reference strain) is susceptible to most insecticides; OPs—L to H (Asia I, Asia II-1; Pyrethroids—M to VH (Asia I, Asia II-1); Neonicotinoids—L to M (Asia I, Asia II-1)	Naveen et al. (2017)
India	2016–2017	Vegetable crops	Not defined	Acephate (OP)—H to VH; triazophos (OP)—M to H; Indoxacarb (Oxadiazine)—N; dinotefuran (neonicotinoid)—L to H; spiromesifen (tetronic acid derivative)—L to H; pyriproxyfen—L to M; flonicamid (pyridine)—L to H	Roy et al. (2019)
Israel	2008–2010	Various vegetables and fresh herbs	B and Q	Thiamethoxam—(Q) VH; imidacloprid (B, Q)—L to H; acetamiprid—(Q)—L to H	Kontsedalov et al. (2012)
Israel	2002–2011	Cotton	B and Q	Pyriproxyfen—(Q)—VH, (B)—L; acetamiprid (Q, B)—L to H; thiamethoxam—(Q, B)—M to VH	Horowitz et al. (2004), Horowitz et al. (2005), Horowitz and Ishaaya (2014)
Pakistan	2002–2007	Cotton and various vegetables	Not defined	OPs—L to M	Ahmad et al. (2010)
Pakistan	2008–2009	Cotton and sunflower	Not defined	Neonicotinoids—L to M; buprofezin—L to M; pyriproxyfen—L	Basit et al. (2013)
Pakistan	2007–2010	Cotton and various vegetables	Not defined	Neonicotinoids—H; diafenthiuron—L to H	Ahmad and Khan (2017)

Table 1 (continued)

Country	Years of collection	Crop	Species/biotype	Resistance to insecticides (N = none; L = low; M = moderate; H = high; VH = very high)*	References
Spain	2006	Tomato and sweet pepper	Q	Azadirachtin—L to M; buprofezin—M to VH; Imidacloprid—L to M; methomyl—L to H; pyridaben—L; pyriproxyfen—L to M; spiromesifen—L	Fernandez et al. (2009)
Spain	2006–2012	Vegetables	Q	Cyantraniliprole—N to L	Gravalos et al. (2015)
Spain	2014–2016	Glasshouse sweet pepper and tomato	Q	Spiromesifen—L to VH; spirotetramat—L to H	Bielza et al. (2019)
Turkey	2000–2001	Cotton	B	Pyrethroids and OPs—M to VH; buprofezin—lower response in the IZMIR strain	Erdogan et al. (2008)
Turkey	2009	Cotton, tomato, cucumber, pepper	MEAM1 (B)	Neonicotinoids: acetamiprid—M to H; imidacloprid—M to VH; thiacloprid—H to VH; thiamethoxam—L to VH	Satar et al. (2018)
Turkey	2011	Cotton, squash, sesame	B	Neonicotinoids: thiamethoxam—L to H; acetamiprid—L to M	Şahin and İkten (2017)
USA, California, Arizona	2003–2005	Cotton and various vegetables	B	Neonicotinoids—H to VH (esp. imidacloprid)	Castle and Prabhaker (2013)
USA, Florida	2000–2007	Especially tomato	B	Neonicotinoids: imidacloprid (systemic bioassay)—L to H; thiamethoxam (systemic bioassay)—L to M	Schuster et al. (2010)
USA, Florida	2008–2010	Mostly tomatoes	B	Neonicotinoids—L; pyrethroids (bifenthrin)—L; buprofezin—L	Caballero et al. (2013)

*e.g., Torres-Villa et al. (2002)

Resistance to pyriproxyfen and buprofezin

Resistance in *B. tabaci* to the Insect Growth Regulators (IGRs), pyriproxyfen and buprofezin has been reported widely from many countries (e.g., Horowitz et al. 2005, 2007; Erdogan et al. 2008; Crowder et al. 2008; Fernandez et al. 2009; Li et al. 2012; Basit et al. 2013; Horowitz and Ishaaya 2014; Roy et al. 2019).

Pyriproxyfen is a potent juvenile hormone (JH) mimic affecting the hormonal balance in insects, suppressing embryogenesis, metamorphosis and adult formation. It has been considered a leading insecticide for controlling whiteflies (Ishaaya and Horowitz 1995; Horowitz et al. 2005; Crowder et al. 2008; Castle et al. 2010), especially against biotype B. Both pyriproxyfen and buprofezin were considered harmless to natural enemies as compared with conventional insecticides. Naranjo et al. (2004) suggested that these selective IGRs can be used in an effective integrated control system for *B. tabaci*. However, its widespread use has resulted in resistance development in Israel since the 1990s (Horowitz et al. 1994; Horowitz et al. 2002, 2005). To delay resistance in *B. tabaci*, the use of pyriproxyfen and buprofezin, especially in cotton fields, was restricted to one application per a cotton season in most Insecticide Resistance Management (IRM) programs, but resistance to these IGRs has evolved and in some cases the use of pyriproxyfen and buprofezin was decreased because of the resistance (ARH, personal communication). Cases of strong resistance to pyriproxyfen have been associated with the Q rather than the B biotype (Horowitz et al. 2002, 2005; Dennehy et al. 2005; Horowitz and Ishaaya 2014). In Israel, since 2009, a significant shift in the biotype ratios has been observed: the B biotype has become predominate over the Q. At the same time, resistance to pyriproxyfen declined considerably (Crowder et al. 2011; Horowitz and Ishaaya 2014). However, simulation models conducted with the B biotype have demonstrated that resistance to pyriproxyfen in this biotype can be managed through modification of operational and environmental factors that can be controlled by the growers (Crowder et al. 2008, 2013; Li et al. 2012).

A study conducted in Arizona, where pyriproxyfen served as a major compound for controlling *B. tabaci* in cotton for over a decade, showed that resistance to this compound increased steadily, and synergism bioassays demonstrated that the increasing resistance to pyriproxyfen was correlated with elevated levels of cytochrome P450 monooxygenases (P450s) and glutathione S-transferases (GSTs) (Ma et al. 2010).

A study conducted with *B. tabaci* MED species employed the DNA microarray technology to compare gene expression levels in pyriproxyfen-resistant and -susceptible populations showed that in the resistant strain many genes implicated in xenobiotic detoxification are upregulated, such as P450s (Ghanim and Kontsedalov 2007), indicating that the resistance to pyriproxyfen could be metabolic. Another study using a recombinantly expressed CYP6CM1, a P450 upregulated in neonicotinoid- and pymetrozine-resistant strains of *B. tabaci*, demonstrated oxidative metabolism by the hydroxylation of pyriproxyfen (Nauen et al. 2015b), thus confirming the potential involvement of P450s in pyriproxyfen resistance.

Resistance to neonicotinoids

Neonicotinoids are among the most effective groups of insecticides for whitefly control. They exhibit systemic and translaminar properties and high residual activity (Takahashi et al. 1992; Elbert et al. 1998; Horowitz et al. 1998). They act especially against sucking insects such as whiteflies, aphids, leafhoppers and various coleopteran pests.

There have been a few review papers summarizing the global aspects of resistance to neonicotinoids (e.g., Nauen and Denholm 2005; Bass et al. 2015); hence, just some important recent studies will be considered below.

In many cases, resistance to neonicotinoids was associated with the Q biotype (e.g., Nauen et al. 2002; Horowitz et al. 2004; Roditakis et al. 2009; Dennehy et al. 2010; Luo et al. 2010), although a few cases of neonicotinoid resistance have been described also in B-biotype strains (Byrne et al. 2003; Schuster et al. 2010; Wang et al. 2010).

Low to moderate levels of resistance to the neonicotinoids imidacloprid and thiamethoxam were detected in Brazil (Silva et al. 2009), whereas in Florida, USA, high levels of resistance to imidacloprid and thiamethoxam were detected in biotype B of *B. tabaci* (Schuster et al. 2010). In Israel, resistance level in Q biotype to thiamethoxam was high and to imidacloprid and acetamiprid was moderate; Q biotype populations have taken over B in crops grown in protected conditions, where resistance outbreaks usually develop after several insecticide applications (Kontsedalov et al. 2012). In Cyprus, moderate to high levels of resistance were detected to imidacloprid (77–392-fold) and thiamethoxam (50–164-fold), but low resistance levels were observed to acetamiprid (Vassiliou et al. 2011). In Crete, very high resistance levels were detected in various whitefly populations for imidacloprid (38–1958-fold). A strong correlation between resistance to imidacloprid and the number of applications with neonicotinoids was observed (Roditakis et al. 2009). Recently, most of the *B. tabaci* populations in Turkey were found to be resistant to neonicotinoids with resistance levels up to 2060-fold for imidacloprid, while resistance to thiamethoxam was low (Satar et al. 2018). In Pakistan, neonicotinoid resistance increased in *B. tabaci* (the biotype was not defined) following intensive use leading to field failures (Ahmad and Khan

2017). In India, high resistance to neonicotinoids in several field populations of *B. tabaci* was detected, especially in Asia I and Asia II-1 strains (Naveen et al. 2017). Reports from China pointed out that the increase in resistance to neonicotinoids was mainly in biotype Q. While biotype B remained susceptible to acetamiprid, imidacloprid and thiamethoxam, field strains of biotype Q expressed moderate to high resistance to these insecticides (Luo et al. 2010). In southeastern China, moderate to high levels of resistance were detected in both B and Q biotypes to two neonicotinoids (28–1900-fold to imidacloprid, 29–1200-fold to thiamethoxam) (Wang et al. 2010). In eastern China, some field strains (especially Q biotype) exhibited low to high resistance to two neonicotinoids (imidacloprid and nitenpyram) (Yuan et al. 2012). A recent study conducted in three regions of China with *B. tabaci* Q collected from vegetables in 2011–2013 revealed low to high resistance to neonicotinoid insecticides (Wang et al. 2017). In southeast coast of China, resistance to neonicotinoids in the Q biotype was unstable in open fields, but increased constantly in protected areas (Yao et al. 2017).

