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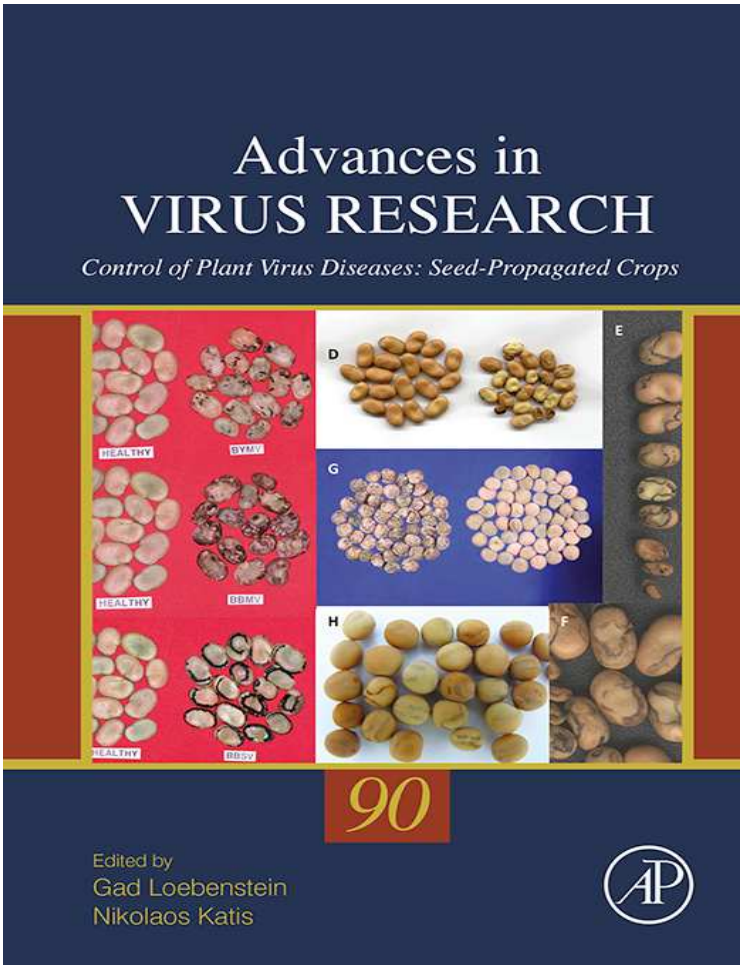

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CHAPTER THREE

Management of Whitefly-Transmitted Viruses in Open-Field Production Systems

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Abstract

Whiteflies are a key pest of crops in open-field production throughout the tropics and subtropics. This is due in large part to the long and diverse list of devastating plant viruses transmitted by these vectors. Open-field production provides many challenges to manage these viruses and in many cases adequate management has not been possible. Diseases caused by whitefly-transmitted viruses have become limiting factors in open-field production of a wide range of crops, i.e., bean golden mosaic disease in beans, tomato yellow leaf curl disease in tomato, cassava mosaic disease and cassava brown streak disease in cassava, and cotton leaf crumple disease in cotton. While host resistance has proven to be the most cost-effective management solution, few examples of host resistance have been developed to date. The main strategy to limit the incidence of virus-infected plants has been the application of insecticides to reduce vector populations aided to some extent by the use of selected cultural practices. However, due to concerns about the effect of insecticides on pollinators, consumer demand for reduced pesticide use, and the ability of the whitefly vectors to develop insecticide-resistance, there is a growing need to develop and deploy strategies that do not rely on insecticides. The reduction in pesticide use will greatly increase the need for genetic resistance to more viruses in more crop plants. Resistance combined with selected IPM strategies could become a viable means to increase yields in crops produced in open fields despite the presence of whitefly-transmitted viruses.

1. INTRODUCTION

Over the last 20 years, viruses transmitted by whiteflies have emerged as a global threat to crop production in a wide range of crops. This emergence is due in large part to the movement of plants and plant parts which distribute both vectors and viruses to new locations (Anderson et al., 2004). Whitefly and whitefly-transmitted viruses are primarily concerns in dicotyledonous crops. Many of the crops that are adversely affected by these viruses

are economically significant and losses occur in both crops for export as well as those critical for subsistence. Many of these viruses are limiting factors in crop production. Some of the greatest losses occur in fiber crops such as cotton; vegetable crops such as cassava, cucurbits, tomato, pepper, common bean, various pulses; agronomic crops such as soybean; and biofuels such as Jatropha. Yield losses, which range from minimal to complete crop failure, depend upon the virus, the crop, the age of the crop at the time of infection, and the incidence of virus-infected plants. Crop resistance to most of these viruses or to feeding by the whitefly vectors has not been developed. In the absence of crop resistance, management of these viruses is usually very challenging, requiring the timely use of numerous management tactics with a heavy reliance on chemicals to limit the feeding, development, and movement of the vector(s).

2. WHITEFLIES AND THE VIRUSES THEY TRANSMIT

2.1. The whiteflies

Whiteflies (Order Hemiptera, Family Aleyrodidae) comprise more than 1500 species in approximately 126 genera (Martin, 2004). Of those many species, only five are known to transmit plant viruses: *Bemisia afer* (Priesner & Hosny), *Bemisia tabaci* species complex, *Parabemisia myricae* Kuwana (bayberry whitefly), *Trialeurodes abutilonea* Haldeman (banded wing whitefly), and *Trialeurodes vaporariorum* Westwood (greenhouse whitefly) (Gamarra et al., 2010; reviews by Hogenhout, Ammar, Whitfield, & Redinbaugh, 2008; Navas-Castillo, Fiallo-Olivé, & Sánchez-Campos, 2011; Ng & Falk, 2006). The diversity of whitefly vectors appears lower than it is in reality due to the current taxonomic organization of the *B. tabaci* species complex. This complex is actually composed of 34 distinguishable entities that are probable species based on both molecular and biological studies (reviewed by Polston, De Barro, & Boykin, 2014). When species names are eventually assigned to these entities, the number of whitefly vector species and the recognized diversity will increase significantly. Other whiteflies reported as vectors include *Trialeurodes ricini* (Misra), which was reported to transmit a begomovirus in Egypt, but this work has not been confirmed by any other reports (Idriss, Abdallah, Aref, Haridy, & Madkour, 1997). In addition, *B. tuberculata* was reported as a vector of viruses associated with frogskin disease of cassava (Angel, Pineda, Nolt, & Velasco, 1990) but phytoplasmas have also been shown to be associated with the disease (Alvarez et al., 2009) and its exact etiology remains uncertain.

Table 3.1 Summary of whitefly species and the virus genera they transmit

Virus family	Virus genus	No. of approved species[a]	Whitefly	Mode of transmission
Betaflexiviridae	*Carlavirus*	3[b]	*Bemisia tabaci* species complex	Nonpersistent/ Semi-persistent
Closteroviridae	*Crinivirus*	1	*Bemisia afer*	Semi-persistent
		4	*Bemisia tabaci* species complex	Semi-persistent
		4	*Trialeurodes abutilonea*	Semi-persistent
		4	*Trialeurodes vaporariorum*	Semi-persistent
Geminiviridae	*Begomovirus*	192	*Bemisia tabaci* species complex	Persistent, nonpropagative
		1	*Trialeurodes ricini*	Unknown
Potyviridae	*Ipomovirus*	4	*Bemisia tabaci* species complex	Semi-persistent
Secoviridae	*Torradovirus*	2[c]	*Bemisia tabaci* species complex	Undetermined
		1	*Trialeurodes vaporariorum*	Undetermined

[a]According to King, Lefkowitz, Adams, and Carstens (2011) except as noted.
[b]Includes *Cucumber vein-clearing virus* (Menzel, Abang, & Winter, 2011).
[c]Includes *Tomato necrotic dwarf virus* (Wintermantel & Hladky, 2013).

Table 3.1 briefly summarizes the families and genera of plant viruses, whitefly species known to transmit at least one species within those genera, and the mode of transmission. Four recent reviews cover these whitefly species and the viruses they transmit in more detail than will be presented here (Hogenhout et al., 2008; Navas-Castillo et al., 2011; Ng & Falk, 2006; Polston et al., 2014).

2.2. The viruses

The plant viruses transmitted by whiteflies have been reviewed extensively and readers are encouraged to consult these references for more detailed descriptions (Jones, 2003; Navas-Castillo et al., 2011; Tzanetakis, Martin, & Wintermantel, 2013; Legg et al., chapter 3).

2.2.1 Betaflexiviridae, Carlavirus

As of 2013, there were 52 virus species in the genus *Carlavirus* (www.ictvonline.org/virusTaxonomy.asp) of which only three, *Cowpea mild mottle virus* (CPMMV), *Cucumber vein-clearing virus* (CuVCV), and *Melon yellowing-associated virus* (MYaV), are known to be transmitted by whiteflies (Menzel et al., 2011; Nagata et al., 2005; Naidu et al., 1998). Carlaviruses are ssRNA viruses and are relatively easy to detect using standard types of assays—ELISA (commercially available for CPMMV) and reverse-transcription PCR. All three have been shown to be transmitted by *B. tabaci* MEAM1 (formerly known as the B biotype) although there is some confusion as to the manner of transmission. CuVCV was transmitted in a semi-persistent manner, while CPMMV has been reported to be transmitted in a nonpersistent manner by some and in a semi-persistent manner by others (Iwaki, Thongmeearkon, Prommin, Honda, & Hibi, 1982; Menzel et al., 2011; Muniyappa & Reddy, 1983; Rosario, Capobianco, Ng, Breitbart, & Polston, 2014). The manner of transmission of MYaV has not been reported. The confusion regarding CPMMV transmission may be due to the lack of identity of the whitefly species used in the studies, the variation among what are currently regarded as isolates of CPMMV but may be different species, as well as differences in methodologies used to determine the manner of transmission.

2.2.2 Closteroviridae, Crinivirus

The last 25 years have seen a rapid increase in the number of described species. These currently number 13 and all are transmitted by whiteflies (www.ictvonline.org/virusTaxonomy.asp). Criniviruses are difficult to recognize as their symptoms are not always apparent and are often readily mistaken for physiological or nutritional disorders or pesticide phytotoxicity. Detection is also difficult as the viruses occur in low concentrations and with less uniform distribution within the plant compared to other viruses. The genus now consists of three separate groups based largely on the sequences of their RNA-dependent RNA polymerase genes and vector transmission characteristics (Tzanetakis et al., 2013; Wintermantel, Hladky, Gulati-Sakhuja, et al., 2009). Criniviruses are transmitted in a semi-persistent manner and do not replicate within their whitefly vectors. Criniviruses can be transmitted by *B. tabaci*, *T. vaporariorum*, and *T. abutilonea* (Wintermantel, 2010). It is possible that additional vector species may exist but have yet to be identified. These three species are often common in areas in which criniviruses are found, and there is a clear relationship between prevalence of vector and

of virus. Once a crinivirus is acquired, whiteflies remain viruliferous for 1–9 days depending on the vector and virus (Wintermantel, 2010; Wisler & Duffus, 2001; Wisler, Duffus, Liu, & Li, 1998). The viruses are not seed-borne, nor are they mechanically transmitted (Tzanetakis et al., 2013).

Like other members of the family *Closteroviridae*, criniviruses have long flexuous rod-shaped virions averaging between 650 and 1000 nm in length (Kreuze, Savenkov, & Valkonen, 2002; Liu, Wisler, & Duffus, 2000). Genomes are predominantly bipartite with RNA1 encoding functions predominantly associated with virus replication, and RNA2 (or RNAs 2 and 3 for *Potato yellow vein virus*) encoding as many as 10 proteins with a range of functions including virus encapsidation, cell-to-cell movement, and vector transmission (King et al., 2011). Crinivirus infections in some crops remain latent for nearly 3 weeks before symptoms appear and others remain latent until plants become coinfected with another virus (Tzanetakis et al., 2013). Such mixed infections can complicate identification of the primary virus causing disease because symptoms resulting from mixed infection with other viruses often induce different symptoms than those resulting from single infections. In other situations, the viruses involved in coinfections are obvious within different sections of infected plants exhibiting symptoms uniquely characteristic of each virus. Numerous studies have demonstrated that interactions between criniviruses and other coinfecting viruses have been known to influence the type and severity of symptoms observed on plants. In many cases, this leads to enhanced disease severity, as has been found with infection of *Sweet potato chlorotic stunt virus* (SPCSV) and members of the *Potyvirus* genus (Karyeija, Kreuze, Gibson, & Valkonen, 2000).

