Chapter 8
The Whitefly *Bemisia tabaci* (Gennadius)

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Abstract The whitefly *Bemisia tabaci* (Gennadius) is a species complex containing at least 35 morphologically indistinguishable cryptic species. Some members of the complex are pests of agricultural and horticultural crops in temperate and tropical regions. During the past 20 years, two species of the complex, Middle East-Asia Minor 1 (hereafter MEAM1) and Mediterranean (hereafter MED), which have been commonly referred to as the B and Q 'biotypes', have risen to international prominence due to their global invasions. In the middle-1990s, the MEAM1 species invaded China most probably with the import of infested plants and seedlings and has become a pest since the late 1990s. In 2003, the MED species of the *B. tabaci* complex was first recorded in China and it is now the dominant species in the Yangtze River Valley and eastern coastal areas. In this chapter, we first reviewed the invasion histories of MEAM1 and MED whiteflies in China and their negative effects. Then, the research progresses on behavior, biotic, environmental and molecular mechanisms of MEAM1 and MED whitefly invasions and replacement of native whitefly species were discussed. Finally, the strategies for whitefly management in China were summarized. These research efforts have provided solid foundation for future investigations on the molecular mechanisms of whitefly invasions and are expected to open important avenues for the discovery of novel strategies for whitefly management in China.

Keywords *Bemisia tabaci* • China • Invasion • Management • Whitefly

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8.1 Introduction

The whitefly *Bemisia tabaci* (Gennadius) is a phloem-feeding insect that lives predominantly in temperate and tropical regions (Byrne and Bellows 1991; Naranjo et al. 2010). It is highly polyphagous and attack more than 600 plant species including food, vegetable, fiber and ornamental host plants under field and greenhouse conditions (Brown 1995). *Bemisia tabaci* is now recognized as a species complex containing at least 35 cryptic species (Boykin and De Barro 2014; De Barro et al. 2011; Liu et al. 2012; Xu et al. 2010a). Some members of the complex are considerable pests of ornamental, vegetable and cotton production, causing damages directly through feeding and indirectly through the transmission of plant viruses (Fig. 8.1) (Naranjo et al. 2010). During the past 20 years, two species of the complex, Middle East-Asia Minor 1 (hereafter MEAM1) and Mediterranean (hereafter MED), which have been commonly referred to as B and Q whiteflies, have risen to international prominence due to their global invasions (Dalton 2006; De Barro et al. 2011; Liu et al. 2007). The invasive MEAM1 has been considered as one of the world's top 100 invasive species according to the International Union for the Conservation of Nature and Natural Resources (IUCN) (http://www.issg.org) and are regulated species in a number of countries, e.g., Australia, Africa, China, EU, and United States. Similarly, the MED species has also begun to invade a large number of countries in Africa, Asia, Europe and America from the Mediterranean region.

Fig. 8.1 Whiteflies cause damage directly through feeding and indirectly through the transmission of begomoviruses

Interestingly, despite MEAM1 and MED species of the *B. tabaci* complex are highly invasive, other members of the complex apparently lack the capacity to invade and establish in neighboring regions. It suggests that the invasive ability for MEAM1 and MED is actually uncommon. Therefore, unraveling the process and mechanism of whitefly invasions may be crucial to advance studies on their biology and introduce new methods to control them. In this review, we will outline the invasion processes and mechanisms of MEAM1 and MED whiteflies in China and then summarize the recent developments in the management of *B. tabaci*. These research efforts have provided valuable information for future investigations on the molecular mechanisms of whitefly invasions and are expected to open important avenues for the discovery of novel strategies for whitefly management.

8.2 The Invasion of *B. tabaci* in China

Although the invasions of *B. tabaci* have caused devastating consequences worldwide, the invasion history and processes of MEAM1 and MED have been poorly documented in most instances. The whitefly *B. tabaci* was first recorded in China in 1949. However, for several decades, this insect was not considered as a severe agricultural pest. In the middle-1990s, the MEAM1 species invaded China most probably with the import of infested plants and seedlings (Luo et al. 2002; Zhang 2000). Subsequently *B. tabaci* has gradually become a severe agricultural pest and significantly threatened the vegetable production in China since the late 1990s. The exotic MEAM1 whitefly species was found to be the dominant species in many agricultural production regions in 1990s (Luo et al. 2002). For example, among the 23 *B. tabaci* populations collected from 1999 to 2001 from 14 provinces, 17 populations were MEAM1. Interestingly, MEAM1 whiteflies mainly occur in regions near the coast or with convenient transportation while only six populations are other species distributed in the inland or mountainous regions (Qiu et al. 2003a). It was also found that during the invasion of *B. tabaci* MEAM1, a number of native whitefly species have been completely replaced in many regions, such as in Zhejiang Province, China during 2004–2006 (Liu et al. 2007).

In 2003, one population collected from poinsettia in Yunnan Province was identified as *B. tabaci* MED based on the mitochondrial cytochrome oxidase subunit I (mtCOI) gene (Chu et al. 2005). Later on, Chu et al. (2012) examined the whitefly populations collected from ten provinces and found that MED was only occasionally detected in Yunnan, Beijing and Henan and MEAM1 was still the dominant species in China. However, in the subsequent years, *B. tabaci* MED was detected in many regions in China and has replaced the previously well-established MEAM1. For instance, in 2001, among the 22 whitefly populations collected from 15 provinces, MED were found in 19 populations (Teng et al. 2010) . Of the 14 samples collected from 2008 to 2009, nine populations belonged to MED, three were MEAM1, and two were a mixture of MED and MEAM1 (Wang et al. 2010b). Hu et al. (2011) found that during June 2009 to March 2010 among the 16 provinces in south and east China, 12 provinces had MED. Pan et al. (2012) found that, for the 55 populations collected from 18 provinces, 43 populations were composed of MED. These data demonstrate that though the exotic MEAM1 was predominant across China in the past, the MED is now the dominant species in the Yangtze River and eastern coastal areas, and MEAM1 is the predominant species only in the south and south eastern coastal areas.