Neonicotinoids target the insect nicotinic acetylcholine receptor (nAChR) in the central nervous system and disrupt nerve transmission leading to paralysis and death within short time (Tomizawa and Casida 2005). As the affinity of these compounds to mammalian nAChRs is very low, and some could be applied and taken up systemically by plants such as imidacloprid, or can by directly treated to seeds, they became very popular, and management programs heavily relied on using neonicotinoids (Jeschke et al. 2011). Enhanced detoxification is reported as the main mechanism for conferring resistance against imidacloprid in strains of both *B. tabaci* MEAM1 and MED (Nauen et al. 2002; Rauch and Nauen 2003). Karunker et al. (2008) have shown by measuring the expression of 11 P450 genes that CYP6CM1 overexpression was tightly associated with imidacloprid resistance. It was also shown that heterologously expressed CYP6CM1 could metabolize imidacloprid and other neonicotinoids in vitro (Karunker et al. 2009) and that its expression and protein level is correlated with the degree of resistance in field-collected populations (Roditakis et al. 2011). A recent computational study suggested that lower levels of dinotefuran resistance in such whitefly strains are due to differences in binding to CYP6CM1 (Meng et al. 2016), a finding validated for the new butenolide insecticide flupyradifurone and the sulfoximine insecticide sulfoxaflor, both not belonging to the neonicotinoids, but targeting insect nAChRs (Jeschke et al. 2015; Nauen et al. 2015a). Nevertheless, this enzyme has the potential to be used for the screening of field populations for resistance against imidacloprid using diagnostic tools such as ELISA (Nauen et al. 2015a). A predominantly metabolic mechanism of resistance was also confirmed by work conducted by Feng et al. (2010) in China. In this study, a thiamethoxam-resistant population was cross-resistant to other neonicotinoids. Synergism assays revealed that the inhibition of P450s strongly synergized neonicotinoid efficacy, a finding supported by increased enzyme activity in resistant strains (Feng et al. 2010). Metabolically based neonicotinoid cross-resistance has also been reported from other parts of China (Wang et al. 2009). Similar results were reported from Turkey, where field-collected populations of *B. tabaci* showed high levels of resistance to different neonicotinoids driven by metabolic mechanisms (Satar et al. 2018).

Recently, *B. tabaci* resistance to insecticides, especially neonicotinoids, has been increasingly investigated by employing RNAseq analysis to screen for (less obvious) mechanisms of resistance. Such experiments also enrich the available datasets of genes, gene expression data and pathways involved in resistance. A study conducted on the MED species of *B. tabaci* used RNAseq analyses to profile the expression patterns of different detoxification genes including P450s, GSTs and carboxylesterases, as potential candidate genes contributing to insecticide resistance (Ilias et al. 2015). The study demonstrated the overexpression of P450s from the CYP2, CYP3 and CYP4 clades, with CYP6CM1 being the major player. Interestingly, in this study, ten unigenes-encoding nAChRs subunits were identified, but none of those showed polymorphism that could be linked to neonicotinoid resistance when compared to a susceptible reference strain (Ilias et al. 2015).

Ketoenols

Ketoenols are a relatively new class of insecticides and known as derivatives of tetronic acids (spiromesifen) and tetramic acids (spirotetramat). Both compounds are active against whiteflies and act as inhibitors of lipid biosynthesis by targeting acetyl-CoA carboxylase, thus being particularly active against juveniles, but also affecting female fecundity (Bretschneider et al. 2003; Nauen et al. 2005). Several reports have indicated the absence of cross-resistance between spiromesifen and other major commonly used insecticides from different chemical groups such as neonicotinoids and pyriproxyfen (Nauen and Konanz 2005; Prabhaker et al. 2008; Kontsedalov et al. 2009). Spirotetramat is a systemic insecticide with phloem and xylem mobility for the control of a broader spectrum of sucking insects, including aphids, whiteflies, psyllids and scales. Similar to spiromesifen, it is particularly effective against juvenile stages and it significantly reduces fecundity and fertility of *B. tabaci* females (Brück et al. 2009).

Fernandez et al. (2009) reported low resistance level to spiromesifen (1- to sevenfold) in populations of Q biotype collected in southeastern Spain, and Roy et al. (2019) found in India low to moderate resistance (8- to 32-fold) to this insecticide. However, recently, several field strains that were assayed in Spain for resistance to these two insecticides exhibited very high resistance to spiromesifen (> 10,000-fold) and cross-resistance to spirotetramat, but to a much lower extent (130-fold) (Bielza et al. 2019).

Diamides

Diamide insecticides represent the most recent class of chemistry introduced to the market approximately 13 years ago (Nauen and Steinbach 2016). Five diamide insecticides, i.e., the phthalic diamide, flubendiamide and the anthranilic diamides chlorantraniliprole, cyclaniliprole, tetraniliprole and cyantraniliprole, have so far been commercialized. Flubendiamide and chlorantraniliprole are potent against lepidopteran pests, while cyantraniliprole also targets sucking pests such as whiteflies and aphids (Sattelle et al. 2008; Lahm et al. 2009). These compounds act on insect ryanodine receptors, large tetrameric calcium release channels located in neuromuscular tissues.

Studies on the molecular mechanisms of diamide resistance in lepidopteran pests, especially the diamondback moth *Plutella xylostella* and the tomato leaf miner *Tuta absoluta*, have revealed RyR target-site mutations with strong functional implications for diamide binding, while metabolic mechanisms of resistance based on elevated levels of detoxification enzymes were not sufficiently studied (Nauen and Steinbach 2016).

In *B. tabaci*, a short time after cyantraniliprole use in China, low to moderate resistance has evolved to this diamide, especially in the Q biotype (MED) of *B. tabaci* (Yao et al. 2017; Wang et al. 2018), whereas in European countries such as Spain, Italy and Greece no variation in susceptibility to cyantraniliprole was detected yet (Gravalos et al. 2015).

Other insecticides

Other important insecticides frequently used to control *B. tabaci* include pymetrozine, a transient receptor protein vanillin (TRPV) channel modulator of chordotonal organs. However, pymetrozine cross-resistance has been described in neonicotinoid-resistant strains of both B and Q biotype whiteflies from different regions worldwide (Gorman et al. 2010). The cross-resistance is mainly driven by the overexpression of CYP6CM1 as shown by another study showing the hydroxylation of pymetrozine by functionally expressed CYP6CM1 (Nauen et al. 2013, 2015b).

Bemisia tabaci resistance management

The most common solutions to control *B. tabaci* pest attacks have been insecticides, because of their efficacy and convenience (e.g., Palumbo et al. 2001; Horowitz et al. 2011). However, using insecticides alone is harmful to natural enemies and the environment, and in addition, intensive use of chemical insecticides results in development of resistance with striking phenotypes that may jeopardize pest control efficacy.

There are a number of major principles for successful resistance management at a technical level to be followed in chemical control, including (a) insecticides should be used according to label recommendations; (b) select insecticides based on known local efficacy and selectivity (IPM); (c) rotate insecticides from different Modes of Action (MoAs) employing a ‘MoA treatment windows’ approach; and (d) nonchemical control methods should be incorporated (IPM). The entire above are essential for the successful implementation of IRM strategies (Table 2). However, a nontechnical parameter that can affect the success of resistance management schemes is the understanding of the resistance mechanisms to avoid cross-resistance issues compromising a developed IRM strategy. Ideally, IRM is supported by educational courses and communication plans as advocated by the Insecticide Resistance Action Committee (IRAC) (Sparks and Nauen 2015).

“Window” programs—rotation of modes of action and insecticide applications

It has been demonstrated that selection pressure enforced by the frequent use of insecticides is the main driving force for the development of resistance via the gradual selection of the individuals carrying the resistant alleles (Georghiou and Lagunes-Tejeda 1991; Denholm and Rowland 1992). However, applying the same insecticide MoA frequently in sequence, within a crop cycle, was a very common practice, particularly for novel and highly effective products. The resistance selection process can be interrupted by using insecticides of different MoAs based on IRAC’s MoA classification scheme (Sparks and Nauen 2015). The rationale behind this strategy is that insecticides of different modes of action usually select for different resistance mechanisms (Sparks and Nauen 2015). Cross-resistance exceptions to the aforementioned rule have been demonstrated, e.g., neonicotinoids and pymetrozine (Gorman et al. 2010; Nauen et al. 2013). In addition, the development of a multiple resistance cannot be excluded if selection pressure is of

Table 2 Current statuses and future prospects of alternative whitefly control methods implemented in integrated and/or biological pest management schemes (see text for details)

Strategy	Product	Current status and prospects
Prevention methods	Insect proof netting on ventilation openings	Extensively adopted with minor regional exceptions
	UV-blocking films	Limited use with a stable trend, adopted mainly in crops practicing biological control
	Reflective mulches	Limited use in greenhouse crops/trend unknown
	Ground cover crops	Limited use/not applied in greenhouse crops
	Use of supplementary UV-radiation	Currently at experimental level/not applied
Mass trapping	Yellow traps	Extensively adopted with minor exceptions
Entomopathogenic fungi	*Lecanicillium lecanii*, *Beauveria bassiana*	Used with IPM schemes/limited adoption
Natural enemies	Predators	Mainly *Amblyseius swirskii* and Mirid species, extensively adopted with minor regional and crop exceptions
	Parasitoids	Mainly *Eretmocerus* sp extensively adopted with minor exceptions
Conservation		Extensively adopted in open field crop, gradually implemented in greenhouse crops with an increasing trend
Essential oils and plant extracts		Limited use with an increasing trend supported by novel products in the market
Biotechnological insecticides	RNAi	Currently experimental level/not applied

extreme level (Roditakis et al. 2005). Thus, it is essential to take into account all available information when a rotation of insecticides of different MoAs is designed. In addition, selecting the most appropriate chemical from available, officially registered products depends on various parameters such as the crop stage, post-harvest interval, use of beneficial/pollinators in the crop, the infestation level, the presence of other coexisting pests and resistance history in the crop. A list of available MoAs and chemicals that could be used in rotation schemes for whitefly control is provided in Table 3.