2.2.3 Geminiviridae, Begomovirus

The single-stranded circular DNA viruses in the genus *Begomovirus* and family *Geminiviridae* are the most studied of the whitefly-transmitted viruses. This is also the largest genus of whitefly-transmitted viruses with almost 200 recognized species (King et al., 2011). Transmission of these viruses by members of the *B. tabaci* species complex is persistent and nonpropagative (reviewed by Navas-Castillo et al., 2011). While there is no specificity of transmission of begomovirus species by members of the *B. tabaci* species complex, it has been shown that different members transmit the same virus with different efficiencies (Bedford, Briddon, Brown, Rosell, & Markham, 1994; Caciagli, Bosco, & Albitar, 1995; Idris, Smith, & Brown, 2001; Jiang, De Blas, Bedford, Nombela, & Muniz, 2004; Li, Hu, Xu, & Liu, 2010; McGrath & Harrison, 1995). For example, under the same conditions,

whiteflies of the MEAM1 and Mediterranean clades transmitted *Tomato yellow leaf curl virus* (TYLCV) with equal efficiency, while whiteflies of the Asia II-1 clade transmitted the same virus about half as efficiently (Li et al., 2010). Differences in transmission efficiency have been shown to be due to the feeding habits and preferences of the vectors for the plant hosts used for acquisition and transmission. Efficiency is also affected by differences in the amount and distribution of begomoviruses among plant hosts (Azzam et al., 1994). The presence of selected endosymbionts (ex. *Hamiltonella spp.*) has also been shown to affect the transmission efficiency of begomoviruses (Gottlieb et al., 2010; Su et al., 2012). It has also been shown that at least one begomovirus can alter the settling, probing, and feeding behavior of the whitefly, thereby altering the transmission efficiency (Moreno-Delafuente, Garzo, Moreno, & Fereres, 2013).

2.2.4 Potyviridae, Ipomovirus

Species in the genus *Ipomovirus* are the only members of the family *Potyviridae* (single-stranded plus sense RNA genome) that are transmitted by whiteflies. Of the six approved species in this genus, four have been confirmed to be transmitted by members of the *B. tabaci* species complex at relatively low efficiencies (often below 50%) and in a semi-persistent manner. *Cassava brown streak virus* (CBSV) was shown to be transmitted by *B. tabaci* but not by *B. afer* (Maruthi et al., 2005). *Cucumber vein-yellowing virus* (CVYV) was shown to be transmitted in a semi-persistent manner by *B. tabaci* (Harpaz & Cohen, 1965; Mansour & Al-Musa, 1993). More recently, *Squash vein-yellowing virus* was demonstrated to be transmitted in a semi-persistent manner by *B. tabaci* MEAM1 (S. Webb, personal communication; Webb, Adkins, & Reitz, 2012). An eggplant-infecting strain of *Tomato mild mottling virus* (formerly Eggplant mild leaf mottle virus) was also recently shown to be transmitted in a semi-persistent manner by *B. tabaci* MEAM1 (Dombrovsky, Sapkota, Lachman, Pearlsman, & Antignus, 2013).

2.2.5 Secoviridae, Torradovirus

The *Torradovirus* genus (single-stranded plus sense RNA genome) is a recently established taxon with two approved species—*Tomato torrado virus* (ToTV) and *Tomato marchitez virus* (syn. Tomato apex necrosis virus), and four additional potential species, *Tomato chocolate virus*, *Tomato chocolate spot virus*, *Tomato necrotic dwarf virus* (ToNDV), and *Cassava torrado-like virus* (CsTLV) (Carvajal-Yepes et al., 2014; King et al., 2011; Larsen,

Duffus, & Liu, 1984; Verbeek, Dullemans, van den Heuvel, Maris, & van der Vlugt, 2007; Wintermantel & Hladky, 2013; www.ictvonline.org/virusTaxonomy.asp). Although little is currently known about the relationship of these recently emerged viruses with whiteflies, details are beginning to emerge. ToTV has been shown to be transmitted by members of the *B. tabaci* species complex and *T. vaporariorum* (Pospieszny et al., 2007; Amari et al., 2008). ToNDV was shown to be transmitted by *B. tabaci* New World1 during initial studies, and later by *B. tabaci* MEAM1 (Larsen et al., 1984; W. M. Wintermantel, pers. comm). Transmission of at least three torradovirus species by multiple whitefly species was recently shown to occur in a semi-persistent manner, requiring acquisistion and transmission periods of at least 2 hours (Verbeek, van Bekkum, Dullemans, & van der Vlugt, 2014).

3. MANAGEMENT OF WHITEFLY-TRANSMITTED VIRUSES USING PESTICIDES

Whiteflies are often managed primarily through multiple applications of a wide range of insecticides. In the absence of genetic resistance, insecticides play the dominant role in reducing whitefly populations and limiting the spread of viruses. This is true in the case of well-developed integrated management programs and even more so in cases where such recommendations do not exist. A wide range of insecticides is labeled for use against whiteflies (Table 3.2). These include pesticides with 11 different classifications of modes of action, as well as those that do not have an established mode of action. These insecticides vary in their target (whitefly eggs, immatures, and/or adults) and in their efficacy.

Optimal use of these pesticides requires several considerations. Selection of the insecticide and timing of application are best when applied using the results of field scouts who monitor whitefly populations. Insecticides should be used in a rotation where insecticides with different modes of action are applied so that development of resistance to any one pesticide by the whiteflies is prevented or delayed.

Of all the insecticides available the one class that has had the greatest impact on the management of whitefly-transmitted viruses is the neonicotinoids. These are generally applied as a soil drench or spray and due to their systemic and translaminar mobility within the plants are readily accessible to the feeding whiteflies. Their effect on whiteflies is rapid; they reduce whitefly populations very quickly and can impair the ability of whiteflies to transmit many plant viruses. The use of neonicotinoids expanded

Table 3.2 Summary of pesticides[a] recommended for use against whiteflies

Main group no. Primary site of action[b]	MoA code	Chemical subgroup or exemplifying active ingredient	Active ingredient	Notes
1 Acetylcholinesterase (AChE) inhibitors Nerve action	1A	Carbamates	Oxamyl	
	1B	Organophosphates	Methamidophos	Mix with a pyrethroid for whitefly control
			Acephate	Does not control silverleaf or sweet potato whiteflies
2 GABA-gated chloride channel antagonists Nerve action	2A	Cyclodiene, organochlorines	Endosulfan	
3 Sodium channel modulators Nerve action	3A	Pyrethroids, pyrethrins	Beta-cyfluthrin, bifenthrin, esfenvalerate, gamma-cyhalothrin, lambda-cyhalothrin, pyrethrins + piperonyl butoxide,[c] zeta-cyermethrin	
4 Nicotinic acetylcholine receptor (nAChR) agonists Nerve action	4A	Neonicotinoids	Acetamiprid, clothianidin, dinotefuran, imidacloprid, thiamethoxam	Foliar or soil drench

Continued

Table 3.2 Summary of pesticides recommended for use against whiteflies—cont'd

Main group no. Primary site of action	MoA code	Chemical subgroup or exemplifying active ingredient	Active ingredient	Notes
7 Juvenile hormone mimics Growth regulation	7C	Pyriproxyfen	Pyriproxyfen	Immatures of banded wing whitefly and silverleaf whitefly
9 Modulators of chordotonal organs Nerve action	9B	Pymetrozine	Pymetrozine	
15 Inhibitors of chitin biosynthesis, type 0 Growth regulation	15	Benzoylureas	Novaluron	
16 Inhibitors of chitin biosynthesis, type 1 Growth regulation	16	Buprofezin	Buprofezin	
21 Mitochondrial complex I electron transport inhibitors Energy metabolism	21A	METI acaricides and insecticides	Fenpyroxymate	
23 Inhibitors of acetyl CoA carboxylase Lipid synthesis, growth regulation	23	Tetronic and tetramic acid derivatives	Spiromesifen	Eggs and immatures
			Spirotetramat	
28 Ryanodine receptor modulators Nerve and muscle action	28	Diamides	Chlorantraniliprole	

Table 3.2 Summary of pesticides recommended for use against whiteflies—cont'd

Main group no. Primary site of action	MoA code	Chemical subgroup or exemplifying active ingredient	Active ingredient	Notes
Mixes of more than one active ingredient	3A, 28		Lambda-cyhalothrin, chlorantraniliprole	
	3A, 4A		Bifenthrin	
	3A, 4A		Bifenthrin, imidacloprid	
	3A, 4A		Lambda-cyhalothrin, thiamethoxan	
	3A, 6		Bifenthrin, Avermectin B1	
	3A, UN		Pyrethrins, azadirachtin	
	4A, 28		Thiamethoxam, chlorantraniliprole	
	16, 28		Buprofezin, flubendiamide	
UN Compounds of unknown or uncertain MoA	UN	Azadirachtin	Azadirachtin	
Not classified by IRAC	–	*n/a*	*Beauveria bassiana, Chromobacterium subtsugae* strain PRAA4-1, extract of *Chenopodium ambroisiodes,* extract of neem oil, insecticidal oil, insecticidal soap, *Isaria fumosorosea* Apopka strain 97	

[a]This is not an exhaustive list but does present a wide range of pesticides with reported activity against whiteflies. This list was prepared using the Vegetable Production Handbook for Florida 2013–2014 (www.omagdigital.com/publication/?i=175403).
[b]Uses the IRAC MoA Classification Scheme(Feb 2014, www.irac-online.org).
[c]Piperonyl butoxide is used as a synergist.

greatly over the last 20 years in terms of the number of crops to which they were applied as well as to the locations where they were routinely used. Until resistance to neonicotinoids develops in the whitefly population, this class of insecticides makes it possible to grow crops in many locations where whiteflies and the viruses they transmit exist.

Unfortunately, the neonicotinoids have been reported to have adverse effects on pollinators such as the European honeybee, bumble bees, birds, and they have been reported to contribute to Colony Collapse Disorder (CCD) (Blacquière, Smagghe, van Gestel, & Mommaerts, 2012; Desneux, Decourtye, & Delpuech, 2007; Mineau & Palmer, 2013). While the cause of CCD has not been resolved, the neonicotinoids have been implicated to play several roles that would be expected to contribute to a decline in pollinators. Honeybees exposed to neonicotinoids have been shown to have increased susceptibility to pathogens (Alaux et al., 2009; Di Prisco et al., 2013; Wu, Smart, Anelli, & Sheppard, 2012); impaired flight navigation, memory, and communication (Eiri & Nieh, 2012); reduced rates of foraging success and colony survival (Henry et al., 2012); and impaired olfactory learning and memory formation (Williamson & Wright, 2013). Studies with bumble bees have shown similar results (Whitehorn, O'Connor, Wackers, & Goulson, 2012) and neonicotinoids have been implicated as one of the causes of the dramatic decline in bumble bee diversity and populations in North America over the last 20 years (Cameron et al., 2011). However, recent studies have questioned these results suggesting that previous studies used abnormally high rates of exposure to neonicotinoids and that adverse effects were not seen at rates that pollinators would be expected to encounter in the field (Elston, Thompson, & Walters, 2013; Epstein et al., 2012). The most recent report from the USDA and EPA concludes that neonicotinoids are a less significant contributor than other factors in causing bee declines (Epstein et al., 2012).

The results of these studies have concerned both environmentalists and agriculturists. The lack of neonicotinoids will be likely to have a negative impact on the management of whitefly-transmitted viruses in the field. In the EU, three neonicotinoids (clothianidin, imidacloprid, and thiametoxam) have been banned from use for 2 years on flowering crops where bees actively forage but allowed on crops where bees are less active (http://www.nytimes.com/2013/04/30/business/global/30iht-eubees30.html?_r=2&; Gross, 2013). In the United States, the response has been more pragmatic and piecemeal. Although the US Environmental Protection Agency has been sued and petitioned to limit the use of neonicotinoids, no ban has as yet been imposed. However, adjustments on a piecemeal

basis are taking place. For example, use of neonicotinoids for control of Citrus greening has been modified to continue its use but to minimize the exposure of honeybees (http://www.freshfromflorida.com/Divisions-Offices/Agricultural-Environmental-Services/Consumer-Services/Florida-Bee-Protection/Citrus-Greening).