8.3 Invasion Mechanisms

The population dynamics of *B. tabaci* is governed entirely by four processes – birth, death, immigration and emigration. Each of them is governed by a wide array of interacting biotic and abiotic factors that determine whitefly occurrence and abundance over time and space (Naranjo et al. 2010). During the last decade, a number of factors that contribute to the invasion and spread of MEAM1 and MED in China have been investigated, such as mating interactions (Liu et al. 2007), host plant adaptation (Xu et al. 2015a), insecticide resistance (Pan et al. 2015), virus-vector-host mutualism (Luan et al. 2013a) and the roles of endosymbionts (Bing et al. 2013; Himler et al. 2011). These studies suggest that the successful invasions of MEAM1 and MED in China is largely due to their intrinsic biological traits, such as high insecticide resistance, wide host range and strong reproduction capacity. These findings will help us to develop novel strategies to manage the invasion and spread of MEAM1 and MED in China.

8.3.1 Asymmetric Mating Interactions

Reproductive interference is one of the major factors mediating species exclusion among insects. Liu et al. (2007) found that asymmetric mating interactions between different cryptic species of *B. tabaci* species complex was a driving force contributing to widespread invasions of the MEAM1 species in China and Australia. The authors conducted long-term field surveys, caged population experiments, and detailed behavioral observations in Zhejiang, China, and Queensland, Australia, to investigate the invasion process and its underlying behavioral mechanisms. During invasion and displacement, they found that the increased frequency of copulation led to increased production of female progeny among invaders, as well as reduced copulation and female production in indigenous genetic groups. Such asymmetric mating interactions may be critical to determining the capacity of a haplodiploid invader and the consequences for its closely related indigenous organisms.

The cryptic species MEAM1 and MED of *B. tabaci* complex have invaded many parts of the world and often exhibit niche overlap and reproductive interference. However, contrasting patterns of competitive displacement between the two invaders have been observed. Sun et al. (2014) investigated the role of reproductive interference on species exclusion between MEAM1 and MED in China. In mixed cohorts of the two species, MEAM1 always excluded MED in a few generations when the initial proportion of MEAM1 was $\geqslant 0.25$. Importantly, as MEAM1 increased in relative abundance, MED populations became increasingly male-biased. All these results suggest that MEAM1 should have a stronger reproductive interference than MED, leading to reduced frequency of copulation and female progeny in MED. These findings not only reveal the importance of reproductive interference in the competitive interactions between the two invasive whiteflies, but also provide a valuable framework against which the effects of other factors mediating species exclusion can be explored (Sun et al. 2014).

8.3.2 Host Plant Adaptation

The capacity of the MEAM1 and MED species of *B. tabaci* species complex to invade has often been linked to their presumed wider host range than the indigenous competitors. To determine whether the invasive MEAM1 species and the indigenous Asia II 1 whitefly species, commonly referred to as the 'ZHJ2 biotype', differ in their ability to use different host plants, Xu et al. (2011) compared their development, survival and reproduction on eight crop species/cultivars that are commonly cultivated in Zhejiang, China. Of the eight host plants tested, MEAM1 performed substantially better than ZHJ2 on squash, tomato and tobacco; MEAM1 and ZHJ2 preformed equally well on cotton and sweet potato, while ZHJ2 performed better than MEAM1 on kidney bean and pepper. These results indicate that while MEAM1 generally has a wider host range than many indigenous *B. tabaci*, an indigenous *B. tabaci* can perform as well as or better on some host plants. This suggests that the differential capacity to use various host plants between whitefly species is important in mediating the process of invasions by an alien whitefly species. Sun et al. (2013a) also examined the effects of host plants on the competitive interactions between the two species in the laboratory. When cohorts with equal abundance of MEAM1 and MED were set up on different host plants, MEAM1 displaced MED on cabbage and tomato in five and seven generations, respectively, but MED displaced MEAM1 on pepper in two generations.

Despite its importance, few studies have addressed the molecular mechanisms of *B. tabaci* against major plant secondary defense compounds. Alon et al. (2012) compared the gene expression between *B. tabaci* adults on wild-type *Nicotiana tabacum* plants or transgenic plants constitutively activating the phenylpropanoid/flavonoids biosynthetic pathway. Both the SSH and cDNA microarray analyses indicated a complex interaction between *B. tabaci* and secondary defense metabolites produced by the phenylpropanoids/flavonoids pathway, such as expression of detoxification, immunity, oxidative stress and general stress related genes. However, the elevated transcriptional activity was not accompanied by reduction of whitefly reproductive performance, indicating high adaptability of *B. tabaci* to this large group of plant secondary defense metabolites (Alon et al. 2012). The same research group also investigated the effects of aliphatic and indolic glucosinolates on the expression of detoxification genes in MEAM1 and MED whiteflies (Elbaz et al. 2012). The result suggests that the two species use rather different strategies to cope with plant defense responses. While MEAM1 utilizes inducible defenses, MED invests significant resources in being always ‘ready’ for a challenge (Elbaz et al. 2012). Xu et al. (2015a) compared the performance of the invasive MEAM1 and the indigenous Asia II 3 whitefly species following host plant transfer from a suitable host (cotton) to an unsuitable host (tobacco) and analyzed their transcriptional responses. Transcriptional analysis showed that the patterns of gene regulation were very different with most of the genes up-regulated in MEAM1 but down-regulated in Asia II 3. Compared to the constitutive high expression of detoxification genes in MEAM1, most of the detoxification genes were down-regulated in Asia II 3. Enzymatic activities of P450, GST and esterase further verified that the detoxification of MEAM1 was much higher than that of Asia II 3. These results reveal obvious differences in response to host transfer in MEAM1 and Asia II 3.