The most widely followed MoA rotation approach in IRM is that suggested by IRAC (www.irac-online.org), namely the 'MoA treatment windows' approach, where several rules apply for the proper implementation of the particular rotation scheme. The basic aim of the IRAC strategy is to avoid treating consecutive generations of the target pest with insecticides of the same MoA. Multiple applications with chemicals of the same MoA are allowed within a generation 'window.' As the generation time for *B. tabaci* ranges between 24 and 30 days, a generation 'window' is set to 30 days for simplicity. Additional required applications beyond the 30-day window should be performed with insecticides of a different MoA. A compound with a specific MoA should not be reused, unless a 60-day interval is allowed (i.e., approximately two generations). In addition, all applications should strictly follow the product label with regard to the rate, the target pest, the method and number of applications.

Insecticide mixtures

Application of insecticide mixtures was used extensively for controlling whiteflies as a tactic for managing insecticide resistance in *B. tabaci*. (Horowitz and Ishaaya 1996; Denholm et al. 1998; Castle et al. 2002). This approach was based on mixing chemicals of different MoAs lacking cross-resistance (Denholm and Rowland 1992; Horowitz and Ishaaya 1996) that could delay resistance development, because mechanisms required to resist both insecticides simultaneously commonly exist in scarcity in a pest population (Georghiou 1994). Unfortunately, the intensive use of synergized insecticides, particularly of OPs and pyrethroids for whitefly control (Denholm et al. 1998), resulted in high resistance levels to both chemicals and major pest control failures (Dennehy and Williams 1997). The insecticide mixtures approach has been thoroughly investigated in numerous pest systems and still remains controversial since several assumptions pertain in each case, dictating the overall success of the method (Cloyd 2010; South and Hastings 2018). The Insecticide Resistance Action Committee (IRAC) provides more detailed information on the use of insecticide mixtures and their value in IRM and pest control in general (refer to www.irac-online.org). Despite the extensive discussion on this topic, the use of insecticide mixtures is still wildly adopted in *B. tabaci* management.

Sustainable IPM approaches

Whitefly control can rely on various methods alternative or complementary to chemical insecticides. Prevention

Table 3 Insecticide modes of action and chemical classes for whitefly resistance management; the availability of different chemical classes depends on regional registrations and therefore varies (MoA classification according to IRAC (Sparks and Nauen 2015)

IRAC group	Mode of action	IRAC subgroup	Chemical class/Chemicals
1	Acetylcholinesterase inhibitors	A	Carbamates
		B	Organophosphates
3	Sodium channel modulators	A	Pyrethroids
4	nAChR competitive modulators	A	Neonicotinoids
		C	Sulfoxaflor
		D	Flupyradifurone
7	Juvenile hormone mimics	C	Pyriproxyfen
9	TRPV channel modulators	B	Pymetrozine
		D	Afidopyropen
12	Inhibitors of mitochondrial ATP synthase	A	Diafenthiuron
15	Inhibitors of chitin biosynthesis affecting CHS1	None	Benzoylureas
16	Inhibitors of chitin biosynthesis, type 1	None	Buprofezin
21	Mitochondrial complex I inhibitors	A	METI's
23	Inhibitors of acetyl-CoA carboxylase	None	Spirotetramat
28	Ryanodine receptor modulators	None	Cyantraniliprole
29	Chordotonal organ modulators, undefined	None	Flonicamid
UN	Compounds of unknown MoA	None	Azadirachtin
UNF	Fungal agents of unknown or uncertain MoA	None	e.g., *Beauveria bassiana*
UNE	Botanical essence	None	e.g., fatty acids

methods such as insect proof netting on greenhouse ventilation openings, UV-blocking films (Monci et al. 2004; Chiel et al. 2006; Horowitz et al. 2011; Monci et al. 2019), reflective mulches (Greer and Dole 2003; Simmons et al. 2010; Rajasri et al. 2011) or ground cover crops (Hilje and Stansly 2008) have been adopted to varying extent. Novel approaches such as the use of supplementary UV radiation (Prieto-Ruiz et al. 2019) may also be a promising addition in the immediate future. Mass trapping with sticky traps has been used extensively, in various forms, having as basis of yellow-colored sticky surfaces (Lu et al. 2012); however, sticky traps are also important tools for whitefly population monitoring (Gerling and Horowitz 1984).

Entomopathogenic fungi have been suggested for whitefly control (Lacey et al. 1999; Wraight et al. 2000; Cuthbertson and Walters 2005); however, this approach was adopted to a limited extent in practice. Nonetheless, recent progress may provide novel tools and a larger market share (Garrido-Jurado et al. 2017; Anwar et al. 2018; Jaber et al. 2018; Santos et al. 2018; do Nascimento Silva et al. 2019) without the adverse effect of resistance development (Gao et al. 2017). One of the major principles of IPM programs is the use of natural enemies, such as predators and parasitoids (Gerling et al. 2001; Horowitz et al. 2011). Numerous predators have been reported praying on whiteflies, in which the phytoseiid mite *Amblyseius swirskii* (Athias-Henriot) can be considered among the most important. Its introduction to the market has changed the balance of plant protection practices against *B. tabaci* in favor of IPM (Nomikou et al. 2001; van der Blom et al. 2008; Calvo et al. 2009, 2012). Mirid bugs like *Nesidiocoris tenuis* (Reuter) and *Macrolophus* sp have been introduced as generalist predators for many pests including *B. tabaci* (Alomar et al. 2006; Arnó et al. 2010). Parasitoids are also key biocontrol agents, playing a major role in IPM for whiteflies. Among others, aphelinids *Encarisa* sp and *Eretmocerus* sp have been successfully incorporated in IPM schemes (Foltyn and Gerling 1985; Heinz and Nelson 1996; Van Lenteren et al. 1997; Qiu et al. 2004).

In field crops, it was demonstrated that the conservation of natural enemies is a key element in IPM programs, since they serve as efficient factors for the control of *B. tabaci* (Naranjo and Akey 2005; Naranjo and Ellsworth 2009a; Vandervoet et al. 2018; Togni et al. 2019). Several years back, the cotton crops served as a model, where the concept of natural enemies' conservation was conceived and implemented, altering the pest status of whiteflies in the cotton growing system of Arizona (Naranjo et al. 2002; Naranjo and Ellsworth 2009b). The idea of conservation was also adopted, with modifications, in greenhouse crops, by modifying the flora surrounding greenhouses (Rodríguez et al. 2018, Roditakis pers. comm.).

Essential oils and plant extracts have been extensively investigated for their activity on *B. tabaci* (Kim et al. 2011; Baldin et al. 2013; Deletre et al. 2016; Vite-Vallejo et al. 2018; Wagan et al. 2018; Cruz-Estrada et al. 2019); however, their use is currently limited. Biotechnological insecticides based on RNA interference (RNAi) that specifically silence the function of vital genes can serve as potential novel pest management tools, though not yet technically feasible (Ghanim et al. 2007; Upadhyay et al. 2011). However, the proof of concept has been provided (Malik et al. 2016; Luo et al. 2017) and several studies demonstrate promising results (Raza et al. 2016; Vyas et al. 2017).

Many of the aforementioned approaches are key element of sustainable IPM schemes that promote alternative pest management tactics and result in substantial reduction of pest pressure and subsequent reduction of insecticide applications making implementation of rational IRM possible.

Farmer education

Scientific evidence of insecticide resistance and IRM schemes can only be useful and contribute to changes in the actual agricultural practice if socioeconomic factors that are occasionally ignored are wisely managed (FAO 2012). These factors include concerns about the cost, the necessity of suggested alterations, the feasibility from a technical perspective and overall a thorough education on resistance management tactics along with its implications in crop protection (FAO 2012). An exceptional example of farmer-level adoption of an IPM program for whiteflies is the case of Arizona. The initiative was driven by governmental officials and academia with great agroecological and financial benefits for the agricultural industry (Naranjo and Ellsworth 2009b). Resistance monitoring is essential for early detection of incipient resistance cases (Ellsworth et al. 2013); of course, this information alone cannot reverse the increasing trend of resistance. The resistance monitoring data should serve as a basis to develop a sustainable resistance management strategy followed by all stakeholders. It is more than evident that acceptance of any IRM strategy at the farmer level is essential for its successful implementation in the management of any pest, including *B. tabaci*.

Conclusion

This paper reviews insecticide resistance and management issues among species of the serious crop pest, *B. tabaci*, focusing mainly on studies published in the past decade. At present, the use of insecticides is the main approach employed to manage *B. tabaci* populations because of their efficacy and convenience. This practice is considered problematic due to both environmental concerns and the widespread insecticide resistance that *B. tabaci* has developed.