4. MANAGEMENT OF WHITEFLY-TRANSMITTED VIRUSES USING CULTURAL PRACTICES

Whiteflies that transmit viruses are most commonly controlled through the use of host plant resistance or the application of insecticides. Cultural practices often play a secondary role in control regimes, but in many circumstances their use can be of critical importance in lessening the dependence on the two main tactics. Consequently, integrated control strategies for whitefly-transmitted viruses frequently include cultural practice components (Stansly & Natwick, 2010). Cultural practices cover a diverse array of activities that are all associated with the manner in which a crop is planted and managed throughout the course of the cropping cycle. Here, we discuss some of the most important and frequently applied cultural practices for the control of whiteflies and the viruses that they transmit.

4.1. Plastic soil mulches

Plastic (polyethylene) soil covers (mulch) are a popular strategy for protection of open-field production against whiteflies and the viruses they transmit (as well as against viruses transmitted by aphids and thrips) (Weintraub & Berlinger, 2004). There are two main approaches to plastic soil mulching—using colored (mainly yellow) plastic that attracts the whiteflies to the mulch instead of to the host, or silver or aluminum coated plastic mulch that strongly reflects light, which acts as a deterrent to the invading whiteflies. Both types of soil mulch interfere with the insect's ability to find the crop, and are most effective early in the season, before the developing plant canopy covers the mulch. Soil mulching is relatively easy to perform, relatively inexpensive, and has added benefits to the grower since mulching can change the plant microclimate; i.e., temperature, humidity, light, water, etc. Moreover, it has been demonstrated that dark mulches that block or reduce light penetration into the soil inhibit germination and growth of weeds, which cannot survive under the mulch (Lament, 1993; Ngouajio & Ernest, 2004). Indeed, in Israel the commercial yellow plastic mulch is actually yellow-on-brown (top side yellow, lower side brown) with a dual effect—protection against insects and inhibition of weeds

(Weintraub & Berlinger, 2004). By inducing favorable conditions for the plant, the mulch can positively affect plant growth and increase yield (Csizinszky, Schuster, & Kring, 1995). However, one of the problems of using plastic mulch is the difficulty of mulch disposal, as polyethylene is not easily degradable.

Yellow plastic mulch—The use of yellow plastic mulch to protect open-field tomato plants from the whitefly-borne TYLCV is a common practice in Israeli agriculture (Cohen & Lapidot, 2007; Polston & Lapidot, 2007). In 1962, Mound tested the attraction of whiteflies to different colors and demonstrated that yellow attracts whiteflies. It was suggested that yellow radiation is a component of the whitefly's host-selection mechanism (Mound, 1962). Testing the effect of yellow plastic mulch on tomato plants Cohen and Melamed-Madjar (1978) found that 28 days after germination (DAG) only 5% of the plants protected by yellow mulch had developed TYLCV symptoms, compared to over 20% of the nonmulched control plants. At 38 DAG, only 10% of the mulched plants exhibited TYLCV symptoms, compared to nearly 100% of the nonmulched control plants. At 48 DAG, 20% of the mulched plants showed TYLCV symptoms, and by 58 DAG incidence of symptomatic plants rose abruptly to 60% TYLCV infection, which was clearly better than the nonmulched control plants, but still unacceptable for the grower. It should be noted that only the yellow mulch, without any application of insecticides, protected the plants. Hence, it was concluded that the protection effect of the yellow mulch lasted about 3–5 weeks after transplanting, which is usually long enough to protect tomato plants during their critical period of susceptibility to begomovirus infection (Levy & Lapidot, 2008; Schuster, Stansly, & Polston, 1996). The effect of the yellow mulch decreases with time probably due to the increase over time of the ratio of plant canopy to mulch.

The controlling effect of yellow mulch is due to a combination of the whitefly's attraction to the yellow color of the mulch and its subsequent death due to dehydration induced by the high temperature of the mulch (Cohen, 1982; Cohen & Lapidot, 2007). It should be noted that the typical Israeli climate is semiarid—high temperature and low humidity. In the tomato-growing regions, soil temperatures exceeding 30 °C are quite common. It was demonstrated that at temperatures above 30 °C, in low-humidity conditions, whiteflies not feeding on a plant dehydrate within an hour (Cohen, 1982).

Another explanation for the effect of yellow mulch comes from the observation that many flying insects, including whiteflies, have higher

landing rates on green-yellow surfaces. Landing induces probing in an attempt to feed, at which time the insect discriminates between "appropriate" and "inappropriate" hosts. If the host is inappropriate, as in the case of plastic mulch, the insect flies a short distance, lands, and probes again. After a number of such inappropriate landings, the insect is likely to fly away entirely (Finch & Collier, 2000; Hilje, Costa, & Stansly, 2001).

Reflective mulch—The successful use of reflective plastic mulch to delay the onset of whitefly infestations and infection by whitefly-transmitted viruses in open-field production is well established (Polston & Lapidot, 2007; Simmons, Kousik, & Levi, 2010; Smith, Koenig, McAuslane, & McSorley, 2000; Summers & Stapleton, 2002). The most effective reflective mulches are entirely or partially aluminized and reflect a lot of daylight. These are believed to reflect both visible and UV light which disorients whiteflies and decreases the landing rate of whiteflies on plants in the field. Like other mulches, the effectiveness decreases as the plant canopy increases and the mulch is covered. Reflective mulches are effective even when whitefly populations are expected to be high. Like the yellow mulch, this approach has the added benefit of interfering with other virus vectors (aphids and thrips), and also affects plant growth and increases yield, especially in cucurbits, which seem to grow better with the light reflected from the mulch (Greer & Dole, 2003). One negative aspect of reflective mulches is the discomfort that it can generate to humans working in the fields. The light can be nearly blinding, and the amount of heat reflected from the mulch makes working in the field nearly intolerable.

Interestingly, while reflective mulches were found to be highly effective in Florida in delaying whitefly infestation and reducing infection rate of tomato plants by the whitefly-transmitted *Tomato mottle virus*, yellow mulches were found to be less effective (Csizinszky, Schuster, & Kring, 1997; Csizinszky, Schuster, & Polston, 1999). The reason for this may be due to the very high level of humidity in Florida. Whiteflies, which were attracted to the yellow mulch probably were not dehydrated as quickly in Florida as they were in Israel, where relative humidity is much lower. Whiteflies attracted to the yellow mulch in Florida were still able to fly to a host plant and feed on it. In a climate with high relative humidity, the yellow mulch may actually attract whiteflies to the crop rather than protect it from whiteflies.

UV-reflective mulch has been used very successfully to reduce incidences of whiteflies and the whitefly-transmitted *Cucurbit leaf crumple virus* (CuLCrV) in zucchini squash (*Cucurbita pepo* L.) (Nyoike, Liburd, & Webb, 2008).

The reflective mulch was used with or without the systemic insecticide imidacloprid. It was found that the reflective mulch alone provided equal protection to squash plants against CuLCrV as did mulch combined with imidacloprid treatment. Hence, since no additional benefits were derived from combining reflective mulch with imidacloprid, it was suggested that the reflective mulch could be used on its own.

4.2. Virus-free seed/planting material

Planting seed or vegetatively propagated planting material that is free of viruses provides a crop with the optimal start to its growth cycle. Vegetatively propagated crops are particularly vulnerable to virus infection, as described in the part of this volume in which they are reviewed. Cassava and sweet potato are the two crops in this category that are most affected by whitefly-transmitted viruses. In sweet potato, which is more widely grown in developed and middle income countries, tissue culture is frequently used for the production of virus-free "seed," and tissue culture with virus indexing is now routinely used throughout growing areas of the United States in foundation seed programs (Clark et al., 2012). In Shangdong Province of China, the country which is the world's largest producer of sweet potato, there has been great success in farmer adoption of virus-free stocks of planting material. An impact assessment of this program demonstrated that more than 80% of the Province's growers were using virus-free seed by the end of a promotional program (Fuglie, Zhang, Salazar, & Walker, 1998). In cassava, tissue culture and virus indexing with thermotherapy has been routinely used for many years as a means of ensuring that germplasm exchanged between continents is free of virus (Frison, 1994). However, it is only recently that these approaches have been used at lower levels of country or region for the provision of virus-free tissue culture plantlets to large-scale "basic seed" producers. Pilot schemes are currently operating in several countries in Africa to develop formalized seed systems that incorporate the production of virus-free seed through tissue culture and certification standards for quality control at the various stages of planting material propagation (Yabeja, Mtunda, Shirima, Kanju, & Legg, 2013).

4.3. Crop placement—In space

Since whiteflies can fly over distances of several kilometers (Blackmer & Byrne, 1993; Cohen, Kern, Harpaz, & Ben Joseph, 1988), and many of

the most important viruses that they transmit are persistent or semi-persistent (Duffus, 1987), new crops planted in proximity to older crops that are infested with whiteflies are vulnerable to being infected by viruses present in the neighboring older fields. Direct relationships between the levels of virus inoculum in surrounding fields and final incidences of virus disease recorded in test plots of the same crop have been demonstrated for both sweet potato (Aritua, Legg, Smit, & Gibson, 1999) and cassava (Legg et al., 1997). In order to minimize the risk of contamination of a new crop from external sources, it is necessary to locate the crop either at a site that is isolated from other infection sources, or that is upwind of the inoculum source (in an environment where there is a consistent prevailing wind). In the southwestern states of the United States, growers avoid planting cotton in close proximity to spring melons for this reason, and similarly, ensure that fall melons or vegetables are not planted too close to cotton (Ellsworth & Martinez-Carrillo, 2001). In cassava, the density of cultivation has been highlighted as a contributing factor to the rapid spread of cassava begomoviruses (Bock, 1994), as has the significance of prevailing wind direction on patterns of spread of these viruses into initially healthy crops (Fargette, Fauquet, Grenier, & Thresh, 1990). "Clean seed" programs for cassava in Tanzania make use of isolated, high elevation sites for pre-basic seed propagation in order to minimize the likelihood of infection by the whitefly-transmitted begomoviruses and CBSVs (Yabeja et al., 2013).

4.4. Crop placement—In time

Patterns of whitefly population increase and decline depend upon several environmental factors, the most important of which are the availability of hosts—determined by the date of planting—and the climatic variables of temperature and precipitation. In general, whiteflies are more abundant during periods of warm weather during which there is active crop growth (resulting from adequate soil moisture) as well as when crop host plants are young and rapidly growing. By careful manipulation of planting dates, therefore, it is often possible to reduce whitefly populations and the resulting incidence of the viruses that they transmit, although this should not be done in a way that makes growing conditions unfavorable for the crop. Mohamed (2012), working on cucurbits in Egypt, observed that using optimal combinations of variety, plant spacing and planting date could result in up to 20-fold reduction in *B. tabaci* populations. In the dry areas of northern Mexico, local regulations governing dates for planting and harvesting

cotton, and enforcing host-free periods were successful in reducing pressure from whitefly populations, although these measures needed to be combined with the strategic but restrained use of insecticides (Ellsworth & Martinez-Carrillo, 2001). In cassava crops in West Africa, rapid increases in cassava mosaic disease (CMD) incidence were recorded in fields between November and June, while the rate of disease increase was much lower from July to October. Seventy percent of this variation could be attributed to whitefly vector numbers, temperature and radiation (Fargette, Jeger, Fauquet, & Fishpool, 1993). Similarly, in Uganda CMD spread was most rapid at one location in March/April, while at two others it was greatest in September/October (Legg, 1995). These patterns offer opportunities to reduce whitefly abundance and consequent virus spread through planting at times of the year when early vigorous stages of crop growth do not correspond with the period during which whiteflies are most abundant.