8.3.3 Roles of Vector–Virus–Plant Interactions in Biological Invasions

Begomoviruses are a group of single stranded DNA viruses exclusively transmitted by the whitefly *B. tabaci* in a persistent, circulative manner (Czosnek and Ghanim 2002). During this process, virions are acquired by the stylet of whitefly vectors from the plant phloem, moving along the esophagus to the midgut, then crossing the gut epithelial cells to the hemocoel, circulating with the hemolymph and reaching the salivary glands, and finally were secreted with saliva (Gray et al. 2014). During the circulation, viruses have engaged host factors or unique strategies for replication, movement, transmission and pathogenesis (Wei et al. 2014). Meanwhile, the insect vectors have evolved immunologic surveillance system against viral invasions (Luan et al. 2011; Wang et al. 2016). Interactions among vector insects, plant viruses and host plants are complex and diverse. These interactions may affect the process of biological invasions and the displacement of indigenous species by invaders when the invasive and indigenous organisms occur with niche overlap. Jiu et al. (2007) compared the performance of the invasive MEAM1 and indigenous Asia II 3 whiteflies on healthy, TbCSV-infected and TYLCCNV-infected tobacco plants. Compared to its performance on healthy plants, the invasive MEAM1 increased its fecundity and longevity significantly when feeding on virus-infected plants. In contrast, the indigenous Asia II 3 species performed similarly on healthy and virus-infected plants. The indirect mutualism between the MEAM1 whitefly and these viruses via their host plants, and the apparent lack of such mutualism for the indigenous whitefly, may contribute to the ability of the MEAM1 whitefly to invade and displace indigenous whiteflies. Interestingly, transcriptional analyses of MEAM1 whiteflies feeding on TYLCCNV-infected and uninfected tobacco plants indicated that the genes involved in the oxidative phosphorylation pathway and detoxification enzyme were down-regulated in whiteflies feeding on virus-infected plants (Luan et al. 2013a). The reduced detoxification activity is likely to attenuate energy costs, thus, enhancing the performance of whiteflies on virus-infected plants (Luan et al. 2013a).

Zhang et al. (2012) found that TYLCCNV and betasatellite coinfection suppresses jasmonic acid defences in the plant. Impairing or enhancing defences mediated by jasmonic acid in the plant enhances or depresses the performance of the whitefly. The result indicate that TYLCCNV can benefit its whitefly vector indirectly, through suppression of jasmonic acid-mediated plant defense (Zhang et al. 2012). To reveal why begomovirus infection can benefit its whitefly vector, Luan et al. (2013b) used a next-generation sequencing technology to identify defense genes differentially regulated in whitefly-infested and/or virus-infected tobacco. The authors found that many of terpenoid synthesis genes were up-regulated in whitefly-infested plants. In contrast, in TYLCCNV-infected leaves, most terpenoid genes were unchanged and five genes were declined. Interestingly, in co-infested plants, most terpenoid genes were unchanged and only three terpenoid genes were up-regulated. This study demonstrates that virus infection can deplete the terpenoid-mediated plant defense against whiteflies, thereby favoring vector–virus mutualism (Luan et al. 2013b). Furthermore, Li et al. (2014b) found that βC1 of TYLCCNV can suppress plant terpene biosynthesis. βC1 directly interacts with the basic helix-loop-helix transcription factor MYC2 to compromise the activation of MYC2-regulated terpene synthase genes, thereby reducing whitefly resistance.

Shi et al. (2013) showed that TYLCV directly and indirectly modified the feeding behavior of *B. tabaci* in favor of MED rather than MEAM1. They further quantified the salicylic acid (SA) titers and relative gene expression of SA in tomato leaves that were infested with viruliferous or non-viruliferous MEAM1 and MED. The authors found that SA titer was always higher in leaves that were infested with viruliferous MEAM1 than with viruliferous MED, whereas the SA titer did not differ between leaves infested with non-viruliferous MEAM1 and MED. Their results also indicate MED may have a mutualistic relationship with TYLCV that results in the reduction of the plant's defense response (Shi et al. 2013). Interestingly, He et al. (2015) found that when feeding on either cotton, a non-host of TYLCCNV, or uninfected tobacco, a host of TYLCCNV, virus-infection of the whiteflies impeded their feeding. Interestingly, when viruliferous whiteflies fed on virus-infected tobacco, their feeding activities were no longer negatively affected; instead, the virus promoted whitefly behaviour related to rapid and effective sap ingestion.

8.3.4 Roles of Endosymbionts in **B. tabaci** *Invasions*

The life history traits of multicellular organisms are often influenced by interactions with symbiotic species. The whitefly *B. tabaci* harbors a primary symbiont "*Candidatus* Portiera aleyrodidarum", which compensates for the deficient nutritional composition of its food sources and a variety of secondary symbionts. Interestingly, all of these secondary symbionts are found in co-localization with the primary symbiont within the same bacteriocytes, which should favor the evolution of strong interactions between symbionts. Recent study showed that *Rickettsia* sp. nr. bellii swept into a population of the invasive MEAM1 in just 6 years. Compared with uninfected whiteflies, Rickettsia-infected whiteflies produced more offspring, had higher survival to adulthood, developed faster, and produced a higher proportion of females (Himler et al. 2011). The *Rickettsia* thus functions as both mutualist and reproductive manipulator. The observed increased performance and sex-ratio bias of infected whiteflies are sufficient to explain the spread of Rickettsia across the southwestern United States.