Bemisia tabaci has evolved resistance to insecticides from most chemical classes including new insecticides. Among the common cryptic species, MED is considered more resistant than the MEAM1 to insecticides such as pyriproxyfen and neonicotinoids; however, in recent years there are other species of *B. tabaci* including MEAM1, Asia I and Asia II-1 that have developed high resistance levels to various groups of insecticides. The mechanisms of resistance in *B. tabaci* are similar to those that have been described from many other pest species, and they are generally classified as metabolic, involving esterase-, glutathione S transferase (GST)- or P450 monooxygenase-based detoxification, or point mutations in the target site. Advanced methods based on the molecular and gene sequence data obtained from resistant and susceptible field-collected *B. tabaci* populations resulted in a better understanding of resistance mechanisms in this pest.

There are several components of IPM-IRM programs applicable to managing the resistance in *B. tabaci*, namely chemical control with selective insecticides, rotation of MoAs, insecticide mixtures, reducing chemical insecticide applications and nonchemical control methods using IPM practices (e.g., biological control, crop plant resistance and physical/mechanical methods). It is hoped that the integration of these methods will contribute to improving the management of the pest, thus helping to guarantee sustainable yields in the future.

Author contributions

ARH wrote the first draft and assembled all co-authors. ARH, MG, ER, RN and II all contributed equally to the formation of the outline and writing the content of this review.

References

Ahmad M, Khan RA (2017) Field-evolved resistance of *Bemisia tabaci* (Hemiptera: Aleyrodidae) to carbodiimide and neonicotinoids in Pakistan. J Econ Entomol 110:1235–1242

Ahmad M, Arif MI, Naveed M (2010) Dynamics of resistance to organophosphate and carbamate insecticides in the cotton whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae) from Pakistan. J Pest Sci 83:409–420

Alomar O, Riudavets J, Castañe C (2006) *Macrolophus caliginosus* in the biological control of *Bemisia tabaci* on greenhouse melons. Biol Control 36:154–162

Alon M, Alon F, Nauen R, Morin S (2008) Organophosphates' resistance in the B-biotype of *Bemisia tabaci* (Hemiptera: Aleyrodidae) is associated with a point mutation in an ace1-type acetylcholinesterase and overexpression of carboxylesterase. Insect Biochem Mol Biol 38:940–949

Anwar W, Ali S, Nawaz K, Iftikhar S, Javed MA, Hashem A, Alqarawi AA, Abd Allah EF, Akhter A (2018) Entomopathogenic fungus *Clonostachys rosea* as a biocontrol agent against whitefly (*Bemisia tabaci*). Biocontrol Sci Technol 28:750–760

Arnó J, Castañé C, Riudavets J, Gabarra R (2010) Risk of damage to tomato crops by the generalist zoophytophagous predator

Nesidiocoris tenuis (Reuter) (Hemiptera: Miridae). Bull Entomol Res 100:105–115

Baldin ELL, Crotti AEM, Wakabayashi KAL, Silva JPGF, Aguiar GP, Souza ES, Veneziani RCS, Groppo M (2013) Plant-derived essential oils affecting settlement and oviposition of *Bemisia tabaci* (Genn.) biotype B on tomato. J Pest Sci 86:301–308

Basit M (2019) Status of insecticide resistance in *Bemisia tabaci*: resistance, cross-resistance, stability of resistance, genetics and fitness costs. Phytoparasitica 47:207–225

Basit M, Saeed S, Saleem MA, Denholm I, Shah M (2013) Detection of resistance, cross-resistance, and stability of resistance to new chemistry insecticides in *Bemisia tabaci* (Homoptera: Aleyrodidae). J Econ Entomol 106:1414–1422

Bass C, Schroeder I, Turberg A, Field LM, Williamson MS (2004) Identification of mutations associated with pyrethroid resistance in the para-type sodium channel of the cat flea, *Ctenocephalides felis*. Insect Biochem Mol Biol 34:1305–1313

Bass C, Denholm I, Williamson MS, Nauen R (2015) The global status of insect resistance to neonicotinoid insecticides. Pestic Biochem Physiol 121:78–87

Bedford ID, Briddon RW, Brown JK, Rosell RC, Markham PG (1994) Geminivirus transmission and biological characterisation of *Bemisia tabaci* (Gennadius) biotypes from different geographic regions. Ann Appl Biol 125:311–325

Bielza P, Moreno I, Belando A, Grávalos C, Izquierdo J, Nauen R (2019) Spiromesifen and spirotetramat resistance in field populations of *Bemisia tabaci* Gennadius in Spain. Pest Manag Sci 75:45–52

Boykin LM, De Barro PJ (2014) A practical guide to identifying members of the *Bemisia tabaci* species complex: and other morphologically identical species. Front Ecol Evol 45:1–5

Boykin LM, Shatters RG Jr, Rosell RC, McKenzie CL, Bagnall RN, De Barro P, Frohlich DR (2007) Global relationships of *Bemisia tabaci* (Hemiptera: Aleyrodidae) revealed using Bayesian analysis of mitochondrial COI DNA sequences. Mol Phylogenet Evol 44:1306–1319

Boykin LM, Armstrong KF, Kubatko L, De Barro P (2012) Species delimitation and global biosecurity. Evol Bioinform 8:1–37

Bretschneider T, Benet-Buchhol J, Fischer R, Nauen R (2003) Spirodiclofen and spiromesifen—novel acaricidal and insecticidal tetronic acid derivatives with a new mode of action. Chimia 57:697–701

Briddon RW (2003) Cotton leaf curl disease, a multicomponent begomovirus complex. Mol Plant Pathol 4:427–434

Brown JK, Frohlich DR, Rosell RC (1995) The sweetpotato or silverleaf whiteflies: biotypes of *Bemisia tabaci* or a species complex? Annu Rev Entomol 40:511–534

Brück E, Elbert A, Fischer R et al (2009) Movento®, an innovative ambimobile insecticide for sucking insect pest control in agriculture: biological profile and field performance. Crop Prot 28:838–844

Byrne DN, Bellows TS Jr (1991) Whitefly biology. Annu Rev Entomol 36:431–457

Byrne FJ, Devonshire AL (1991) In vivo inhibition of esterase and acetylcholinesterase activities by profenofos treatments in the tobacco whitefly *Bemisia tabaci* (Genn)—implications for routine biochemical monitoring of these enzymes. Pestic Biochem Physiol 40:198–204

Byrne FJ, Devonshire AL (1993) Insensitive acetylcholinesterase and esterase polymorphism in susceptible and resistant populations of the tobacco whitefly *Bemisia tabaci* (Genn). Pestic Biochem Physiol 45:34–42

Byrne FJ, Devonshire AL (1997) Kinetics of insensitive acetylcholinesterases in organophosphate-resistant tobacco whitefly, *Bemisia tabaci* (Gennadius) Homoptera: Aleyrodidae). Pestic Biochem Physiol 58:119–124

Byrne FJ, Cahill M, Denholm I, Devonshire AL (1994) A biochemical and toxicological study of the role of insensitive acetylcholinesterase in organophosphorus resistant *Bemisia tabaci* (Homoptera: Aleyrodidae) from Israel. Bull Entomol Res 84:179–184

Byrne FJ, Castle S, Prabhaker N, Toscano N (2003) Biochemical study of resistance to imidacloprid in B biotype *Bemisia tabaci* from Guatemala. Pest Manag Sci 59:347–352

Caballero R, Cyman S, Schuster DJ (2013) Monitoring insecticide resistance in biotype B of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in Florida. Fla Entomol 96:1243–1256

Cahill M, Byrne FJ, Gorman K, Denholm I, Devonshire AL (1995) Pyrethroid and organophosphate resistance in the tobacco whitefly *Bemisia tabaci* (Homoptera: Aleyrodidae). Bull Entomol Res 85:181–187

Cahill M, Denholm I, Byrne FJ, Devonshire AL (1996) Insecticide resistance in *Bemisia tabaci*—current status and implications for management. In: Proceedings of Brighton crop protection conference—pests and diseases, November 18–21 1996. British Crop Protection Council, Farnham, Brighton, UK, pp 75–80

Calvo FJ, Bolckmans K, Belda JE (2009) Development of a biological control-based integrated pest management method for *Bemisia tabaci* for protected sweet pepper crops. Entomol Exp Appl 133:9–18

Calvo FJ, Bolckmans K, Belda JE (2012) Biological control-based IPM in sweet pepper greenhouses using *Amblyseius swirskii* (Acari: Phytoseiidae). Biocontrol Sci Technol 22:1398–1416

Castle SJ, Prabhaker N (2013) Monitoring changes in *Bemisia tabaci* (Hemiptera: Aleyrodidae) susceptibility to neonicotinoid insecticides in Arizona and California. J Econ Entomol 106:1404–1413

Castle SJ, Toscano NC, Prabhaker N, Henneberry TJ, Palumbo JC (2002) Field evaluation of different insecticide use strategies as resistance management and control tactics for *Bemisia tabaci* (Hemiptera: Aleyrodidae). Bull Entomol Res 92:449–460

Castle SJ, Palumbo JC, Prabhaker N, Horowitz AR, Denholm I (2010) Ecological determinants of *Bemisia tabaci* resistance to insecticides. In: Stansly PA, Naranjo SE (eds) Bemisia: bionomics and management of a global pest. Springer, Dordrecht, pp 423–465