4.5. Trap crops

Traps crops have been shown to be effective in reducing populations of whiteflies, and therefore reducing the level of virus infection. In tomatoes in the south-eastern USA, squash planted around tomatoes acted as a trap crop, since whiteflies were more attracted to the squash plants than they were to the tomatoes (Schuster, 2004). Significant reductions in the abundance of *B. tabaci* whitefly adults in tomatoes surrounded by squash, compared with no-squash controls led to important reductions in the incidence of TYLCV in the "protected" tomato crop. There are numerous other examples, which while not relating directly to whitefly-transmitted viruses, nevertheless illustrate the potential benefit provided by trap crops for managing whitefly populations. *B. tabaci* has been shown to settle preferentially on cantaloupes in comparison with cotton (Castle, 2006). In leaf assays, there was a 67% preference for cantaloupes, which rose to 90% in full plant assays. When cantaloupes were planted around cotton crops, populations of eggs and early-stage nymphs on cantaloupe were more than 10 times those in the cotton for 9 out of 12 sampling dates through the season. However, the trap crop effect was not sufficient to prevent the action threshold from being reached. This fact highlights a general feature of cultural practices: they are seldom able to keep whitefly populations below threshold levels and similarly are rarely able to prevent virus transmission when applied in the absence of other "supporting" control measures (Castle, 2006). This is particularly true for whitefly-transmitted viruses, since a population of whiteflies that causes 100% virus infection may be

significantly below a density that would cause physical damage. Tolerance levels for virus-transmitting whiteflies are much lower than those that only cause direct or indirect physical damage.

4.6. Intercropping

Mixtures of crops are not usually cultivated together in commercial agricultural environments. However, mixing crops together in a single field is a common practice in subsistence agricultural systems in developing countries. Breaking up a crop environment typically makes it less readily colonized by weak-flying sucking pests such as whiteflies, and this probably explains why many of the major whitefly outbreaks have been in large-scale commercial production situations. Several experimental examples illustrate the potential benefits of intercropping as a control measure for whiteflies. In Egypt, maize either intercropped or rotated with cucumber, tomato, or squash resulted in lower whitefly abundances in the vegetable crops and significantly lower incidences of CVYV in cucumber, *Squash leaf curl virus* (begomovirus) in squash, or TYLCV in tomato (Abd-Rabou & Simmons, 2012). In zucchini on Hawaii, both okra and sunnhemp planted as intercrops with zucchini resulted in significantly reduced *B. tabaci* whitefly populations, although these reductions did not result in significant yield differences when compared with monocrop controls (Manandhar, Hooks, & Wright, 2009). For cassava in Africa, intercropping experiments have been undertaken in West, Central and East Africa at various times in the last three decades. Mixing cassava with maize in Ivory Coast resulted in modest reductions in CMD incidence with some of the planting schemes tested (Fargette & Fauquet, 1988), and similar results were obtained with both maize and cowpea in Cameroon (Fondong, Thresh, & Zok, 2002). Since some intercrop planting arrangements "worked" while others—using the same intercrop—did not, it has proven difficult to disseminate intercropping extension messages that would be readily understood, and therefore adopted, by growers. This further highlights one of the difficulties in disseminating cultural control technologies—they are relatively knowledge intensive and require the input of substantial training efforts from public extension agencies.

4.7. Physical barriers

Crop colonization by whiteflies, and the virus transmission that may follow, can be hindered by placing physical barriers between flying whiteflies and the crop host plants that they seek. The usual ways of achieving this are

through either temporary or permanent protection. Permanent protection, usually done by enclosing crop plants in permanent or semi-permanent insect-proof housing, is most appropriate for high value crops that are grown on a relatively small scale. For crops grown at a larger scale, where only temporary protection is sufficient, floating row covers or tunnels may be used. In permanent screenhouses, mesh can be used that excludes whiteflies and yet allows aphelinid parasitoids to enter, thereby promoting biological control. Screenhouses are used on a massive scale in the vegetable production zones of southern Europe, most famously including the "visible-from-space" expanse of plastic housing at Almeria, in southern Spain. In addition to providing good overall growing conditions for vegetables produced, the physical protection offered by this housing helps to reduce movement of whiteflies between crops and consequent virus spread. Integrated control strategies that combine protection of crops in screenhouses with biological control have resulted in drastic cuts in the levels of insecticide usage, while at the same time providing a more sustainable solution to the management of whitefly-transmitted viruses. In smaller scale, subsistence-oriented production systems, net tunnels constructed with locally available materials have been piloted for the protection of virus-free sweet potato planting material (Anon, 2012). Experiments conducted in Kenya have shown that over a period of 33 months, the use of these net tunnels led to increases in production and income of >100% (Anon, 2012). For an extended review on physical barriers, please see Chapter 1.

4.8. Physical traps

Whitefly populations can be reduced by physically removing these insects from the air space around crop plants in either protected- or open-field situations. The effect is clearly enhanced through the use of an attractant, which is typically the visual cue of the yellow color. Yellow sticky traps, that attract then kill whiteflies, have mainly been used for monitoring populations of the winged adults (Fishpool & Burban, 1994). In confined areas, such as screenhouses, where the air space is limited, it is possible for such traps to have a significant impact in reducing the overall whitefly population, thereby helping to control virus disease (Xi-Shu et al., 2008). In addition to demonstrating the large beneficial effect of the combined use of yellow sticky traps and biological control using the parasitoid *Eretmocerus* nr. *rajasthanicus*, Xi-Shu et al. (2008) also demonstrated that traps placed parallel to rows of tomato plants caught many more whiteflies than

traps oriented perpendicular to the rows. While the benefits of sticky traps in protected environments have been shown (Lu, Bei, & Zhang, 2012), this same study demonstrated the absence of any significant beneficial effect in field-grown crops.

4.9. Conclusions

A detailed review of cultural control for *B. tabaci* whiteflies (Hilje et al., 2001) noted that there has been a disproportionately small amount of attention given to these approaches, while observing that this is likely a reflection of the difficulty of implementation of some of these measures. Cultural control tactics, such as managing planting dates, rotation systems or crop-free periods require a high degree of local coordination among growers, which is very often difficult to achieve. Other methods such as intercropping or the use of trap crops require substantial changes to the production system. Many successes have nevertheless been achieved, with the most significant coming from the physical protection of crops by using tunnels or screenhouses, isolation of fields, and from the use of virus-free seed. Even where the impacts of specific cultural control tactics are insufficient on their own to control whiteflies and whitefly-transmitted viruses, they may still play an important role in integrated control systems. Consequently, continued research to identify, enhance and implement these approaches within the context of integrated control programs is strongly merited.

5. GENETIC RESISTANCE

Genetic resistance in the host plant is considered highly effective in the defense against viral infection in the field. This is especially true for those viruses that have prolific vectors which can rapidly produce very high populations in the field and are hard to contain. Genetic resistance requires neither environmentally hazardous chemical application nor plant seclusion and can potentially be stable and long lasting. A disadvantage, however, is that genetic resistance requires the identification of resistance loci which are not always available, and in many cases are identified in wild species. Interspecific crossing programs for introgressing resistance from wild species into crop relatives can be long and laborious.

This section will cover issues essential for the development of resistance, such as the development of controlled procedures for inoculation by whiteflies, optimal plant age for resistance screening, breeding for virus resistance, the effect of virus-resistant genotypes on virus epidemiology and more;

elements that are related to all whitefly-transmitted viruses. However, due to the impact of the diseases induced by TYLCV, and to the large body of research and publications available for this virus, this section will emphasize genetic resistance to TYLCV which can be viewed as an example relevant to other whitefly-transmitted viruses.

5.1. Tomato yellow leaf curl virus

TYLCV, a monopartite begomovirus (family *Geminiviridae*) is one of the most devastating viruses in tomatoes in many tropical and subtropical regions worldwide (Lapidot & Friedmann, 2002; Moriones & Navas-Castillo, 2000; Navas-Castillo et al., 2011). Like all begomoviruses, TYLCV is transmitted by the whitefly *B. tabaci* in a circulative and persistent manner (Cohen & Harpaz, 1964; Rubinstein & Czosnek, 1997).

The viral circular ssDNA genome of nearly 2.8 kb contains six open reading frames (ORFs) that are organized directionally, two in the sense orientation and four in the complementary orientation (Gafni, 2003; Gronenborn, 2007; Lapidot & Polston, 2006). The bidirectional ORFs are separated by a ~250-bp intergenic region that contains elements for replication and bidirectional transcription (Gronenborn, 2007; Gutierrez, 1999; Hanley-Bowdoin, Settlage, Orozco, Nagar, & Robertson, 1999; Petty, Coutts, & Buck, 1988).

On the complementary strand, the *C1* gene encodes Rep (replication-associated protein) which is a multifunctional protein involved in viral replication and transcriptional regulation. This is the only viral protein absolutely required for viral replication (Gronenborn, 2007). The *C2* gene encodes TrAP(transcriptional activator protein), which enhances expression of the coat protein, and plays a role in the suppression of host defense responses as well as in viral systemic infection (Bisaro, 2006; Brough, Sunter, Gardiner, & Bisaro, 1992; Etessami, Saunders, Watts, & Stanley, 1991). The *C3* gene encodes the REn (replication enhancer protein) which acts by enhancing viral DNA accumulation in infected plants and interacts with Rep (Sunter, Hartitz, Hormuzdi, Brough, & Bisaro, 1990). The *C4* gene which is embedded within the *C1* gene, but in a different ORF, is implicated in viral pathogenicity and movement (Jupin, De Kouchkovsky, Jouanneau, & Gronenborn, 1994; Rigden, Krake, Rezaian, & Dry, 1994).

On the sense strand, the capsid protein encoded by *V1* is required for whitefly transmission, binds to viral ssDNA, may play a role in systemic

movement, and acts as a nuclear shuttle protein that mediates movement of viral nucleic acid into the host-cell nucleus (Azzam et al., 1994; Briddon, Pinner, Stanley, & Markham, 1990; Kunik, Palanichelvam, Czosnek, Citovsky, & Gafni, 1998; Palanichelvam, Kunik, Citovsky, & Gafni, 1998; Rojas et al., 2001). The product of the *V2* ORF is involved in viral movement (Rojas et al., 2001; Wartig et al., 1997) and has been shown to act as a suppressor of RNA silencing (Zrachya et al., 2007).

TYLCV induces severe yield losses in tomato, which, depending on the age of the plant at the time of infection, can reach 100% (Lapidot et al., 1997; Levy & Lapidot, 2008). Two to three weeks after inoculation, the infected tomato plant displays pronounced disease symptoms that include upward cupping of the leaves, chlorosis of the leaf margins and severe stunting of the entire plant. In many tomato-growing areas, TYLCV has become the limiting factor for production of both open-field and protected cultivation systems (Lapidot & Friedmann, 2002).

TYLCV was first detected and identified in the northern part of Israel, following an outbreak of a new disease in tomatoes in 1959 (Cohen & Harpaz, 1964; Cohen & Lapidot, 2007). Similar disease symptoms associated with high populations of whiteflies were observed on tomatoes grown in the Jordan Valley in the late 1930s (Avidov, 1946). The outbreaks of tomato yellow leaf curl disease (TYLCD), which were sporadic in the 1960s, became a serious economic problem and by end of the 1970s, all tomato-growing regions in the eastern Mediterranean basin were affected by TYLCD (Hanssen & Lapidot, 2012). In the late 1980s, TYLCV particles were isolated and the virus was cloned and sequenced (GenBank accession no. X15656) and found to be a monopartite begomovirus (Navot, Pichersky, Zeidan, Zamir, & Czosnek, 1991). Shortly thereafter, another Mediterranean viral strain inducing TYLCD was cloned and sequenced—*Tomato yellow leaf curl Sardinia virus* (TYLCSV; GenBank accession no. X61153) (Kheyr-Pour et al., 1991). Over the years, especially with the advent of sequencing as a routine procedure, it became apparent that the name TYLCV had been given to a heterogeneous group of more than 10 virus species and their strains, all of which induce very similar disease symptoms in tomato (Moriones & Navas-Castillo, 2000; Navas-Castillo et al., 2011).

TYLCV, most probably emerged from the eastern Mediterranean, spread westward, and subsequently became recognized as a tomato pathogen throughout the Mediterranean basin (Cohen & Lapidot, 2007; Czosnek & Laterrot, 1997; Hanssen & Lapidot, 2012; Hanssen, Lapidot, & Thomma,

2010; Lefeuvre et al., 2010; Navas-Castillo et al., 2011). The disease continued to spread westward into the Caribbean, Central and North America, and eastward toward China, Japan, and Australia. Today, it is present in most tomato-growing areas worldwide (Lefeuvre et al., 2010; Navas-Castillo et al., 2011).