Bing et al. (2013) tested five of the six S-endosymbiont lineages (excluding *Fritschea*) from 340 whitely individuals representing six putative species from China. *Hamiltonella* was detected only in the two exotic invaders, MEAM1 and MED. *Rickettsia* was absent in Asia II 1 and MED, scarce in Asia II 3 (13%), but abundant in Asia II 7 (63.2%), China 1 (84.7%) and MEAM1 (100%). *Wolbachia*, *Cardinium* and *Arsenophonus* were absent in the invasive MEAM1 and MED but mostly abundant in the native putative species. Furthermore, phylogenetic analyses revealed that some S-endosymbionts have several clades and different *B. tabaci* putative species can harbor different clades of a given S-endosymbiont, demonstrating further the complexity of S-endosymbionts in *B. tabaci.* These results demonstrate the variation and diversity of S-endosymbionts in different putative species of *B. tabaci*, especially between invasive and native whiteflies.

Owing to the importance of endosymbionts in whitefly biology, a number of studies have been carried out to reveal the function of whitefly endosymbionts. In order to gain insight into the metabolic role of each symbiont, Rao et al. (2015) analyzed the genome sequences of the primary symbiont *Portiera* and of the secondary symbiont *Hamiltonella* in MED. Sequencing results shows that the genome of *Portiera* is highly reduced (357 kb). It has kept a number of genes encoding most essential amino-acids and carotenoids, but lacks almost all the genes involved in the synthesis of vitamins and cofactors. Interestingly, *Hamiltonella* can not only provide vitamins and cofactors, but also complete the missing steps of some of the pathways of *Portiera*. The data suggests that *Portiera* and *Hamiltonella* are not only complementary but could also be mutually dependent to provide a full complement of nutrients to their hosts. On the other hand, genome analysis revealed that another secondary symbiont *Rickettsia* was unable to synthesize amino acids required for complementing the whitefly nutrition (Zhu et al. 2016). Parallel genomic and transcriptomic analysis further revealed that the host genome contributes multiple metabolic reactions that complement or duplicate *Portiera* function, and that *Hamiltonella* may contribute multiple cofactors and one essential amino acid, lysine. These results shows that bacteria with genomic decay enable host acquisition of complex metabolic pathways by multiple independent horizontal gene transfers from exogenous bacteria (Luan et al. 2015).

8.3.5 Roles of Pesticides Application in **B. tabaci** *Invasions*

At present, more than 50 insecticides have been employed to control the growth of *B. tabaci* populations and viral transmission (Horowitz et al. 2011). However, due to the rapidly rising resistance to insecticides, utilizing chemical agents to control *B. tabaci* is facing ever-increasing difficulties (Dennehy et al. 2010; Wang et al. 2009). During the last 20 years, a number of studies have been carried out to reveal the molecular mechanisms of whitefly resistance to insecticides. Pyriproxyfen is one of the major insecticides used to control the whitefly, however, whitefly resistance to pyriproxyfen has been observed in many regions (Crowder et al. 2007). To investigate the molecular basis underlying this resistance, a cDNA microarray was used to monitor changes in gene expression in a resistant *B. tabaci* population (Ghanim and Kontsedalov 2007). Functional analysis showed that many of the up-regulated ESTs were associated with resistance and xenobiotic detoxification, protein, lipid and carbohydrate metabolism and JH-associated processes (Ghanim and Kontsedalov 2007). Yang et al. (2013b) analyzed the differences between resistant and susceptible stains at both transcriptional and translational levels. Among the 1338 differentially expressed genes, 118 were putatively linked to insecticide resistance. The same research group also compared gene expression in the egg, nymph and adult stages of a thiamethoxam-resistant strain with a susceptible strain using a custom whitefly microarray (Yang et al. 2013a). Gene ontology and bioinformatic analyses revealed that at all life stages many of the DEGs encoded enzymes were involved in metabolic processes and/or metabolism of xenobiotics. In addition, several ATP-binding cassette transporters were highly over-expressed at the adult stage of the TH-R strain and may play a role in resistance by active efflux (Yang et al. 2013a).

The wide application of insecticides in China may be the key factor driving the rapid displacement of MEAM1 by MED. Under laboratory conditions, the MEAM1 can displace MED without the selection of insecticides (Wu et al. 2010). However, field surveys in China after 2003 indicate that in many regions MED has been replacing the earlier invader MEAM1. Sun et al. (2013a) conducted laboratory experiments and field sampling to examine the effects of insecticide application on the competitive interactions between MEAM1 and MED. In the laboratory, MEAM1 displaced MED in five generations on cotton when initial populations of the two species were equal and no insecticide was applied. In contrast, MED displaced MEAM1 in seven and two generations, respectively, when imidacloprid was applied. Field sampling indicated that in a single season MED displaced MEAM1 on crops heavily sprayed with neonicotinoid insecticides but the relative abundance of the two species changed little on crops without insecticide spray. As field populations of MED have lower susceptibility than those of MEAM1 to commonly used insecticides, insecticide application seems to have played a major role in shifting the species competitive interaction in favor of MED in the field. Later on, Pan et al. (2015) confirmed that the rapid replacement of the MEAM1 by MED throughout China is because MED is more tolerant of insecticides. The field monitoring also revealed that the insecticide resistance of MED generally is higher than MEAM1.