Chiel E, Steinberg S, Messika Y, Antignus Y (2006) The effect of UV-absorbing plastic sheet on the attraction and host location ability of three parasitoids: *Aphidius colemani*, *Diglyphus isaea* and *Eretmocerus mundus*. Biocontrol 51:65–78

Chu D, Wan FH, Zhang YJ, Brown JK (2010) Change in the biotype composition of *Bemisia tabaci* in Shandong Province of China from 2005 to 2008. Environ Entomol 39:1028–1036

Chung IH, Kang S, Kim YR, Kim JH, Jung JW, Lee S, Lee SH, Hwang SY (2011) Development of a low-density DNA microarray for diagnosis of target-site mutations of pyrethroid and organophosphate resistance mutations in the whitefly *Bemisia tabaci*. Pest Manag Sci 67(12):1541–1548

Cloyd RA (2010) Pesticide mixtures and rotations: are these viable resistance mitigating strategies. Pest Technol 4:14–18

Costa HS, Brown JK, Sivasupramaniam S, Bird J (1993) Regional distribution, insecticide resistance, and reciprocal crosses between the A and B biotypes of *Bemisia tabaci*. Insect Sci Appl 14:255–266

Crowder DW, Ellers-Kirk C, Yafuso C, Dennehy TJ, Degain BA, Harpold VS, Tabashnik BE, Carrière Y (2008) Inheritance of resistance to pyriproxyfen in *Bemisia tabaci* (Hemiptera: Aleyrodidae) males and females (B biotype). J Econ Entomol 101:927–932

Crowder DW, Horowitz AR, Breslauer H, Rippa M, Kontsedalov S, Ghanim M, Carrière Y (2011) Niche partitioning and stochastic processes shape community structure following whitefly invasions. Basic Appl Ecol 12:685–694

Crowder D, Ellsworth P, Naranjo S, Tabashnik B, Carrie're Y (2013) Modeling resistance to juvenile hormone analogs: linking evolution, ecology, and management. In: Devillers J (ed) Juvenile hormones and juvenoids: modeling biological effects and environmental fate. CRC Press, Boca Raton, pp 99–126

Cruz-Estrada A, Ruiz-Sánchez E, Cristóbal-Alejo J, González-Coloma A, Andrés MF, Gamboa-Angulo M (2019) Medium-chain fatty acids from Eugenia winzerlingii leaves causing insect settling deterrent, nematicidal, and phytotoxic effects. Molecules 24:1724

Cuthbertson AGS, Walters KFA (2005) Pathogenicity of the entomopathogenic fungus, *Lecanicillium muscarium*, against the sweetpotato whitefly *Bemisia tabaci* under laboratory and glasshouse conditions. Mycopathologia 160:315–319

Dângelo RAC, Michereff-Filho M, Campos MR, da Silva PS, Guedes RNC (2018) Insecticide resistance and control failure likelihood of the whitefly *Bemisia tabaci* (MEAM1; B biotype): a neotropical scenario. Ann Appl Biol 172:88–99

De Barro PJ, Liu SS, Boykin LM, Dinsdale A (2011) *Bemisia tabaci*: a statement of species status. Annu Rev Entomol 56:1–19

Deletre E, Chandre F, Barkman B, Menut C, Martin T (2016) Naturally occurring bioactive compounds from four repellent essential oils against *Bemisia tabaci* whiteflies. Pest Manag Sci 72:179–189

Denholm I, Rowland MW (1992) Tactics for managing pesticide resistance in arthropods: theory and practice. Annu Rev Entomol 37:91–112

Denholm I, Cahill M, Byrne FJ, Devonshire AL (1996) Progress with documenting and combating insecticide resistance in Bemisia. In: Gerling D, Mayer RT (eds) Bemisia: 1995 taxonomy, biology, damage, control and management. Intercept Ltd Andover, Hants, pp 577–603

Denholm I, Cahill M, Dennehy TJ, Horowitz AR (1998) Challenges with managing insecticide resistance in agricultural pests, exemplified by the whitefly, *Bemisia tabaci*. Philos Trans R Soc Ser B 353:1757–1767

Dennehy TJ, Williams L (1997) Management of resistance in Bemisia in Arizona cotton. Pestic Sci 51:398–406

Dennehy TJ, Degain BA, Harpold VS, Brown JK, Morin S, Fabrick JA, Byrne FJ, Nichols RL (2005) New challenges to management of whitefly resistance to insecticides in Arizona. University of Arizona, Tucson

Dennehy TJ, Degain BA, Harpold VS, Zaborac M, Morin S, Fabrick JA, Nichols RL, Brown JK, Byrne FJ, Li XC (2010) Extraordinary resistance to insecticides reveals exotic Q biotype of *Bemisia tabaci* in the new world. J Econ Entomol 103:2174–2186

Dinsdale A, Cook L, Riginos C, Buckley YM, De Barro P (2010) Refined global analysis of *Bemisia tabaci* (Gennadius) (Hemiptera: Sternorrhyncha: Aleyroidea) mitochondrial CO1 to identify species level genetic boundaries. Ann Entomol Soc Am 103:196–208

Dittrich V, Ernst GH, Ruesch O, Uk S (1990) Resistance mechanisms in sweetpotato whitefly (Homoptera, Aleyrodidae) populations from Sudan, Turkey, Guatemala, and Nicaragua. J Econ Entomol 83:1665–1670

do Nascimento Silva J, Mascarin GM, de Paula Vieira de Castro R, Castilho LR, Freire DMG (2019) Novel combination of a biosurfactant with entomopathogenic fungi enhances efficacy against *Bemisia* whitefly. Pest Manag Sci. https://doi.org/10.1002/ps.5458

Drabo SF, Gnankine O, Imael HN, Bassolé R, Charles N, Mouton L (2017) Susceptibility of MED-Q1 and MED-Q3 biotypes of *Bemisia tabaci* (Hemiptera: Aleyrodidae) populations to essential and seed oils. J Econ Entomol 110:1031–1038

Elbert A, Nauen R, Leicht W (1998) Imidacloprid, a novel chloronicotinyl insecticide: biological activity and agricultural importance. In: Ishaaya I, Degheele D (eds) Insecticides with novel modes of action: mechanism and application. Springer, Berlin, pp 50–73

Ellsworth PC, Tronstad R, Leser J, Goodell PB, Godfrey LD, Henneberry TJ, Hendrix D, Brushwood D, Naranjo SE, Castle S, Nichols RL (1999) Sticky cotton sources and solutions. IPM Series No. 13. The University of Arizona Cooperative Extension. Publ. #AZ1156. Tucson, p 4. http://ag.arizona.edu/crops/cotton/insects/wf/stickycss.pdf

Ellsworth PC, Li X, Dennehy TJ, Palumbo JC, Castle S, Prabhaker N, Nichols RL (2013) Is monitoring susceptibility of *Bemisia tabaci* to insecticides useful to management? In: First international whitefly symposium, 20–24 May, Kolymbari, Crete, Greece

Erdogan C, Moores GD, Gurkan MO, Gorman KJ, Denholm I (2008) Insecticide resistance and biotype status of populations of the tobacco whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae) from Turkey. Crop Prot 27:600–605

FAO (2012) Guidelines on prevention and management of pesticide resistance. International code of conduct on the distribution and use of pesticides, p 52

Farghaly S (2010a) Identification of mutations in the *Bemisia tabaci* (Genn.) para sodium cannel gene associated with resistance to pyrethroids. Egypt J Agric Res. 88:153–165

Farghaly S (2010b) Biochemical monitoring for resistance in the whitefly *Bemisia tabaci*. Am Euroasian J Agric Environ Sci 8:383–389

Feng Y, Wu Q, Wang S, Chang X, Xie W, Xu B, Zhang Y (2010) Cross-resistance study and biochemical mechanisms of thiamethoxam resistance in B-biotype *Bemisia tabaci* (Hemiptera: Aleyrodidae). Pest Manag Sci 66:313–318

Fernandez E, Gravalos C, Javier Haro P, Cifuentes D, Bielza P (2009) Insecticide resistance status of *Bemisia tabaci* Q-biotype in southeastern Spain. Pest Manag Sci 66:885–891

Foltyn S, Gerling D (1985) The parasitoids of the aleyrodid *Bemisia tabaci* in Israel: development, host preference and discrimination of the aphelinid wasp *Eretmocerus mundus*. Entomol Exp Appl 38:255–260

Gao T, Wang Z, Huang Y, Keyhani NO, Huang Z (2017) Lack of resistance development in *Bemisia tabaci* to Isaria fumosorosea after multiple generations of selection. Sci Rep 7:42727

Garrido-Jurado I, Resquín-Romero G, Amarilla SP, Ríos-Moreno A, Carrasco L, Quesada-Moraga E (2017) Transient endophytic colonization of melon plants by entomopathogenic fungi after foliar application for the control of *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae). J Pest Sci 90:319–330

Georghiou GP (1994) Principles of insecticide resistance management. Phytoprotection 75:51–59

Georghiou GP, Lagunes-Tejeda A (1991) The occurrence of resistance to pesticides in arthropods: an index of cases reported through 1980. In: FAO plant production and protection series

Gerling D, Horowitz AR (1984) Yellow traps for evaluating the population levels and dispersal patterns of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). Ann Entomol Soc Am 77:753–759

Gerling D, Alomar Ò, Arnó J (2001) Biological control of *Bemisia tabaci* using predators and parasitoids. Crop Prot 20:779–799

Ghanim M, Kontsedalov S (2007) Gene expression in pyriproxyfen-resistant *Bemisia tabaci* Q biotype. Pest Manag Sci 63(8):776–783