It should be noted that although TYLCV is primarily known as a pathogen of tomato, the virus can infect other agricultural plants. TYLCV induces severe symptoms in common bean (*Phaseolus vulgaris* L.) (Cohen & Antignus, 1994), the cut-flower lisianthus (*Eustoma grandiflorum*) (Cohen et al., 1995), while pepper (*Capsicum annuum*) was found to be a symptomless host of the virus (Morilla et al., 2005; Polston, Cohen, Sherwood, Ben-Joseph, & Lapidot, 2006).

5.2. Development of a controlled whitefly-mediated inoculation system

To succeed in a breeding program whose aim is to develop resistant cultivars to a virus, or any other pathogen for that matter, one must develop an accurate and reliable mass inoculation and selection system. Since many of the whitefly-transmitted viruses are only poorly if at all transmitted mechanically, it is essential to develop whitefly-mediated inoculation protocols, which will ensure high (preferably 100%) infection rates, and a standardized (as much as possible) inoculum pressure (for a review, see Lapidot, 2007).

Development of a whitefly-mediated inoculation system requires rearing of whiteflies. It requires a dedicated rearing facility suitable for rearing whiteflies on the one hand, but secluded so other insects do not penetrate and whiteflies do not escape. Polston and Capobianco (2013) present a detailed explanation of the conditions and considerations in rearing whiteflies for virus transmission. Maintenance of such a rearing facility is time consuming. Since whitefly populations reach very high numbers in the field, why not rely on spontaneous field inoculation? Surprisingly, spontaneous field infection has been shown to be largely inefficient, as many plants escape infection, even under heavy inoculation pressure (Vidavsky et al., 1998). Following planting of susceptible tomato plants in an area stricken with whiteflies and TYLCV, only 50% of the susceptible tomato plants were infected during the first month after planting. Despite high whitefly populations and available viral inoculum, 10% of the susceptible plants had escaped infection even 90 days after transplanting (Vidavsky et al., 1998). In another study, the percentage of viruliferous whiteflies in the general whitefly population in the field was found to be rather low

(Cohen et al., 1988). Depending on the TYLCV-susceptible host from which the whiteflies were collected, only 3–6% of the whiteflies collected in the field were able to transmit the virus (Cohen et al., 1988).

Spontaneous field inoculation has other disadvantages besides promoting inoculation escapees: field inoculation may lead to milder disease symptoms compared to controlled inoculation, probably due to late and unsynchronized infection. Pico, Diez, and Nuez (1998) assayed cultivated and wild tomato accessions for their resistance to TYLCV. They compared controlled whitefly inoculation with cage inoculation and with spontaneous field inoculation. It was concluded that the response of a resistant source to TYLCV may vary with the inoculation technique used and that controlled greenhouse inoculation corresponded to high inoculum levels, while spontaneous field inoculation corresponded to low inoculum levels. However, despite the low and delayed disease incidence following spontaneous field inoculation, it was possible to discard the most susceptible genotypes with field testing (Pico et al., 1998).

Another problem with spontaneous field inoculation is that there are other pathogens in the field, so a specific virus-resistant plant may become infected by an unrelated virus, or any other pathogen, and erroneously be considered susceptible. For evaluation of resistance to TYLCV in areas where diverse begomoviruses are present, this can be a serious concern. In field inoculation, the whitefly pressure, intensity of inoculation, level of viral inoculum, and plant age at time of inoculation are all unknown and variable. The elapsed time between whitefly acquisition and transmission of the virus is also unknown with regard to its impact in field inoculation. Whiteflies transmit begomoviruses in a persistent, circulative manner. However, it has been shown for a number of begomoviruses including TYLCV that although transmission may continue for the life span of the vector, transmission efficiency declines with time, which is clearly the case for the semi-persistent transmitted crini- and ipomoviruses (Caciagli et al., 1995; Cohen, Duffus, Larsen, Liu, & Flock, 1983; Cohen & Harpaz, 1964; Navas-Castillo et al., 2011; Rubinstein & Czosnek, 1997). Thus, the efficiency of spontaneous field inoculation is unknown and hence not reproducible.

5.3. When should we inoculate?

Another obstacle in the development of TYLCV (as well as other virus) resistance has been the lack of a standard method for the assessment of

resistance (Lapidot, Ben Joseph, Cohen, Machbash, & Levy, 2006). Variability in assay conditions has led to contradictory results, where different resistance levels have been attributed to the same genetic sources (Pico et al., 1998; Vidavsky et al., 1998). The response of a plant to infection by a pathogen may be affected by test conditions such as temperature, light, growth conditions, inoculation pressure, and plant age (or developmental stage) at the time of infection. This latter phenomenon has been referred to as age-related or mature-plant resistance (Loebenstein, 1972). In some instances, it has been shown that mature plants resist or tolerate virus infection much better than plants infected at an early stage of development, leading to what appears (erroneously) to be increased viral resistance (Garcia-Ruiz & Murphy, 2001; Levy & Lapidot, 2008; Moriones, Aramburu, Riudavets, Arno, & Lavina, 1998).

To determine the effects of plant age on the expression of genetic resistance to TYLCV, tomato plants expressing different levels of resistance to TYLCV were inoculated at three different ages—14, 28, and 45 days after sowing (DAS). Resistance was assayed mainly by comparing yield components of inoculated plants to those of control, noninoculated plants of the same line or variety (Levy & Lapidot, 2008). It was found that plant age at inoculation had no effect on disease severity scores of the susceptible varieties, and little or no effect on those of the resistant varieties. In contrast, plant age at inoculation had a significant effect on the yield of all varieties tested. All the varieties suffered a significant yield reduction due to inoculation with TYLCV, but the older the plant was at time of inoculation, the TYLCV-induced yield reduction became smaller. Hence, it was concluded that there is an age-related (or mature-plant) resistance in tomato plants to TYLCV, regardless whether the tomato plants tested were susceptible or resistant to the virus.

The occurrence of age-related resistance raised another question—what is the optimal age for inoculation of the tomato plants when screening for TYLCV resistance? This may depend on the genetic material being screened: if segregating populations are being screened for individual resistant plants, then it is best to inoculate at the earliest possible stage, when the effect of the viral infection is most severe. This way the selected plants will indeed be those expressing the highest level of resistance. If, on the other hand, commercial hybrids are being tested for level of resistance, then inoculation at 28 DAS may be most suitable as most commercial tomato plants are sown in specialized and protected nurseries and transplanted to the field about 28 days later. Thus, from an agricultural point of view, 28 DAS may be

the most appropriate stage for testing commercial hybrids as it mimics inoculation just following transplanting to the field.

5.4. Breeding tomatoes (*Solanum lycopersicum*) for resistance to TYLCV

There have been prolonged efforts to breed tomato cultivars resistant to TYLCV. Since all cultivated tomato accessions at the time were found to be extremely susceptible to the virus, wild tomato species were screened for their response to the virus in order to identify and introgress genes controlling resistance (Ji, Scott, Hanson, Graham, & Maxwell, 2007, reviewed in Lapidot & Friedmann, 2002; Lapidot & Polston, 2006; Vidavsky, 2007). Thus, breeding programs have been based on the introgression of resistance genes from accessions of wild origin into the cultivated tomato. Progress in breeding for TYLCV resistance has been slow, mainly due to the complex genetics of the resistance, the interspecific barriers between the wild and domesticated tomato species, and the need for a reliable screen for resistance to the virus (Ji, Scott, et al., 2007; Lapidot, 2007; Vidavsky, 2007). In spite of these challenges, TYLCV-resistant commercial tomato cultivars are available today from several seed companies.

Sources of resistance to TYLCV have been identified and introgressed from several wild tomato species, including: *Solanum pimpinellifolium*, *S. peruvianum*, *S. chilense*, and *S. habrochaites*. However, until now only five major resistance loci, termed *Ty-1* to *ty-5*, have been characterized and mapped to the tomato genome using molecular DNA markers (Ji, Scott, et al., 2007).

Resistance introgressed from *S. chilense* accession LA1969 was found to be controlled by a major partial dominant gene, termed *Ty-1*, and at least two additional modifier genes (Zamir et al., 1994). *Ty-1* was mapped to the top of chromosome 6, while the two modifiers were mapped to chromosomes 3 and 7 (Zamir et al., 1994). To the best of our knowledge, *Ty-1* is the most utilized TYLCV-resistance locus in tomato breeding programs worldwide, and most TYLCV-resistant commercial hybrids available today carry this locus.

Hanson et al. (2000) analyzed the resistant line H24, which contains resistance introgressed from accession B6013 of *S. habrochaites* (Kalloo & Banerjee, 1990). The authors screened resistant plants using what at the time they thought were three different isolates of TYLCV. It was however later found that those viral isolates were in fact three isolates of *Tomato leaf curl virus* and not TYLCV. The resistance that was found to be dominant was mapped

to the bottom of chromosome 11, and was termed *Ty-2* (Hanson, Green, & Kuo, 2006).

A major partially dominant gene, which was introgressed from *S. chilense* accessions LA2779 and LA1932, was mapped to chromosome 6 and was termed *Ty-3* (Ji, Schuster, & Scott, 2007; Ji & Scott, 2006). The introgression derived from LA2779 was found also to contain *Ty-1*, suggesting a linkage between *Ty-1* and *Ty-3* (Ji, Schuster, et al., 2007). Indeed, in a recent study, it was shown that *Ty-1* and *Ty-3* are allelic, and that *Ty-1/Ty-3* code for an RNA-dependent RNA polymerase, suggesting that the resistance induced by these loci is via RNA silencing (Verlaan et al., 2011, 2013). The detailed mechanism of how TYLCV-resistance is mediated by *Ty-1/Ty-3* has yet to be elucidated.

Ty-4 was introgressed from *S. chilense* LA1932 and has been mapped to the long arm of chromosome 3. This locus is considered to be a minor one as it only accounted for 16% of the resistance when combined with *Ty-3* (Ji, Scott, Schuster, & Maxwell, 2009).

The TYLCV-resistant line TY172, carrying *Ty-5*, is thought to be derived from four different accessions formerly assigned as *S. peruvianum*: PI 126926, PI 126930, PI 390681, and LA0441 (Friedmann, Lapidot, Cohen, & Pilowsky, 1998). LA0441 was later subclassified as *S. arcanum* (Peralta, Knapp, & Spooner, 2005). TY172 is highly resistant to TYLCV: it produces minimal symptoms following infection and allows only low levels of viral DNA, and exhibited the highest level of resistance in a field trial which compared yield components of various resistant accessions following inoculation with TYLCV (Friedmann et al., 1998; Lapidot et al., 1997). Classical genetic studies have suggested that the resistance in TY172 is controlled by three genes exerting a partially dominant effect (Friedmann et al., 1998). Gene mapping showed that the resistance in TY172 was controlled by a previously unknown major recessive QTL, and four additional minor QTLs (Anbinder et al., 2009). The major QTL was mapped to chromosome 4 and was designated *Ty-5*.

Recently, the recessive resistance in the old commercial cultivar Tyking (Royal Sluis, The Netherlands) has been shown to colocalize with the resistance in TY172 (Hutton, Scott, & Schuster, 2012). The authors suggested that since one of the populations used by Anbinder et al. (2009) also showed recessive gene action that the locus in TY172 should therefore be renamed *ty-5*. Resistance derived from the cultivar Tyking has been used in many breeding programs. Interestingly, Bian et al. (2007) determined that resistance in the tomato line Fla. 653 was controlled by a recessive allele termed

tgr-1. Fla. 653 has resistance derived from "Tyking" and is homozygous for *ty-5* (Hutton et al., 2012). In another study, Giordano, Silva-Lobo, Santana, Fonseca, and Boiteux (2005) also identified a recessive allele (termed *tcm-1*) derived from Tyking that was effective against bipartite begomoviruses. Hence, Hutton et al. (2012) hypothesized that both *tgr-1* and *tcm-1* describe the *ty-5* allele from Tyking, and speculated that this allele was introgressed from *S. peruvianum*.

5.5. Effect of TYLCV-resistant genotypes on virus epidemiology

As the use of TYLCV-resistant tomato cultivars in open-field cultivation becomes a common practice, the need to assess the potential effect of resistant varieties in TYLCV epidemiology becomes apparent. The potential of TYLCV-infected resistant genotypes to serve as virus reservoirs was studied in a greenhouse study (Lapidot, Friedmann, Pilowsky, Ben Joseph, & Cohen, 2001), and more recently in a field study (Srinivasan, Riley, Diffie, Sparks, & Adkins, 2012). In the first study, four different tomato genotypes exhibiting different levels of TYLCV resistance, ranging from fully susceptible to highly resistant, served as TYLCV-infected source plants. The survival and TYLCV acquisition and transmission rates for whiteflies having fed on the different infected tomato genotypes were examined.