For instance, Luo et al. (2010) found that MEAM1 remained largely susceptible to acetamiprid, imidacloprid, and thiamethoxam, whereas MED expressed 20–170 folds resistance to these insecticides. These studies strongly support the hypothesis that insecticide use reverses the MEAM1-MED competition in China and allows MED to displace MEAM1 in different regions.

8.3.6 Adaptation of **B. tabaci** *to Heat Stress*

In nature, whiteflies are continuously exposed to abiotic stresses. The great adaptability of MEAM1 to harsh temperature conditions plays a major role in its rapid invasions and spread. Results of the comparative studies demonstrated that MEAM1 whiteflies possess greater tolerance to harsh temperatures than the greenhouse whitefly *T. vaporariorum* and some of the native whitefly species (Cui et al. 2008; Gao et al. 2015). The MEAM1 adults showed greater ability to adapt to higher temperature than *T. vaporariorum* under laboratory conditions. The thermal thresholds for survival of MEAM1 and *T. vaporariorum* were 45 °C and 43 °C, respectively. Fecundity of the MEAM1 was not significantly affected after 1 h heat shock, whereas that of *T. vaporariorum* was decreased (Cui et al. 2008). Mahadav et al. (2009) compared the expression patterns of MEAM1 and MED under 25 °C and 40 °C heat stress using microarray. The authors found that compared to the treatment of MED, exposure of MEAM1 to heat stress was accompanied by rapid alteration of gene expression. These differences might be due to better adaptation of one species over another and might eventually lead to change of MEAM1 and MED distribution (Mahadav et al. 2009). To reveal why females are more heat resistant than males, Lu and Wan (2008) identified the DEGs in male and female whiteflies, respectively. The authors found that difference of heat-resistance under heat-shock condition was associated with DEGs between *B. tabaci* sexes.

8.3.7 Genetic Base of **B. tabaci** *Invasions*

The recent advancement in genomic technologies offers great opportunities for a better understanding of the complex mechanisms underlying whitefly invasions (Edwards and Papanicolaou 2012). With the development of high performance sequencing technology, transcript profiling techniques allow the simultaneous examination of thousands of genes, and can be utilized to study changes in gene expression (Gibbons et al. 2009). In 2010, a new short read sequencing technology (Illumina) was employed to analyze the transcriptome of the MED. A total of 168,900 distinct sequences were assembled. Based on similarity search with known proteins, 27,290 sequences with a cut-off E-value of 10^{-5} were identified (Wang et al. 2010a). In 2011, Wang et al. (2011) re-sequenced the transcriptome of the invasive MEAM1 whitefly using Illumina and compared it with the MED transcriptome. The comparison revealed that the level of sequence divergence in coding region was 0.83%, strongly supporting to the previous proposition that MEAM1 and MED whiteflies are two species. This study further showed that 24 genes, which have evolved in response to positive selection, were involved in metabolism and insecticide resistance. These genes might contribute to the divergence of the two whitefly species (Wang et al. 2011). To reveal the possible mechanism of whitefly invasions, 52,535 transcriptome sequences were identified from the native Asia II 3 species (Wang et al. 2012). Comparison of the sequence divergence between the transcriptomes of Asia II 3 and the invasive species MEAM1 and MED indicated that the overall divergence of coding sequences between the orthologous gene pairs of Asia II 3 and MEAM1, and that between Asia II 3 and MED, was 1.73 and 1.84%, respectively, much higher than that between MEAM1 and MED (0.83%). The data also demonstrated that the most divergent gene classes between the native and invasive species were related to cytochrome P450, glutathione metabolism and oxidative phosphorylation, which seemed relevant to the invasion, displacement and speciation of the species in the *B. tabaci* complex (Wang et al. 2012).

Wang et al. (2013) further examined the transcriptional difference between the two invasive whitefly species, MEAM1 and MED, and one indigenous whitefly species Asia II 3. The results showed that 2422 genes between MEAM1 and MED; 3073 genes between MEAM1 and Asia II 3; and 3644 genes between MED and Asia II 3 were differentially expressed. Carbohydrate, amino acid and glycerolipid metabolisms were more active in MEAM1 and MED than in Asia II 3. Furthermore, the majority of genes involved in basic metabolism and detoxification were expressed at a higher level in MEAM1 and MED than in Asia II 3, which might be responsible for their higher resistance to insecticides and environmental stresses (Wang et al. 2013). Sequencing and comparison of the gut transcriptomes of MEAM1 and MED revealed that many genes related to detoxification were expressed at an elevated level in the gut of MED compared to MEAM1, which might be responsible for the MED's higher resistance to insecticides and environmental stresses (Ye et al. 2014). Xu et al. (2015a) compared the transcriptional responses of MEAM1 and Asia II 3 whitefly species following host plant transfer from a suitable host (cotton) to an unsuitable host (tobacco). Transcriptional analysis showed that compared to the constitutive high expression of detoxification genes in MEAM1, most of the detoxification genes were down-regulated in Asia II 3. Enzymatic activities of P450, GST and esterase further verified that the detoxification of MEAM1 was much higher than that of Asia II 3. These results reveal obvious differences in responses of MEAM1 and Asia II 3 to host transfer.