Ghanim M, Kontsedalov S, Czosnek H (2007) Tissue-specific gene silencing by RNA interference in the whitefly *Bemisia tabaci* (Gennadius). Insect Biochem Mol Biol 37:732–738

Gorman K, Slater R, Blande JD, Clarke A, Wren J, McCaffery A, Denholm I (2010) Cross-resistance relationships between neonicotinoids and pymetrozine in *Bemisia tabaci* (Hemiptera: Aleyrodidae). Pest Manag Sci 66:1186–1190

Gravalos C, Fernandez E, Belando A, Moreno I, Ros C, Bielza P (2015) Cross-resistance and baseline susceptibility of Mediterranean strains of *Bemisia tabaci* to cyantraniliprole. Pest Manag Sci 71:1030–1036

Greer L, Dole JM (2003) Aluminum foil, aluminium-painted, plastic, and degradable mulches increase yields and decrease insect-vectored viral diseases of vegetables. Horttechnology 13:276–284

Guirao P, Beitia F, Cenis JL (1997) Biotype determination of Spanish populations of *Bemisia tabaci* (Hemiptera: Aleyrodidae). Bull Entomol Res 87:587–593

Heinz KM, Nelson JM (1996) Interspecific interactions among natural enemies of Bemisia in an inundative biological control program. Biol Control 6:384–393

Henneberry TJ, Faust RM (2008) Introduction. In: Gould J et al (eds) Classical biological control of *Bemisia tabaci* in the United States. Springer, Berlin

Hequet E, Henneberry TJ, Nichols RL (eds) (2007) Sticky cotton: causes, effects, and prevention. USDA-ARS Technical Bulletin No 1915

Hilje L, Stansly PA (2008) Living ground covers for management of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) and tomato yellow mottle virus (ToYMoV) in Costa Rica. Crop Prot 27:10–16

Hogenhout SA, Ammar ED, Whitfield AE, Redinbaugh MG (2008) Insect vector interactions with persistently transmitted viruses. Annu Rev Phytopathol 46:327–359

Horowitz AR, Ishaaya I (1996) Chemical control of *Bemisia tabaci*—management and application. In: Gerling D, Mayer RT (eds) Bemisia: 1995 taxonomy, biology, damage, control and management. Intercept Ltd Andover, Hants, pp 537–556

Horowitz AR, Ishaaya I (2014) Dynamics of biotypes B and Q of the whitefly *Bemisia tabaci* and its impact on insecticide resistance. Pest Manag Sci 70:1568–1572

Horowitz AR, Forer G, Ishaaya I (1994) Managing resistance in *Bemisia tabaci* in Israel with emphasis on cotton. Pestic Sci 42:113–122

Horowitz AR, Mendelson Z, Weintraub PG, Ishaaya I (1998) Comparative toxicity of foliar and systemic applications of two chloronicotinyl insecticides, acetamiprid and imidacloprid, against the cotton whitefly, *Bemisia tabaci*. Bull Entomol Res 88:437–442

Horowitz AR, Kontsedalov S, Denholm I, Ishaaya I (2002) Dynamics of insecticide resistance in *Bemisia tabaci*—a case study with an insect growth regulator. Pest Manag Sci 58:1096–1100

Horowitz AR, Denholm I, Gorman K, Cenis JL, Kontsedalov S, Ishaaya I (2003) Biotype Q of *Bemisia tabaci* identified in Israel. Phytoparasitica 31:94–98

Horowitz AR, Kontsedalov S, Ishaaya I (2004) Dynamics of resistance to the neonicotinoids acetamiprid and thiamethoxam in *Bemisia tabaci* (Homoptera: Aleyrodidae). J Econ Entomol 97:2051–2056

Horowitz AR, Kontsedalov S, Khasdan V, Ishaaya I (2005) Biotypes B and Q of *Bemisia tabaci* and their relevance to neonicotinoid and pyriproxyfen resistance. Arch Insect Biochem Physiol 58:216–225

Horowitz R, Denholm I, Morin S (2007) Resistance to insecticides in the TYLCV vector, *Bemisia tabaci*. In: Czosnek H (ed) Tomato yellow leaf curl virus disease. Springer, Dordrecht, pp 305–325

Horowitz AR, Antignus Y, Gerling D (2011) Management of *Bemisia tabaci* Whiteflies. In: Thompson WMO (ed) The whitefly, *Bemisia tabaci* (Homoptera: Aleyrodidae) interaction with geminivirus-infected host plants. Springer, Dordrecht, pp 293–322

Hu J, Zhang X, Jiang Z, Zhang F, Liu Y, Li Z, Zhang Z (2017) New putative cryptic species detection and genetic network analysis of *Bemisia tabaci* (Hempitera: Aleyrodidae) in China based on mitochondrial COI sequences. Mitochondrial DNA Part A 29:474–484

Ilias A, Lagnel J, Kapantaidaki DE, Roditakis E, Tsigenopoulos CS, Vontas J, Tsagkarakou A (2015) Transcription analysis of neonicotinoid resistance in Mediterranean (MED) populations of *B. tabaci* reveal novel cytochrome P450s, but no nAChR mutations associated with the phenotype. BMC Genom 16:939

Ishaaya I, Horowitz AR (1995) Pyriproxyfen, a novel insect growth regulator for controlling whiteflies: mechanism and resistance management. Pestic Sci 43:227–232

Jaber LR, Araj SE, Qasem JR (2018) Compatibility of endophytic fungal entomopathogens with plant extracts for the management of sweetpotato whitefly *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae). Biol Control 117:164–171

Jeschke P, Nauen R, Schindler M, Elbert A (2011) Overview of the status and global strategy for neonicotinoids. J Agric Food Chem 59:2897–2908

Jeschke P, Nauen R, Gutbrod O, Beck ME, Mathiesen S, Haas M, Velten R (2015) Flupyradifurone (Sivanto™) and its novel butenolide pharmacophore: structural considerations. Pestic Biochem Physiol 121:21–38

Jones DR (2003) Plant viruses transmitted by whiteflies. Eur J Plant Pathol 109:195–219

Karunker I, Benting J, Lueke B, Ponge T, Nauen R, Roditakis E, Vontas J, Gorman K, Denholm I, Morin S (2008) Over-expression of cytochrome P450 CYP6CM1 is associated with high resistance to imidacloprid in the B and Q biotypes of *Bemisia tabaci* (Hemiptera: Aleyrodidae). Insect Biochem Mol Biol 38:634–644

Karunker I, Morou E, Nikou D, Nauen R, Sertchook R, Stevenson BJ, Paine MJ, Morin S, Vontas J (2009) Structural model and functional characterization of the *Bemisia tabaci* CYP6CM1vQ, a cytochrome P450 associated with high levels of imidacloprid resistance. Insect Biochem Mol Biol 39(10):697–706

Kim SI, Chae SH, Youn HS, Yeon SH, Ahn YJ (2011) Contact and fumigant toxicity of plant essential oils and efficacy of spray formulations containing the oils against B- and Q-biotypes of *Bemisia tabaci*. Pest Manag Sci 67:1093–1099

Kontsedalov S, Zchori-Fein E, Chiel E, Gottlieb Y, Inbar M, Ghanim M (2008) The presence of Rickettsia is associated with increased susceptibility of *Bemisia tabaci* (Homoptera: Aleyrodidae) to insecticides. Pest Manag Sci 64:789–792

Kontsedalov S, Gottlieb Y, Ishaaya I, Nauen R, Horowitz R, Ghanim M (2009) Toxicity of spiromesifen to the developmental stages of *Bemisia tabaci* biotype B. Pest Manag Sci 65:5–13

Kontsedalov S, Abu-Moch F, Lebedev G, Czosnek H, Horowitz AR, Ghanim M (2012) *Bemisia tabaci* biotype dynamics and resistance to insecticides in Israel during the years 2008–2010. J Integr Agric 11:312–320

Lacey LA, Kirk AA, Millar L, Mercadier G, Vidal C (1999) Ovicidal and larvicidal activity of conidia and blastospores of *Paecilomyces fumosoroseus* (Deuteromycotina: Hyphomycetes) against *Bemisia argentifolii* (Homoptera: Aleyrodidae) with a description of a bioassay system allowing prolonged survival of control insects. Biocontrol Sci Technol 9:9–18

Lahm GP, Cordova D, Barry JD (2009) New and selective ryanodine receptor activators for insect control. Bioorg Med Chem 17:4127–4133

Lee SH, Yoon KS, Williamson MS, Goodson SJ, Takano-Lee M, Edman JD et al (2000) Molecular analysis of kdr-like resistance in permethrin-resistant strains of head lice, *Pediculus capitis*. Pestic Biochem Physiol 66:130–143

Legg JP, Shirima R, Tajebe LS, Guastella D, Boniface S, Jeremiah S, Nsami E, Chikoti P, Rapisarda C (2014) Biology and management of *Bemisia* whitefly vectors of cassava virus pandemics in Africa. Pest Manag Sci 70:1446–1453

Li X, Degain BA, Harpold VS, Marçon PG, Nichols RL, Fournier AJ, Naranjo SE, Palumbo JC, Ellsworth PC (2012) Baseline susceptibilities of B- and Q-biotype *Bemisia tabaci* to anthranilic diamides in Arizona. Pest Manag Sci 68:83–91

Li HR, Pan HP, Tao YL, Zhang YJ, Chu D (2017) Population genetics of an alien whitefly in China: implications for its dispersal and invasion success. Sci Rep 7:2228. https://doi.org/10.1038/s41598-017-02433-5