Whitefly survival rates following feeding on the different source plants at 21 days postinoculation (DPI), shortly after the appearance of disease symptoms, were similar regardless of the plant genotype from which the virus was acquired. Significant differences in whitefly survival rates were found after whiteflies had fed on the infected source plants at 35 DPI, with the whitefly survival rate increasing with higher levels of resistance displayed by the source plant. This may have been due to the deleterious effect of TYLCV on the infected plant. At 35 DPI, the susceptible and moderately resistant genotypes exhibited pronounced disease symptoms, presumably making the plant less suitable for whitefly feeding. In contrast, the highly resistant genotypes hardly showed any disease symptoms, which would favor whitefly survival (Lapidot et al., 2001).

The TYLCV level in the whiteflies following feeding could be directly correlated to the virus level in the source plant: the higher the level in the source plant, the higher the TYLCV level in the whitefly. This correlation was the same, regardless of the time of feeding—21 or 35 DPI—and regardless of the state of the source plants. The severity of disease symptoms exhibited by the source plants did not seem to affect TYLCV acquisition by the whiteflies.

The transmission rate of whiteflies that had fed on infected source plants at 21 DPI was negatively correlated with the level of resistance displayed by the source plant. Therefore, the higher the resistance, the lower the transmission rate. However, at 35 DPI, transmission rates from the susceptible plants were lowest, presumably due to their poor condition. Transmission rates from source plants displaying a medium level of resistance were highest, with rates declining following feeding on source plants displaying higher levels of TYLCV resistance (Lapidot et al., 2001).

Based on these results, the authors postulated that a TYLCV-infected field of susceptible tomato plants might serve as a high-risk virus reservoir early after infection. However, as the plants deteriorate due to expression of disease symptoms, the potential of these plants to serve as a virus source declines. In contrast, a field of moderately resistant plants might serve as an effective virus reservoir throughout the season as plants do not deteriorate as badly as the susceptible genotypes. However, following infection in the field, highly resistant tomato genotypes pose the lowest risk to surrounding plants in terms of outbreaks of viral epidemics (Lapidot et al., 2001).

In the second study, Srinivasan et al. (2012) evaluated the effect of four different TYLCV-resistant and two susceptible commercial hybrids on whitefly population and TYLCV acquisition and transmission in the field, as well as in a greenhouse study. The different genotypes were evaluated in the field in two consecutive years. It was found that although whitefly populations in the field were not uniformly distributed, the different tomato genotypes exhibited minor differences in their ability to support whitefly populations. TYLCV-infection rate in the field was also the same among the different tomato genotypes, although the susceptible genotypes showed severe symptoms while most of the resistant genotypes showed no disease symptoms. TYLCV levels in whiteflies following acquisition from resistant genotypes were lower than from susceptible genotypes. These observations are consistent with the earlier study by Lapidot et al. (2001). However, in contrast to the earlier study, transmission rates following TYLCV acquisition from the different resistant and susceptible genotypes were the same—transmission ranged from 55% to 85% but the differences were not statistically significant (Srinivasan et al., 2012). There were a number of differences in the execution of the experiments between the two studies, but the main one was that while Lapidot et al. (2001) used a single whitefly per plant in the transmission experiments, Srinivasan et al. (2012) used 20 whiteflies per plant. This and other differences in experimental procedure could easily account for the differences in results. Nevertheless, Srinivasan

et al. (2012) argued that their results demonstrate that under conditions of heavy inoculum and high vector pressure, similar to field conditions in many instances, TYLCV acquisition from resistant genotypes may result in efficient transmission to susceptible ones. Hence, they argue that tomato genotypes with a high level of TYLCV-resistance do not pose a lower risk to surrounding plants in the field (Srinivasan et al., 2012).

5.6. Bean (*P. vulgaris*) resistance to TYLCV

In 1997, an outbreak of an unknown disease in common bean (*P. vulgaris*) that caused severe losses was reported in Southern Spain (Navas-Castillo, Sanchez-Campos, & Diaz, 1999). The incidences of the unknown disease reached 80% in some fields. Symptoms consisted of downward curling, crumpling, thickening and elongation of leaves, and severe stunting of the plant. When infected early, plants showed dramatic stunting and abortion of new inflorescences, and production was entirely lost. It was soon discovered that causal agent of the disease was TYLCV. Moreover, since beans were used in Spain as an intercrop between tomato seasons, the bean plants served as a TYLCV reservoir and caused an increase in TYLCV epidemics in the tomatoes that were planted following the bean harvest (Sanchez Campos et al., 1999). It was concluded that there is a need for TYLCV-resistant bean cultivars (Navas-Castillo et al., 1999).

In Israel, it has been known for quite some time that common bean is susceptible to infection by TYLCV (Cohen & Antignus, 1994). Still, there have been no reports in Israel of TYLCV epidemics in beans, despite the fact that beans are grown in Israel and that TYLCV and its whitefly vector are present in all agricultural areas of the country. The major bean season in Israel is in early spring, thus, beans are planted and harvested before the build-up of large whitefly populations (see Section 4.4). However, this by itself does not seem to explain the lack of TYLCV epidemics in bean. It was postulated that the bean varieties being used by the growers were not susceptible to the virus. Hence, commercial varieties of common bean were screened for resistance to TYLCV (Lapidot, 2002). Out of the 42 varieties that were tested, 24 were found to be susceptible: the plants exhibited severe symptoms and accumulated high levels of viral DNA. Eighteen varieties were found to be resistant to the virus: one variety showed mild symptoms, while 17 showed no symptoms following inoculation. From the 17 symptomless varieties, plants of three varieties contained viral DNA while no viral DNA was detected in the plants of the other 14 varieties.

According to companies selling bean seeds, the two most popular bean varieties grown in Israel were found to be resistant to TYLCV (Lapidot, 2002). This may explain their popularity as well as the freedom from TYLCV epidemics in bean in Israel.

When the effect of bean plant age on viral inoculation by whiteflies was assayed, it was found that the success rate of TYLCV infection was highly dependent on bean plant age with the highest infection rates occurring in 14-day-old plants. Infection rates decreased when the inoculated plants were either younger or older than the optimum age of 14-day-old. A strong effect of plant age on infection success was also found when bean plants were inoculated with a different begomovirus, *Bean golden yellow mosaic virus* (BGYMV) (Morales & Niessen, 1988). Infection rates dropped from 100% infection in plants inoculated when they were 7-day-old plants, to 0% infection in plants inoculated at 12 days. Thus, the same phenomenon is observed in both studies—a distinct dependence of the rate of infection success with bean plant age.

In another study Monci, Garcia-Andres, Maldonado, and Moriones (2005) screened *P. vulgaris* breeding lines both in the field and in the greenhouse for resistance to TYLCV. High levels of resistance were found in the GG12 breeding line. There were no disease symptoms under field conditions as well as after controlled inoculation in the greenhouse. Following inoculation of segregating populations, the resistance was found to be controlled by a single dominant gene. Although the resistant plants did not show disease symptoms following inoculation with TYLCV, it was found that virus replication was not inhibited. Rather, it was found that viral systemic accumulation was strongly restricted in the resistant plants, suggesting that cell-to-cell or long-distance viral movement was impaired (Monci et al., 2005).

Recent reports indicate that TYLCV continues to be a problem for bean growers in southern Spain (Segundo et al., 2008), in Iran (Hedesh, Shams-Bakhsh, & Mozafari, 2011) and recently infection of common bean by TYLCV was also reported in China (Ji et al., 2012). However, it should be noted that in Latin America, where bean is a staple food, the most severe whitefly-transmitted diseases in bean cultivation are bean golden mosaic disease (BGMD) which is largely induced by the begomoviruses *Bean golden mosaic virus* and BGYMV. Indeed, major efforts are being made to breed common bean for resistance to BGMD (Morales & Jones, 2004).

5.7. Genetic resistance to the whitefly

As with development of viral resistance in the host, a potentially excellent control method against whiteflies and the viruses they transmit would be the development of whitefly resistance in the target host. There are several means by which resistance against insects can function. The presence of some plant secondary metabolites dissuades insects from settling on plants, in turn preventing the steady feeding that can lead to toxicity or virus transmission. Other metabolites may prevent oviposition, thereby reducing vector populations (Bleeker et al., 2011; Mutschler & Wintermantel, 2006; Nombela & Muniz, 2010). Resistance against whiteflies will complement resistance against the viruses they transmit and potentially reduce reliance on insecticides by reducing the frequency or the number (or both) of insecticide applications required to minimize insect populations. Host resistance to whiteflies can be combined with other methods of whitefly control. In a recent study, two whitefly-resistant genotypes of *Citrullus colocynthis* (L.), a wild relative of cultivated watermelon, were tested in the field in combination with the use of a reflective soil mulch, and were found to reduce whitefly populations (Simmons et al., 2010). The authors suggested that combining the use of reflective mulch and host plant resistance could additively suppress whitefly infestation. Although effective whitefly resistance has so far only been identified in a limited number of host plants (Nombela & Muniz, 2010; Simmons & Levi, 2002), and is mostly found in wild relatives of crop plants, the potential remains for such resistance in a number of crops that are affected by whiteflies and whitefly-transmitted viruses. Resistance to whitefly in some cotton genotypes reduced the number of insecticide applications required, thus lowering production costs while ensuring a marketable product (Chu et al., 1998). Host plant resistance to *B. tabaci* MEAM1 has been reported in two exotic melon accessions also identified as sources of resistance to *Cucurbit yellow stunting disorder virus* (CYSDV): PI 313970 and TGR-1551. Low-level resistance to *B. tabaci* MEAM1 was identified in PI 313970 in both greenhouse (Simmons & McCreight, 1996) and open-field (Boissot, Lafortune, Pavis, & Sauvion, 2003) studies. Similarly, TGR-1551 expressed low-level resistance to *B. tabaci* MED in a greenhouse study (Soria, López-Sesé, & Gómez-Guillamón, 1999). Other recent examples of the potential value of host plant resistance to whiteflies include the use of acylsugar-mediated resistance in tomato to reduce spread of TYLCV (Rodríguez-López et al., 2011). It was shown that in a no-choice experiment, 28 days after release of

viruliferous whiteflies 60–80% (depending on the season) of the control tomato plants (*cv.* Moneymaker) were infected with TYLCV, while only 15–20% of the whitefly-resistant plants were infected. Similarly, preliminary studies using tomato breeding lines expressing acylsugars derived from a different wild *Solanum* species slowed the rate of infection by the crinivirus, *Tomato infectious chlorosis virus* in southern California fields (Mutschler & Wintermantel, 2006).

6. CASE STUDY 1: MANAGING BEGOMOVIRUSES AND IPOMOVIRUSES IN CASSAVA

Cassava is affected by three groups of whitefly-transmitted viruses: the cassava mosaic geminiviruses (CMGs), the CBSVs, and the CsTLVs. CMGs are present in both Africa (nine species) and South Asia (two species), CBSVs are present in coastal East Africa and the Great Lakes region of Central Africa (two species) and one newly described species, CsTLV—has been described from Colombia in Latin America (see Chapter XX which provides more detail on the cassava viruses). The CMGs and CBSVs are the biggest economic constraints to cassava production and have therefore been the subject of most of the effort to develop management programs. The CMGs cause CMD (Bock & Woods, 1983; Storey, 1936) which reduces plant growth, may lead to stunting and can cause yield losses of up to 90% in affected plants (Thresh, Fargette, & Otim-Nape, 1994). The CBSVs cause cassava brown streak disease (CBSD) (Hillocks, Raya, & Thresh, 1996; Storey, 1936; Winter et al., 2010). CBSD has a less obvious effect on cassava foliage than CMD, but causes a brown necrotic rot in the tuberous roots of affected plants. Yield losses of up to 70% have been reported (Hillocks, Raya, Mtunda, & Kiozia, 2001). Together, these two diseases cause more than US$ 1 billion of production losses annually in Africa (Legg, Owor, Sseruwagi, & Ndunguru, 2006; Thresh, Otim-Nape, Legg, & Fargette, 1997). CMD has been a target of control measures since the time of the earliest epidemics in the 1920s (Thresh & Cooter, 2005), while CBSD only began to "attract" more research attention since 2004, as it began to spread beyond its former confined distribution in coastal East Africa. Several major programs are currently being implemented to control both diseases in Africa.