8.4 Management of *B. tabaci*

8.4.1 Monitoring and Treatment Decisions

By collecting information of several factors (e.g., longitude, latitude, altitude, average annual rainfall, average annual temperature and its range, average temperature in January and July, annual highest and lowest temperature) at whitefly occurred spots in China and analyzing with Maxent prediction model, Ren et al. (2011) reported that South and East China, as well as the southern part of North China were suitable for *B. tabaci* distribution. Using life table data of *B. tabaci* and 10 years' climate information in different regions in China, Ren et al. (2011) warned that *B. tabaci* may have 11–15 generations in Guangdong, Guangxi and Hainan provinces, 7–15 generations in Shandong, Henan and Chongqing areas, and one generation in Tibet and Qinhai provinces. Based on this result, a monitoring and early warning platform has been established (http://www.ipm.ioz.ac.cn/them_gefeng/fenshi/index.as).

The use of yellow sticky cards (24 cm × 20 cm) is an important method of monitoring whitefly populations in the wild. Five yellow sticky cards were put in every 667 m^2 field using 5-points or "Z"-shaped methods, and replaced with new ones every 10 days. The upper edge of the card was kept at an equal level to or slightly above the plants. If the number of adult whitefly captured on the cards reached 0.25–0.5 adult/cm^2, biological control measures should be taken; while it reached 3–4 adult/cm^2, chemical control measures should be taken to suppress the outbreak of *B. tabaci* (Ren et al. 2014). Sampling via leaf-turn method was also adopted. For Solanaceous and Cucurbitaceae plants, the third and fourth leaf from the top was sampled; while for vegetables such as cabbage and Chinese kale, the young leaves in plant heart part were sampled. If the number of adult whitefly reached 0.5–2 adult/leaf, biological control measures should be taken; while it reached 5–6 adult/leaf, environmental friendly insecticides should be sprayed (Tian et al. 2015). Such action threshold has been defined as the level of pest populations at which control should be implemented to avoid significant damages to crops (Dik and Albajes 1999), while an "economic injury level" (EIL) requires more rigorous criteria employing economic consideration. Related to market and environmental conditions in China, an economic injury level of 18 adult *B. tabaci* per cucumber plant at the four-leaf stage was determined (Shen et al. 2005); for greenhouse tomato, a level of 13.6 adults per 100 leaves was established (Cao and Cao 2011); while for cabbage, an economic threshold of 6.0–6.8 adults per plant in the seedling stage and 2.1–3.8 adults per plant in the rosette stage were determined (Wang 2007).

8.4.2 Cultural Control

Cultural control is to improve crop system to make the environment less favorable to pest reproduction, dispersal, survival and damage, while more suitable to natural enemies. Cultural control options for *B. tabaci* include the use of physical barriers or other barriers to prevent the pest from reaching the crop, adjusting planting dates, planting in low infestation areas, rotation with non-susceptible crops, destroying crop residues and selecting resistant crops or cultivars (Ren et al. 2001).

Planting Dates One way to reduce whitefly infestations is to adjust planting dates to avoid the heaviest insect migration periods or crop overlap. Early planting in spring or delayed planting in fall can be an effective way to avoid whiteflies, since they reproduce more rapidly under hot and dry conditions. Highly susceptible crops such as cucurbits, crucifers and tomatoes should avoid to be planted when whitefly migration is expected.

Crop Termination Whitefly infestations most often occur in fields where damages ever occurred. Susceptible crops should not be planted near infestation sources. Godfrey et al. (2008) suggested that cotton should be planted at least one-half mile upwind from other key host crops, such as melons, tomatoes, from key ornamental plants, and from key weed species that harbor *B. tabaci*. Infected plants should be removed and destroyed, and susceptible crops should not be grown continuously. It is reported that *B. tabaci* can continue to increase up to 6 weeks after final cotton irrigation even following defoliation since red eye pupa were able to continue development to the adult stage on cotton leaves that abscised and fell from the plants (Nuessly et al. 1994). Thus crop residues, which can harbor whitefly and virus inoculum, should be rapidly and completely destroyed after the final harvest.

Water and Fertility Management Water and fertility management play important roles as cultural control methods in whitefly management. Overuse of nitrogen fertilizer will greatly increase whitefly numbers and honeydew production thus exacerbate damages from *B. tabaci* infestations (Bi et al. 2001, 2005). Higher populations of *B. tabaci* were observed on water-stressed cotton as compared to well-watered plants (Flint et al. 1996). However, *B. tabaci* feeding on well-watered plants produced more honeydew and sugars per gram of honeydew than on water stressed cotton (Henneberry et al. 2002).

8.4.3 Host Plant Resistance

Planting varieties that are resistant to *B. tabaci* and associated viruses (e.g., tomato yellow leaf curl virus, TYLCV) is a preferred solution for minimizing damages caused by whitefly at the early stage. The *Mi-1* gene, present in many varieties of cultivated tomato (*Solanum lycopersicum* L.) and introduced into this plant from its wild relative, *S. peruvianum*, regulates resistance to *B. tabaci*, aphid *Macrosiphum* *euphorbiae* and root-knot nematodes *Meloidogyne* spp. (Roberts and Thomason 1986; Rossi et al. 1998; Nombela et al. 2001). However, tomato varieties bearing *Mi-1* gene has not been widely used in China yet. A number of studies on different plant varieties resistant to this pest have been carried out in China during the last decade. Studies have compared the biotic potential of whiteflies in different cultivated plants such as tomato, cucumber, beans, eggplant, peanut, squash and pepper in China (Ren et al. 2001; Xu et al. 2010b; Sun et al. 2013b; Wu 2013; Ji 2015).