Liu SS, Colvin J, De Barro PJ (2012) Species concepts as applied to the whitefly *Bemisia tabaci* systematics: how many species are there? J Integr Agric 11:176–186

Lu Y, Bei Y, Zhang J (2012) Are yellow sticky traps an effective method for control of sweetpotato whitefly, *Bemisia tabaci*, in the greenhouse or field? J Insect Sci 12:113

Luo C, Jones CM, Zhang F, Denholm I, Gorman K (2010) Insecticide resistance in *Bemisia tabaci* biotype Q (Hemiptera: Aleyrodidae) from China. Crop Prot 29:429–434

Luo Y, Chen Q, Luan J, Chung SH, Van Eck J, Turgeon R, Douglas AE (2017) Towards an understanding of the molecular basis of effective RNAi against a global insect pest, the whitefly *Bemisia tabaci*. Insect Biochem Mol Biol 88:21–29

Ma D, Gorman KJ, Devine GJ, Luo W, Denholm I (2007) The biotype and insecticide-resistance status of whiteflies, *Bemisia tabaci* (Hemiptera: Aleyrodidae), invading cropping systems in Xinjiang Uygur Autonomous Region, northwestern China. Crop Prot 26:612–617

Ma W, Li X, Dennehy TJ, Lei C, Wang M, Degain BA, Nichols RL (2010) Pyriproxyfen resistance of *Bemisia tabaci* (Homoptera: Aleyrodidae) biotype B: metabolic mechanism. J Econ Entomol 103:158–165

Malik HJ, Raza A, Amin I, Scheffler JA, Scheffler BE, Brown JK, Mansoor S (2016) RNAi-mediated mortality of the whitefly through transgenic expression of double-stranded RNA homologous to acetylcholinesterase and ecdysone receptor in tobacco plants. Sci Rep 6:38469. https://doi.org/10.1038/srep38469

McKenzie CL, Bethke JA, Byrne FJ, Chamberlin JR, Dennehy TJ, Dickey AM, Gilrein D, Hall PM, Ludwig S, Oetting RD, Osborne LS, Schmale L, Shatters RG Jr (2012) Distribution of *Bemisia tabaci* (Hemiptera: Aleyrodidae) biotypes in North America after the Q invasion. J Econ Entomol 105:753–766

Meng X, Zhu C, Feng Y, Li W, Shao X, Xu Z, Chemg J, Li Z (2016) Computational insights into the different resistance mechanism of imidacloprid versus dinotefuran in *Bemisia tabaci*. J Agric Food Chem 64:1231–1238

Monci F, García-Andrés S, Sánchez F, Moriones E, Espí E, Salmerón A (2004) Tomato yellow leaf curl disease control with UV-blocking plastic covers in commercial plastichouses of Southern Spain. In: Acta Hortic. International Society for Horticultural Science, pp 537–542

Monci F, García-Andrés S, Sánchez-Campos S, Fernández-Muñoz R, Díaz-Pendón JA, Moriones E (2019) Use of systemic acquired resistance and whitefly optical barriers to reduce tomato yellow leaf curl disease damage to tomato crops. Plant Dis 103:1181–1188

Morin S, Williamson MS, Goodson SJ, Brown JK, Tabashnik BE, Dennehy TJ (2002) Mutations in the *Bemisia tabaci* para sodium channel gene associated with resistance to a pyrethroid plus organophosphate mixture. Insect Biochem Mol Biol 32:1781–1791

Mota-Sanchez D, Wise JC (2019) The arthropod pesticide resistance database. Michigan State University. http://www.pesticideresistance

Naranjo SE, Akey DH (2005) Conservation of natural enemies in cotton: comparative selectivity of acetamiprid in the management of *Bemisia tabaci*. Pest Manag Sci 61:555–566

Naranjo SE, Ellsworth PC (2009a) Fifty years of the integrated control concept: moving the model and implementation forward in Arizona. Pest Manag Sci 65:1267–1286

Naranjo SE, Ellsworth PC (2009b) The contribution of conservation biological control to integrated management of *Bemisia tabaci* in cotton. Biol Con 51:458–470

Naranjo SE, Ellsworth PC, Chu CC, Henneberry TJ (2002) Conservation of predatory arthropods in cotton: role of action thresholds for *Bemisia tabaci* (Homoptera: Aleyrodidae). J Econ Entomol 95:682–691

Naranjo SE, Ellsworth PC, Hagler JR (2004) Conservation of natural enemies in cotton: role of insect growth regulators in management of *Bemisia tabaci*. Biol Control 30:52–72

Nauen R, Denholm I (2005) Resistance of insect pests to neonicotinoid insecticides: current status and future prospects. Arch Insect Biochem Physiol 58:200–215

Nauen R, Konanz S (2005) Spiromesifen as a new chemical option for resistance management in whiteflies and spider mites. Pflanzenschutz-Nachr Bayer 58:485–502

Nauen R, Steinbach D (2016) Resistance to diamide insecticides in lepidopteran pests. In: Horowitz AR, Ishaaya I (eds) Advances in insect control and resistance management. Springer, Berlin, pp 219–240

Nauen R, Stumpf N, Elbert A (2002) Toxicological and mechanistic studies on neonicotinoid cross resistance in Q-type *Bemisia tabaci* (Hemiptera: Aleyrodidae). Pest Manag Sci 58:868–875

Nauen R, Schnorbach HJ, Elbert A (2005) The biological profile of spiromesifen (Oberon®)—a new tetronic acid insecticide/acaricide. Pflanzenschutz -Nachr Bayer 58:417–440

Nauen R, Vontas J, Kaussmann M, Wölfel K (2013) Pymetrozine is hydroxylated by CYP6CM1, a cytochrome P450 conferring neonicotinoid resistance in *Bemisia tabaci*. Pest Manag Sci 69:457–461

Nauen R, Jeschke P, Velten R, Beck ME, Ebbinghaus-Kintscher U, Thielert W, Wölfel K, Haas M, Kunz K, Raupach G (2015a) Flupyradifurone: a brief profile of a new butenolide insecticide. Pest Manag Sci 71:850–862

Nauen R, Wölfel K, Lueke B, Myridakis A, Tsakireli D, Roditakis E, Tsagkarakou A, Stephanou E, Vontas J (2015b) Development of a lateral flow test to detect metabolic resistance in *Bemisia tabaci* mediated by CYP6CM1, a cytochrome P450 with broad spectrum catalytic efficiency. Pestic Biochem Physiol 121:3–11

Naveen NC, Chaubey R, Kumar D, Rebijith KB, Rajagopal R, Subrahmanyam B, Subramanian S (2017) Insecticide resistance status in the whitefly, *Bemisia tabaci* genetic groups Asia-I, Asia-II-1 and Asia-II-7 on the Indian subcontinent. Sci Rep 7:40634. https://doi.org/10.1038/srep40634

Nomikou M, Janssen A, Schraag R, Sabelis MW (2001) Phytoseiid predators as potential biological control agents for *Bemisia tabaci*. Exp Appl Acarol 25:271–291

Oliveira MRV, Henneberry TJ, Anderson P (2001) History, current status, and collaborative research projects for *Bemisia tabaci*. Crop Prot 20:709–723

Palumbo JC, Horowitz AR, Prabhaker N (2001) Insecticidal control and resistance management for *Bemisia tabaci*. Crop Prot 20:739–765

Parrella G, Scassillo L, Giorgini M (2012) Evidence for a new genetic variant in the *Bemisia tabaci* species complex and the prevalence of the biotype Q in southern Italy. J Pest Sci 85:227–238

Perring TM (2001) The *Bemisia tabaci* species complex. Crop Prot 20:725–737

Perring TM, Cooper DA, Rodriguez RJ, Farrar CA, Bellows TS (1993) Identification of a whitefly species by genomic and behavioral studies. Science 259:74–77

Prabhaker N, Castle SJ, Buckelew L, Toscano NC (2008) Baseline susceptibility of *Bemisia tabaci* B biotype (Hemiptera: Aleyrodidae) populations from California and Arizona to spiromesifen. J Econ Entomol 101:174–181

Prieto-Ruiz I, Garzo E, Moreno A, Dáder B, Medina P, Viñuela E, Fereres A (2019) Supplementary UV radiation on eggplants indirectly deters *Bemisia tabaci* settlement without altering the predatory orientation of their biological control agents *Nesidiocoris tenuis* and Sphaerophoria rueppellii. J Pest Sci 92:1057–1070

Qiu YT, van Lenteren JC, Drost YC, Posthuma-Doodeman CJAM (2004) Life-history parameters of *Encarsia formosa*, *Eretmocerus eremicus* and *E. mundus*, aphelinid parasitoids of *Bemisia argentifolii* (Hemiptera: Aleyrodidae). Eur J Entomol 101:83–94

Rajasri M, Prasada Rao RDVJ, Vijaya Lakshmi K, Loka Reddy K (2011) Effect of different mulches on the incidence of Tomato leaf curl virus and its vector whitefly *Bemisia tabaci* in tomato. In: Acta Hort. International Society for Horticultural Science, pp 215–221

Rauch N, Nauen R (2003) Identification of biochemical markers linked to neonicotinoid cross-resistance in *Bemisia tabaci* (Hemiptera: Aleyrodidae). Arch Insect Biochem Physiol 54:165–176

Raza A, Malik HJ, Shafiq M, Amin I, Scheffler JA, Scheffler BE, Mansoor S (2016) RNA interference based approach to down regulate osmoregulators of whitefly (*Bemisia tabaci*): potential technology for the control of whitefly. PLoS ONE 11(4):e0153883. https://doi.org/10.1371/journal.pone.0153883