6.1. Principal components of management strategies for cassava viruses

Cassava is a vegetatively propagated crop, and in almost all farming situations, new crops are planted using cuttings taken from mature stems.

Breeders use true botanical seed as part of their germplasm development work, and very rarely, tissue culture plantlets may be used to establish cassava plantings. The general use of vegetatively propagated cuttings for planting means that viruses may be readily carried from one crop to the next through planting material—leading to virus build-up or "degeneration"—unless preventive measures are taken. CMGs are transmitted persistently by *B. tabaci* (Dubern, 1994), while CBSVs are transmitted semi-persistently by the same insect (Jeremiah, 2012). These modes of transmission have important impacts on the epidemiological characteristics of CMD and CBSD (Legg et al., 2011) and therefore determine which control approaches are most suitable. In both cases, however, the suite of control tactics is similar and includes: host plant resistance, phytosanitation, other cultural control approaches, and vector control. Integrated management strategies combine several of these tactics to make the overall control impact stronger and more sustainable.

6.2. Host plant resistance to cassava viruses

Sources of resistance for both CMD and CBSD have been derived from introgressing resistance genes into cultivated cassava from wild relatives (Jennings, 1994). For CMD resistance, this has also been augmented through crosses with West African landraces which have contributed the single dominant gene—CMD2 (Akano, Dixon, Mba, Barrera, & Fregene, 2002). The speed and efficiency of cassava resistance breeding is currently being enhanced through the application of both molecular markers and next-generation sequencing approaches (Rabbi et al., 2014). Several of the most CMD-resistant varieties, bred using conventional approaches, are virtually immune to infection by CMGs. By contrast, conventional breeding has been relatively less successful in identifying and deploying high levels of resistance to CBSVs. For these ipomoviruses, transgenic approaches—based on RNAi technology—offer great potential for combining resistance to CBSVs with the farmer-preferred quality characteristics that are already present in conventionally bred CMD-resistant varieties. High levels of resistance have been demonstrated in cassava plants transformed with constructs derived from coat protein sequences of CBSVs (Yadav et al., 2011), and several transformed cassava varieties are currently being evaluated in confined field trials in Uganda and Kenya (Taylor et al., 2012).

6.3. Phytosanitation

Establishing new cassava plantings with healthy cuttings and maintaining the health of those plantings over the course of the growing season using

phytosanitary practices have long been advocated as important approaches to managing cassava virus diseases (Calvert & Thresh, 2002). Plants derived from CMD-free cuttings yield significantly more than others established from infected cuttings, even if the initially healthy plants become infected during the course of the growing season (Fauquet & Fargette, 1990; Thresh, Fargette, et al., 1994). Furthermore, the later that plants become infected, the smaller the yield penalty (Thresh, Fargette, et al., 1994). Tissue culture (TC) is used by several strategically important laboratories and institutions to produce and exchange virus-indexed TC plantlets (Frison, 1994). Meristem tip culture combined with thermotherapy is effective in "cleaning up" cassava germplasm through virus elimination (Kartha & Gamborg, 1975). The primarily subsistence nature of the cassava crop in areas most affected by viruses, however, means that TC methods are not generally used to produce virus-free planting stock for larger scale field applications, as is done for other vegetatively propagated crops, such as sweet potato.

Roguing and selection of disease-free stems are widely advocated for the management of both CMD and CBSD. The differing patterns of spread of the viruses that cause these diseases, however, mean that these methods are not equally effective for the two diseases. Whitefly spread over medium to long distances is an important feature of the epidemiology of the CMGs, which means that roguing operations can be ineffective. The shorter distance spread of the semi-persistent CBSVs offers greater potential for managing CBSD through area-wide phytosanitation incorporating roguing. The cryptic symptoms of CBSD mean that effective training on accurate symptom recognition needs to be incorporated into phytosanitation programs.

6.4. Other cultural practices

Several other cultural practices have been used in attempts to control CMD and CBSD. Examples of these are presented in Section 4.2 and include managing the placement of the crop in space and/or time, and intercropping. The greatest benefits can be achieved by planting cassava crops in such a way that the degree of infestation by whitefly vectors is reduced. This can be achieved most effectively by planting during a season where the young crop growth stages occur at a time when whiteflies are not abundant, or by selecting a location for planting that is unfavorable for whiteflies. Intercropping may provide marginal benefits in reducing infection by CMGs (Fondong et al., 2002), but the relative success of control outcomes depends

on the intercrop design, and the benefits offered are probably outweighed by the difficulties entailed in modifying the farming system.

6.5. Vector control

Super-abundant populations of *B. tabaci* whiteflies have driven the expansion of the pandemics of severe CMD and CBSD through large parts of East and Central Africa (Legg et al., 2011, 2014). However, surprisingly little attention has been directed toward the development and application of control tactics for this insect vector. Currently, there is virtually no field-level management of whiteflies being undertaken in cassava plantings in either Africa or South Asia, where whitefly-borne viruses are the major constraint.

Since cassava is grown primarily as a subsistence crop, there is little current use of inputs—either fertilizer or pesticides—in its cultivation in Africa. There has been some use of imidacloprid, or neonicotinoid equivalents, but typically only in experimental situations where whitefly exclusion is required in order to make comparisons between virus-infected and uninfected plants or between plots infected with different virus species (Owor, Legg, Okao-Okuja, Obonyo, & Ogenga-Latigo, 2004). As the commercialization of the crop progresses, however, it is likely that insecticides will see more widespread use in production.

Attempts have been made to determine whether sources of whitefly resistance (to *Aleurotrachelus socialis* Bondar) carried by some Latin American cassava genotypes (e.g., MEcu72) are also effective against African cassava *B. tabaci*. Although abundances of *B. tabaci* on these genotypes were significantly lower than the average for African cassava genotypes, the degree of resistance was much less than that recorded for *A. socialis* (Omongo et al., 2012). There is considerable current interest, however, in investigating the potential for the use of RNAi technologies involving the transformation of cassava plants with gene constructs that have the potential to provide much higher levels of whitefly resistance than are currently available. Some of the first practical examples of this for *Bemisia* control have recently been demonstrated (Upadhyay et al., 2011).

A diverse set of natural enemies have been reported from *B. tabaci* in several African countries, of which the most widely occurring are the aphelinid parasitoid wasps, *Encarsia* spp. and *Eretmocerus* spp. (Legg & James, 2005). Significant levels of parasitism have been reported, and there may be opportunities for these to be enhanced through manipulation of the cropping environment. However, the local parasitoids may only make an effective

contribution to whitefly control if part of a multicomponent integrated management approach (Asiimwe et al., 2007). Although classical biological control has proven highly effective against pests introduced to Africa, such as the cassava mealybug [*Phenacoccus manihoti* Mat. -Ferr.] and the cassava green mite [*Mononychellus tanajoa* (Bondar)], the prospects of similar success for *Bemisia* seem less promising, since this genus of whiteflies is considered to be indigenous to Africa (Campbell, Steffen-Campbell, & Gill, 1996). Introductions of *Eretmocerus hayati* Rose & Zolnerowich to Australia for the control of *B. tabaci* MEAM1 have been highly successful, however, as this exotic parasitoid species has greatly augmented the existing activity of the 11 local species of *Eretmocerus* and *Encarsia* reported to attack *B. tabaci* (De Barro & Coombs, 2009). This success has encouraged recent initiatives to introduce *E. hayati* to East Africa to evaluate its potential effectiveness against African cassava-colonizing *B. tabaci*. Biological control is unlikely to be effective in a single-component control strategy and offers greatest potential as a component within an integrated whitefly management strategy also incorporating host plant resistance and cultural methods.

6.6. Integrated control strategies

The term integrated control has most commonly been used to refer to the combination of pesticide application with other management tactics, very often with a goal of reducing overall levels of pesticide usage (Naranjo & Ellsworth, 2009). Since pesticides are not usually used by cassava growers in Africa and South Asia, this term has rarely been used to describe multicomponent control strategies. Such approaches have been widely used for cassava virus disease management, however, and have primarily involved the combination of host plant virus resistance and phytosanitary measures to protect the health of cassava plants before and after planting. As cassava virus disease pandemics have spread through large parts of East and Central Africa, governments, NGOs and international partners have responded through the mass deployment of resistant varieties (Walsh, 2012). The initial target of these mitigation efforts was the pandemic of severe CMD, whose most rapid period of spread occurred during the 1990s, and the varieties multiplied had high levels of CMD resistance (Dixon et al., 2003; Legg, Kapinga, Teri, & Whyte, 1999; Thresh, Otim-Nape, & Jennings, 1994). Since the mid-2000s, these large-scale germplasm "roll-out" programs have been coupled with the application of quality management protocols (QMP), which comprise procedures for the assurance of specified minimum virus disease levels

in multiplied and disseminated crops of improved cassava varieties (Jennings, 1994). In order to strengthen standards and avoid inadvertent spread of cryptic CBSD infection, a large-scale virus testing program was undertaken during the Great Lakes Cassava Initiative—a six-country regional cassava virus management program (Smith, 2014). By combining virus testing at a small number of high-level germplasm multiplication sites, with the large-scale application of QMP measures at primary (regional), secondary (district), and tertiary (community) multiplication sites, it was possible to deliver high-quality planting material with little or no cassava virus disease to the ultimate targets of the program—small-scale growers. Although the initial stages of this effort were hindered by the lack of resistance to CBSD in varieties being multiplied, improvements were achieved through the course of the initiative as CBSD-tolerant varieties were identified and incorporated.

On-going and future targets for cassava virus disease control work will be to improve resistance to CBSD using both conventional and transgenic methods, identify sources of whitefly resistance, and combine the use of improved germplasm with other cultural and biological controls to strengthen the effectiveness of integrated control. Looking further ahead, the significant risks of spread of cassava viruses, both within and between the continents in which cassava is grown (Africa, Asia, and Latin America), demand that great attention is given to strengthening surveillance and quarantine procedures.

7. CASE STUDY 2: MANAGEMENT OF CRINIVIRUSES

There is a tremendous amount of research on management of begomoviruses, but only a limited amount of information on management of other types of whitefly-transmitted viruses. This section will address management of criniviruses (reviewed by Tzanetakis et al., 2013), which share a number of similarities with begomoviruses, but differ greatly in mode of transmission by whitefly vectors and therefore management.

Over the past 25 years, the number of members in this genus has expanded through identification and characterization of new viruses affecting a wide range of crop and weed hosts throughout tropical and subtropical areas of the world where whitefly vectors are prevalent, as well as in greenhouse production facilities. In the 1980s, *Lettuce infectious yellows virus* and *Beet pseudo-yellows virus* (BPYV) were the only well-known whitefly-transmitted viruses with virions composed of flexuous rods, and it was

not until many years later that BPYV was added to the genus after genome analysis confirmed that it too was bipartite like other members. Throughout the 1990s and beyond, a wide array of criniviruses have been characterized (Celix, Lopez-Sese, Almarza, Gomez-Guillamon, & Rodriguez-Cerezo, 1996; Duffus, Larsen, & Liu, 1986; Duffus, Liu, & Wisler, 1996; Duffus, Liu, Wisler, & Li, 1996; Liu, Li, Wisler, & Duffus, 1997; Martin, 2004; Martın, Velasco, Segundo, Cuadrado, & Janssen, 2008; Okuda, Okazaki, Yamasaki, Okuda, & Sugiyama, 2010; Salazar, Muller, Querci, Zapata, & Owens, 2000; Tzanetakis et al., 2004; Winter et al., 1992) and the genus now consists of three separate groups based largely on genetic relationships and vector transmission characteristics (Tzanetakis et al., 2013; Wintermantel, Hladky, Gulati-Sakhuja, et al., 2009).