8.4.4 Physical Control

Fine-mesh nylon screen (normally pore diameter 0.125 mm) can be used in greenhouse production to reduce the potential for infestation of greenhouse pests including whitefly, flower thrips, aphid and leafminer. Under field conditions, several types of barriers can reduce whitefly problems, including reflective mulches that tend to repel whiteflies, oil-coated yellow mulches that act as a trap for whiteflies, floating row covers that exclude whiteflies during the vegetative growth of crops, as well as barrier and trap crops (Ren et al. 2001; Tian et al. 2015).

Yellow sticky cards were also used to trap whitefly adults, especially in greenhouse condition. It is suggested that yellow sticky card (24 cm × 20 cm) could trap whitefly efficiently when placed vertically among plants and one card per 3–5 m, kept the upper edge of the card at an equal level or slightly above the plants (Qiu and Ren 2006; Chen et al. 2012).

8.4.5 Biological Control

In China, a number of natural enemies of *B. tabaci* have been recorded including 56 species of parasitoids, mainly belonging to the genera *Eretmocerus* and *Encarsia*; 54 species of arthropod predators, dominated by lady beetles and lacewings in Coleoptera and Neuroptera; and seven species of entomopathogenic fungi (Li et al. 2011). More than ten species of parasitoids and predators are commercially available in China now (Table 8.1).

Parasitoids *Encarsia bimaculata* and *Eretmocerus* sp. nr. *furuhashii* are the two dominate species parasitizing *B. tabaci* in South China, while the population of *Encarsia formosa* is abundant in north China in protected fields, and *Eretmocerus hayati* is abundant in Xinjiang province, located in northwest China, on cotton in fields (Li et al. 2011; Abuduhani et al. 2013; Zhang et al. 2015).

Among the four Aphelinid species which are commercially available in China (Table 8.1), *Encarsia sophia* (formerly known as *En. transvena*) is a solitary, arrhenotokous, heteronomous autoparasitoid. For this species, fertilized eggs are laid in whitefly nymphs and developed into female progeny, while the unfertilized eggs are

Table 8.1 Biological control parasitoids and predators commercially available in China

Biocontrol insects	Company/commercial facility	Location
Parasitoids		
Encarsia formosa	Quentian ™ Bio-Tech Co., LTD	Beijing
	NewLand™ BioControl Service Co., Ltd	Changchun, Jilin Province
	LandGreen® BioTech Service	Beijing
	TIANYI® Biologicaol Control	Hengshui, Hebei Province
	Beijing Academy of Agriculture and Forestry Sciences	Beijing
Encarsia sophia	Quentian ™ Bio-Tech Co., LTD	Beijing
	LandGreen® BioTech Service	Beijing
	TIANYI® Biologicaol Control	Hengshui, Hebei Province
	Institute of Plant Protection, Chinese Academy of Agricultural Sciences	Beijing
	Beijing Academy of Agriculture and Forestry Sciences	Beijing
Eretmocerus mundus	Quentian ™ Bio-Tech Co., LTD	Beijing
Eremocerus hayati	Institute of Plant Protection, Chinese Academy of Agricultural Sciences	Beijing
Predator mites		
Neoseiulus cucumeris	Quentian ™ Bio-Tech Co., LTD	Beijing
	LandGreen® BioTech Service	Beijing
	Fujian Yanxuan Bio-preventing and Controlling Technology Co., Ltd.	Fuzhou, Fujian Province
Predator ladybird		
Delphastus catalinae	Quentian ™ Bio-Tech Co., LTD	Beijing
	LandGreen® BioTech Service	Beijing
Harmonia axyridis	Quentian ™ Bio-Tech Co., LTD	Beijing
	NewLand™ BioControl Service Co., Ltd	Changchun, Jilin Province
	LandGreen® BioTech Service	Beijing
	Beijing Academy of Agriculture and Forestry Sciences	Beijing
Propylea japonica	Quentian ™ Bio-Tech Co., LTD	Beijing
	LandGreen® BioTech Service	Beijing
Serangium japonicum	Quentian ™ Bio-Tech Co., LTD	Beijing
Predatory stink bug		
Orius sauteri	Quentian ™ Bio-Tech Co., LTD	Beijing
	LandGreen® BioTech Service	Beijing
Orius minutus	Quentian ™ Bio-Tech Co., LTD	Beijing

(continued)

Table 8.1 (continued)

Biocontrol insects	Company/commercial facility	Location
Lacewing		
Chrysopa pallens	Quentian ™ Bio-Tech Co., LTD	Beijing
	LandGreen® BioTech Service	Beijing

Modified from Yang et al. (2014)

laid externally on immature parasitoids inside the whitefly host, either on conspecific species or on heterospecific primary parasitoids, and developed into male progeny (Hunter and Kelly 1998). It is originated from Pakistan, and currently present across northern and southern China (Yang et al. 2012; Li et al. 2011). *Er. hayati* is a primary, solitary parasitoid which oviposits externally under the nymphal host (Yang and Wan 2011). After eclosion, the first instar larva penetrates the host from underneath and develops internally. Both of these two parasitoids attack all nymphal stages (N1-N4) of *B. tabaci*, while *En. sophia* prefer old instar and *Er. hayati* prefer young ones (Yang and Wan 2011). Although *Er. hayati* is capable of high parasitism on *B. tabaci*, its field population often fluctuates because of the severe consumption of hosts by adults (Yang et al. 2012; Xu et al. 2015b). The combined release of the autoparasitoid *En. sophia* will stabilize the effect of *Er. hayati* (Xu et al. 2015b, 2016; Huang et al. 2016).