Roditakis E, Roditakis NE, Tsagkarakou A (2005) Insecticide resistance in *Bemisia tabaci* (Homoptera: Aleyrodidae) populations from Crete. Pest Manag Sci 61:577–582

Roditakis E, Tsagkarakou A, Vontas J (2006) Identification of mutations in the para sodium channel of *Bemisia tabaci* from Crete, associated with resistance to pyrethroids. Pestic Biochem Physiol 85:161–166

Roditakis E, Grispou M, Morou E, Kristoffersen JB, Roditakis N, Nauen R, Vontas J, Tsagkarakou A (2009) Current status of insecticide resistance in Q biotype *Bemisia tabaci* populations from Crete. Pest Manag Sci 65:313–322

Roditakis E, Morou E, Tsagkarakou A, Riga M, Nauen R, Paine M, Morin S, Vontas J (2011) Assessment of the *Bemisia tabaci* CYP6CM1vQ transcript and protein levels in laboratory and field-derived imidacloprid-resistant insects and cross-metabolism potential of the recombinant enzyme. Insect Sci 18:23–29

Rodríguez E, González M, Paredes D, Campos M, Benítez E (2018) Selecting native perennial plants for ecological intensification in Mediterranean greenhouse horticulture. Bull Entomol Res 108:694–704

Roy D, Bhattacharjee T, Biswas A et al (2019) Resistance monitoring for conventional and new chemistry insecticides on *Bemisia tabaci* genetic group Asia-I in major vegetable crops from India. Phytoparasitica 47:55–66

Şahin I, İkten C (2017) Neonicotinoid resistance in *Bemisia tabaci* (Genn., 1889) (Hemiptera: Aleyrodidae) populations from Antalya, Turkey. Türk Entomol Derg 41:169–175

Sanchez-Campos S, Navas-Castillo J, Camero R, Soria C, Diaz JA, Moriones E (1999) Displacement of *tomato yellow leaf curl virus* (TYLCV-Sr) by TYLCV-Is in tomato epidemics in Spain. Phytopathol 89:1038–1043

Santos TTMD, Quintela ED, Mascarin GM, Santana MV (2018) Enhanced mortality of *Bemisia tabaci* nymphs by *Isaria javanica* combined with sublethal doses of chemical insecticides. J Appl Entomol 142:598–609

Satar G, Ulusoy MR, Nauen R, Dong K (2018) Neonicotinoid insecticide resistance among populations of *Bemisia tabaci* in the Mediterranean region of Turkey. Bull Insectol 71:171–177

Sattelle DB, Cordova D, Cheek TR (2008) Insect ryanodine receptors: molecular targets for novel pest control chemicals. Invertebr Neurosci 8:107–119

Schuler TH, Martinez-Torres D, Thompson AJ, Denholm I, Devonshire AL, Duce IR et al (1998) Toxicological, electrophysiological, and molecular characterisation of knockdown resistance to pyrethroid insecticides in the diamondback moth, *Plutella xylostella* (L.). Pestic Biochem Physiol 59:169–182

Schuster DJ, Mann RS, Toapanta M, Cordero R, Thompson S, Cyman S, Shurtleff A, Morris Ii RF (2010) Monitoring neonicotinoid resistance in biotype B of *Bemisia tabaci* in Florida. Pest Manag Sci 66:186–195

Silva LD, Omoto C, Bleicher E, Dourado PM (2009) Monitoring the susceptibility to insecticides in *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) populations from Brazil. Neotrop Entomol 38:116–125

Simmons AM, Kousik CS, Levi A (2010) Combining reflective mulch and host plant resistance for sweetpotato whitefly (Hemiptera: Aleyrodidae) management in watermelon. Crop Prot 29:898–902

South A, Hastings IM (2018) Insecticide resistance evolution with mixtures and sequences: a model-based explanation. Malar J 17:80

Sparks TC, Nauen R (2015) IRAC: mode of action classification and insecticide resistance management. Pestic Biochem Physiol 121:122–128

Stansly PA, Naranjo SE (2010) Bemisia: bionomics and management of a global pest. Springer, Dordrecht

Takahashi H, Mitsui J, Takausa N, Matsud M, Yoneda H, Suszuki J, Ishimitsi K, Kishimoto T (1992) NI-25, a new type of systemic and broad spectrum insecticide. In: Proceedings of 1992 Brighton crop protection conference—pests and diseases, vol 1, pp 88–96

Teng X, Wan FH, Chu D (2010) *Bemisia tabaci* biotype Q dominates other biotypes across China. Fla Entomol 93:363–368

Togni PHB, Venzon M, Souza LM, Santos JPCR, Sujii ER (2019) Biodiversity provides whitefly biological control based on farm management. J Pest Sci 92:393–403

Tomizawa M, Casida JE (2005) Neonicotinoid insecticide toxicity: mechanisms of selective action. Annu Rev Pharmacol Toxicol 45:247–268

Torres-Villa LM, Rodŕiguez-Molina MC, Lacasa-Plasencia A, Bielza-Lino P, Rodŕiguez-del-Rincón A (2002) Pyrethroid resistance of *Helicoverpa armigera* in Spain: current status and agroecological perspective. Agric Ecosyst Environ 93:55–66

Tsagkarakou A, Nikou D, Roditakis E, Sharvit M, Morin S, Vontas J (2009) Molecular diagnostics for detecting pyrethroid and organophosphate resistance mutations in the Q biotype of the whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae). Pestic Biochem Physiol 94:49–54

Upadhyay SK, Chandrashekar K, Thakur N, Verma PC, Borgio JF, Singh PK, Tuli R (2011) RNA interference for the control of whiteflies (*Bemisia tabaci*) by oral route. J Biosci 36:153–161

Van Der Blom J, Robledo A, Torres S, Sánchez JA, Contreras M (2008) Control biológico de plagas en Almería: revolución verde después de dos décadas. Phytoma España 198:42–47

Van Lenteren JC, Drost YC, Van Roermund HJW, Posthuma-Doodeman CJAM (1997) Aphelinid parasitoids as sustainable biological control agents in greenhouses. J Appl Entomol 121:473–485

Vandervoet TF, Ellsworth PC, Carrière Y, Naranjo SE (2018) Quantifying conservation biological control for management of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in cotton. J Econ Entomol 111:1056–1068

Vassiliou V, Emmanouilidou M, Perrakis A, Morou E, Vontas J, Tsagkarakou A, Roditakis E (2011) Insecticide resistance in *Bemisia tabaci* from Cyprus. Insect Sci 18:30–39

Vite-Vallejo O, Barajas-Fernández MG, Saavedra-Aguilar M, Cardoso-Taketa A (2018) Insecticidal effects of ethanolic extracts of *Chenopodium ambrosioides*, *Piper nigrum*, *Thymus vulgaris*, and *Origanum vulgare* against *Bemisia tabaci*. Southwest Entomol 43:383–393

Vyas M, Raza A, Ali MY, Ashraf MA, Mansoor S, Shahid AA, Brown JK (2017) Knock down of whitefly gut gene expression and mortality by orally delivered gut gene-specific dsRNAs. PLoS ONE 12(1):e0168921. https://doi.org/10.1371/journal.pone.0168921

Wagan TA, Cai W, Hua H (2018) Repellency, toxicity, and anti-oviposition of essential oil of Gardenia jasminoides and its four major chemical components against whiteflies and mites. Sci Rep 8:9375. https://doi.org/10.1038/s41598-018-27366-5

Wang Z, Yao M, Wu Y (2009) Cross-resistance, inheritance and biochemical mechanisms of imidacloprid resistance in B-biotype *Bemisia tabaci*. Pest Manag Sci 65(11):1189–1194

Wang Z, Yan H, Yang Y, Wu Y (2010) Biotype and insecticide resistance status of the whitefly *Bemisia tabaci* from China. Pest Manag Sci 66:1360–1366

Wang S, Zhang Y, Yang X, Xie W, Wu Q (2017) Resistance monitoring for eight insecticides on the sweetpotato whitefly (Hemiptera: Aleyrodidae) in China. J Econ Entomol 110:660–666

Wang R, Wang J, Che W, Luo C (2018) First report of field resistance to cyantraniliprole, a new anthranilic diamide insecticide, on *Bemisia tabaci* MED in China. J Integr Agric 16:60345–60347

Watanabe LFM, Bello VH, De Marchi BR et al (2019) Performance and competitive displacement of *Bemisia tabaci* MEAM1 and MED cryptic species on different host plants. Crop Prot 124:104860

Wraight SP, Carruthers RI, Jaronski ST, Bradley O, Garza CJ, Galaini W (2000) Evaluation of entomopathogenic fungi *Beauveria bassiana* and *Paecilomyces fumosoroseus* for microbial control of the silverleaf whitefly, *Bemisia argentifolii*. Biol Control 17:203–217

Xu J, De Barro PJ, Liu SS (2010) Reproductive incompatibility among genetic groups of *Bemisia tabaci* supports the proposition that the whitefly is a cryptic species complex. Bull Entomol Res 100:359–366

Yao FL, Zheng Y, Huang XY, Ding XL et al (2017) Dynamics of *Bemisia tabaci* biotypes and insecticide resistance in Fujian province in China during 2005–2014. Sci Rep 7:40803. https://doi.org/10.1038/srep40803

Yuan L, Wang SL, Zhou JC, Du YZ, Zhang YJ, Wang JJ (2012) Status of insecticide resistance and associated mutations in Q-biotype of whitefly, *Bemisia tabaci*, from eastern China. Crop Prot 31:67–71