Symptoms of criniviruses are not always as apparent as those of other plant viruses. Whereas begomoviruses often produce bright yellow symptoms on leaves, along with distortion and curling, criniviruses often cause symptoms that are readily mistaken for physiological or nutritional disorders or pesticide phytotoxicity. Depending on the host plant affected, these symptoms include interveinal yellowing of leaves, an associated loss of photosynthetic capability, leaf brittleness, reduced plant vigor, yield reductions, and early senescence (Tzanetakis et al., 2013; Wintermantel, 2010). Many crinivirus infections remain latent for nearly 3 weeks before symptoms appear, and as a result these viruses can be moved on transplants without knowledge the plants are infected. Symptoms are usually most apparent on the middle and older parts of plants, with new growth appearing normal and symptoms progressing toward newer growth over time. In a few crops, including strawberry and sweet potato, crinivirus infection can remain latent until plants become coinfected with another virus resulting in symptom development due to synergism between the crinivirus and the coinfecting virus.

Such mixed infections can complicate identification of the primary virus causing disease because symptoms resulting from mixed infection with other viruses often induce different symptoms than those resulting from single infections. In other situations, the viruses involved in coinfections are obvious with different sections of infected plants exhibiting symptoms uniquely characteristic of each virus. An example would be CYSDV infection of melon with coinfection by either a begomovirus or potyvirus. All three types of virus produce unique symptoms on melon. CYSDV produces interveinal yellowing beginning near the crown and progressing outward down the vines, whereas mosaic symptoms resulting from infection by *Watermelon*

mosaic virus or leaf curl symptoms resulting from CuLCrV are usually found near the ends of vines.

Numerous studies have demonstrated that interactions between criniviruses and other coinfecting viruses have been known to influence the type and severity of symptoms observed on plants. In most documented cases, this leads to enhanced disease severity, as has been found with infection of SPCSV and members of the Potyvirus genus (Karyeija et al., 2000). Similar effects were later found with coinfection between SPCSV and viruses of other genera and families (Cuellar, De Souza, Barrantes, Fuentes, & Kreuze, 2011; Untiveros, Fuentes, & Salazar, 2007). In some hosts, such as strawberry, coinfection involving a crinivirus and another virus produces severe symptoms, whereas plants infected by either virus alone remained asymptomatic (Tzanetakis, Wintermantel, et al., 2006; Tzanetakis et al., 2004). Much remains to be determined regarding the interactions between the coinfecting viruses and their hosts and how this leads to increased severity; however, such interactions complicate management of virus diseases in the field.

7.1. CYSDV: Managing crinivirus infection in the field

CYSDV was widely studied following its establishment in the Imperial Valley of California. In the fall of 2006, CYSDV was identified affecting cucurbit production throughout the southwestern US (California and Arizona), as well as nearby Sonora in Mexico, resulting in widespread infection of the fall melon crop (Brown, Guerreo, Matheron, Olsen, & Idris, 2007; Kuo, Rojas, Gilbertson, & Wintermantel, 2007). Although at that time it was believed the host range of CYSDV was restricted to cucurbit crops (Celix et al., 1996), the virus survived the largely cucurbit-free winter months to infect a limited number of plants the following spring, and again infect nearly the entire fall crop in 2007. This pattern is now well established in the region. Populations of *B. tabaci* accumulate gradually during the spring melon season, with infection developing late in the season with only limited impact on yield during the spring season (Chu et al., 2007). In contrast, the exceptionally high populations of *B. tabaci* during the fall melon season in the desert region of southwestern US results in rapid and efficient transmission of CYSDV to melon, with infection occurring in seedling plants. Following the establishment of CYSDV in the region, research demonstrated that the virus was able to infect a broad range of common weed and crop plants prevalent in the desert production region (Wintermantel, Hladky, Cortez, et al.,

2009; Wintermantel, Hladky, Gulati-Sakhuja, et al., 2009). The establishment of CYSDV in this important region where most US winter melons are produced prompted an aggressive research effort toward development of effective management strategies for control of the virus and to mitigate CYSDV-induced losses.

7.2. Identification and management of crop and weed reservoir hosts

Studies demonstrated that the presence of several weed or alternate crop hosts in the region, most of which were symptomless when infected (Wintermantel, Hladky, Cortez, et al., 2009). Subsequent work focused on determining which of these newly identified hosts were of epidemiological significance. Although CYSDV was able to infect several weed hosts as well as lettuce (*Lactuca sativa*) and snap bean (*P. vulgaris*), titers were much lower in non-cucurbit hosts than in melon and other cucurbits (Wintermantel, Gilbertson, & Natwick, 2014). In some cases, the CYSDV titer in the host plant was directly related to the efficiency of virus transmission to melon; however, in several host plants transmission rates did not correspond to virus titer, indicating a complex relationship influencing the ability of different host plants to serve as efficient virus reservoirs for transmission to melon. Importantly, one of the most widely planted crops in the region, alfalfa (*Medicago sativa*), although a host of CYSDV, is very inefficient as a source for transmission of the virus to cucurbits (Wintermantel et al., 2014). Knowledge of reservoir hosts is important toward reducing sources of virus in the field through reduction of source plants when possible. By targeting weed management against virus reservoir hosts and plants on which the whitefly vector feeds or reproduces, spread of the virus can be limited when combined with other practices.

7.3. Genetic resistance to the virus

Traditionally, management of whitefly-transmitted viruses in the desert production regions of the southwestern US has been predominantly through control of the whitefly vector using insecticidal control. Several neonicotinoid formulations are currently used in conjunction with other chemistries, for control of *B. tabaci* populations. Still, even aggressive insecticidal methods are ineffective at reducing populations of *B. tabaci* MEAM1 (the whitefly vector common in the southwestern US) sufficiently to

mitigate virus spread. CYSDV has established itself in the wild hosts and cultivated crops of the region, and insecticidal control alone has not been sufficient to obtain marketable melons when plants become infected early as occurs during the fall production season. Therefore, an aggressive resistance breeding program was developed. A number of laboratories are focused on development of CYSDV resistance, particularly in cucumber and cantaloupe melon (Aguilar, Abad, & Aranda, 2006; Eid, Abou-Jawdah, El-Mohtar, Sobh, & Havey, 2006; López-Sesé & Gómez-Guillamón, 2000; Marco, Aguilar, Abad, Gomez-Guillamon, & Aranda, 2003; McCreight & Wintermantel, 2011). Interestingly, the first few years of research on host plant resistance to CYSDV in California's Imperial Valley were conducted without any measures to control *B. tabaci* MEAM1, but it became evident that control of this insect was essential for resistance to CYSDV to be more fully expressed. Recent studies have shown that combining host plant resistance with effective vector control has been very effective at maximizing the effectiveness of resistance (McCreight J. D. & Wintermantel W. M., unpublished) and offers potential for improved management in production fields once resistance is introgressed into cultivated melon.

In cantaloupe melon, each resistance source has the potential to reduce severity, but breeding studies have demonstrated that combining resistance sources results in stronger resistance than can be achieved with individual genes (McCreight & Wintermantel, 2011). There are currently two independent sources of resistance to CYSDV in melon germplasm: TGR-1551 from Zimbabwe (López-Sesé & Gómez-Guillamón, 2000) and PI 313970 from India (McCreight & Wintermantel, 2008). Resistance in TGR-1551 was initially reported to be dominant (López-Sesé & Gómez-Guillamón, 2000); however, it is possible the resistance may be codominant and complex (Sinclair, 2003). Alternatively, CYSDV resistance in TGR-1551 may be affected by environmental variation (Rubio, Abou-Jawdah, Lin, & Falk, 2001). Most importantly, although the resistance in TGR-1551 can be effective, its performance has been variable depending on the conditions and locations where it has been evaluated. The single recessive gene for resistance in PI 313970 (McCreight & Wintermantel, 2011) can also reduce disease severity in the field, but the exceptionally high populations of viruliferous whiteflies that occur in the southwestern US during the summer and fall can be too much for this resistance source alone. Results of a cross of PI 313970 × TGR-1551 in 2009 and 2010 suggest the possibility of higher and more uniform levels of resistance when their

genes are combined (McCreight & Wintermantel, 2011). However, introgression of these sources of resistance from exotic melons into commercially favored sweet cantaloupe melon is a formidable task.

7.4. Crinivirus management in transplanted crops

Many field crops begin in nurseries with propagation by seed or through cuttings or runners. In some crops, grafting is increasing in popularity as a means of introducing vigorous or highly resistant root systems that will benefit the plant once it is transplanted to the field. Any movement or manipulation of plant material inherently introduces the risk of virus infection. It is critical that nursery operations routinely monitor grafting stock for the most critical viruses that could affect the crop once it is in the field. This is particularly important when nursery facilities are located in areas known to harbor viruses of concern for the nursery crop or their insect vectors. Although such measures are important for preventing infection of nursery stock with all viruses, it is an especially significant concern with regard to criniviruses. As noted, criniviruses have a lengthy latent period in most host plants ranging from slightly under 3–4 weeks depending on the plant and virus. Due to the extended latent period, a crinivirus introduced in the nursery can easily remain symptomless until it is transplanted in the field, resulting in introduction of the virus to the initial field and potentially to an entire production region. Although criniviruses are not as easily graft-transmitted as many other plant viruses, these viruses can be introduced to healthy plant material through graft unions. They are also maintained in rooted cuttings and can be difficult to monitor. *Strawberry pallidosis-associated virus* is known to increase in titer during the winter months, but titers can decrease to nearly undetectable levels during the summer (Tzanetakis et al., 2004). Such cycling of virus titers may occur with other crinivirus infections as well, but such studies have not been conducted. Consequently, effective monitoring should be performed on nursery stock throughout the year, not only as plants are prepared for movement to the field.

7.5. Summary

Successful management of criniviruses in field production systems is best achieved through integrated pest management (IPM). Resources available increased tremendously over the past decade as the library of epidemiological knowledge of this important and emerging genus has grown. Host range information is largely established for most members of the genus and sources

of host plant resistance are being developed for some. Effective management of weed hosts and carefully managed crop rotation and proximity will reduce spread among fields. It is anticipated that new sources of host plant resistance against both criniviruses and their whitefly vectors will continue to be identified, adding to the arsenal of protective measures available for crop production. Currently there are a number of options for insecticidal control of whitefly vectors. Effective management to prolong functionality of insecticides, coupled with virus and/or insect resistance will also be valuable for management of criniviruses in field production systems. Admittedly, identification of resistance sources will require time for some of the more recently characterized members of the genus. However, through strategic use of host plant and/or insect resistance when available, monitoring and internal management of nursery stock, and efficient use of pesticides, crinivirus infection of field crops can be minimized.

8. CONCLUDING REMARKS

Whiteflies have become a key pest in modern agriculture, mainly in open-field production. This is largely due to the long list of devastating plant viruses transmitted by the whiteflies. Some of the diseases caused by whitefly-transmitted viruses have become a limiting factor in open-field production, and important examples include: BGMD in beans, TYLCD in tomato, CMD and CBSD in cassava, and Cotton leaf curl disease (CLCuD) in cotton. The main strategy to stop whitefly infestation in the field is the application of insecticides. However, due to growing consumer demand for cleaner produce, and the whitefly's ability to develop insecticide-resistance, there is a growing demand to reduce insecticide application. This will increase the need for effective IPM strategies to reduce infestation by whiteflies and the viruses they transmit. Genetic resistance in the host—to the whitefly as well as to the whitefly-transmitted viruses, combined with other IPM strategies could become a viable solution to open-field production in the days of reduced application of insecticides.

Management of whitefly-transmitted viruses is challenging. While host resistance to the virus is the best approach, the number and diversity of the viruses and crops affected mean that there are few examples of diseases being managed by this approach. The importance of resistance for management of these viruses cannot be overstated, and as such there is a tremendous need to develop resistance to whitefly-transmitted viruses in many crops. In most

cases, the focus of management is the reduction in whitefly populations and the reduction of inoculum sources.

The most effective management schemes that reduce whitefly populations and limit virus spread are those that use multiple approaches simultaneously. This also involves professional crop scouts who can help tailor the timing and type of insecticide application to keep costs as low as possible and maximize effectiveness. These schemes can be expensive and demanding of resources and education and work best when there is a support structure to provide data essential for development and use of appropriate management tools (Adkins et al., 2011). Knowledge of the alternative hosts of the virus, the identity and feeding preferences of the vector, information on expected changes in whitefly populations throughout the year, and knowledge of alternative hosts of the whitefly all contribute to the design of effective management recommendations. Growers that lack such resources cannot manage these viruses very effectively and often must abandon the crop for alternative crops that are not affected. Further investments in the development of host resistance as well as in the development of effective integrated management tactics will allow us to produce both food and biofuel crops despite the presence of these viruses and their vector.

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