Predators The lady beetle *Axinoscymnus cardilobus* is a dominant predator of *B. tabaci* in south China, while *Harmonia axyridis* and *Propylea japonica* are dominant predators species in north China (Zhang et al. 2007a, b; Li et al. 2011). *H. axyridis* is a generalist predator extensively employed as a biological control agent in China (Koch 2003). This ladybird species exhibits significantly lower selectivity for *B. tabaci* and a reduced reproduction rate when fed on *B. tabaci* (Tan et al. 2016). However, its generalist character could be helpful in controlling secondary pests. Besides, when it was released in combination with whitefly parasitoids, *En. sophia* and *En. formosa*, *H. axyridis* showed a significant preference for non-parasitized nymphs as prey; and both parasitoid species parasitized more *B. tabaci* as compared to the wasps were released either alone or mixed with the other parasitoid (Tan et al. 2016). This combination release of predator and parasitoids enhanced whitefly control. Li et al. (2014a) also reported an enhanced control effects on *B. tabaci* by combined release of *Orius sauteri*, a generalist predatory stink bug, with *En. formosa*.

Entomopathogenic Fungi Several species of entomopathogenic fungi active against *B. tabaci* are commercially available in China, including *Beauveria bassiana*, *Aschersonia aleyrodis*, *Verticillium lecanii*, and *Isaria fumosorosea*. *B. bassiana* could significantly decrease the survival rate of *B. tabaci* nymphs while increase developmental time and pre-oviposition period (Xia et al. 2013). *A. aleyrodis* could parasitize on 1–3 instar nymphs of *B. tabaci*, and had no contradicted effect on whitefly parasitoid *Eretmocerus* sp. (Qiu et al. 2003b). *I. fumosorosea* infected all immature stages and adults of *B. tabaci* (Tian et al. 2014). *V. lecanii* showed deterrent activity to *B. tabaci* adults and contact toxicity to *B. tabaci* nymphs (Wang et al. 2006). However, *V. lecanii* required high humidity to be effective, this shortage could be made up by using *V. lecanii* toxic (Hong et al. 2011). The deterrent and anti-feeding activity of *V. lecanii* toxic-VIII on *B. tabaci* adults was tested as 41% and 23%, respectively (Hong et al. 2011). Restricted by environmental factors such as temperature and humility, the effect of entomopathogenic fungi in *B. tabaci* management was slow and not very stable. Recent researches revealed that when *I. fumosorosea* combined with thiamethoxam or imidacloprid, and *B. bassiana* combined with non-ionic surfactants, a synergic effect on *B. tabaci* was observed (Mascarin et al. 2014; Zou et al. 2014).

8.4.6 Chemical Control

Even the system of organic crops production inclines to employ increasing biological control measures, chemical control is indispensable when *B. tabaci* occurs in high density and quick eliminating effect is required. However, *B. tabaci* can develop resistance not only to conventional insecticides in China, but also to a number of new insecticides, such as pyriproxyfen, acetamiprid, imidacloprid, and thiamethoxam, especially MED (Crowder et al. 2007; Luo et al. 2010). Besides, thiamethoxam was highly toxic to *Serangium japonicum*, a predator ladybeetle, regardless of exposure routes (e.g., residue contact, egg-dip, and systemic treatment) (Yao et al. 2015). Therefore, thiamethoxam should be used with caution in IPM of *B. tabaci*. Some environmental friendly insecticides, avermectin, spinetoram, sulfozaflor and cyantraniliprole, are recommended to be applied in *B. tabaci* management (Keyimu et al. 2014; Xie et al. 2014).

8.5 Concluding Remarks

Even though many field surveys have been conducted to monitor the spread of *B. tabaci* during the last 15 years, our understanding of the invasion processes of MEAM1 and MED in China remain largely observational and anecdotal. This is mainly due to the lack of efficient methods to easily distinguish different whitefly species in the field and the presence of the *B. tabaci* species complex. Nevertheless, the current surveys have clearly showed that while MEAM1 was dominate near 2000, MED has replaced MEAM1 in many regions of China now. During the last decade, we have identified multiple factors that contribute to the invasions of *B. tabaci* into new regions and habitats, such as mating interactions, host plant adaptation, insecticide resistance, virus-vector-host mutualism and the roles of endosymbionts. Those studies obviously suggest that the successful invasions of MEAM1 and MED in China are largely due to their intrinsic traits, such as high insecticide resistance, wide host range and strong reproduction capacity. More comparative studies on the biological characteristics between invasive and indigenous species may provide better understanding of the mechanism underlying invasions and displacement. It is also crucial to identify the key factors that contribute to the unique features of MEAM1 and MED. The obtained knowledge will help us to develop new strategies to control the spread of invasive *B. tabaci* in China. At this stage, Chinese farmers mainly rely on insecticides as immediate solutions to *B. tabaci* problems. However, the use of insecticides impairs the benefits of consumers and regulators concerned with food safety and environmental protection. This conflict leads to interest and development in alternative control measures. In response, Integrated Pest Management (IPM) has been the main paradigm in modern pest control. In China, IPM has been developed in the last decade with a combination of tactics including cultural control methods, resistant plant varieties, physical control such as mechanical screen and yellow sticky cards, biological control by natural enemies, and the judicious use of insecticides based on sampling and economic thresholds. In the production of some high-value crops, the *B. tabaci* IPM has been tested to be effective and been gradually adopted in organic farms. However, for most farmers, considering the IPM cost and knowledge access, chemical measures are still the prior choice. Thus, the wide demonstration and dissemination of *B. tabaci* IPM in end-users to improve the implement of environmental friendly measures to control *B. tabaci* needs extensive devotion from regulators and researchers.

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