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Plant-mediated whitefly–begomovirus interactions: research progress and future prospects

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Abstract

Plant-mediated interactions between begomoviruses and whiteflies exert important influences on the population dynamics of vectors and the epidemiology of plant diseases. In this article, we synthesize the relevant literature to identify patterns to the interactions. We then review studies on the ecological, biochemical and molecular mechanisms underlying the interactions and finally elaborate on the most interesting issues for future research. The interactions between begomoviruses and the insect vector, the whitefly *Bemisia tabaci*, via their shared host plants can be mutualistic, neutral or negative. However, in contrast to a pattern of improved performance of vectors on virus-infected plants that has been observed with persistently transmitted RNA viruses, the number of cases exhibiting mutualistic, neutral or negative effects in the indirect interactions between begomoviruses and whiteflies appear evenly distributed. With regard to the mechanisms of plant-mediated positive effects on whiteflies, two case studies indicate that suppression of plant defence and/or alteration in plant nutrition as a result of virus infection can be important. Our review shows that we are only just beginning to understand the tripartite interactions between begomoviruses, whiteflies and plants. Future efforts in this area should try to expand the number and diversity of pathosystems for investigation to reveal the patterns of interactions, to investigate the molecular and biochemical mechanisms of the interactions using a multidisciplinary approach, and to examine the virus–plant–vector interactions in the field and in natural plant communities.

Keywords: insect vector, plant virus, plant–virus–vector interaction, persistently transmitted virus, vector performance, vector behaviour

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Introduction

The whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is a cryptic species complex composed of more than 35 morphologically indistinguishable species (De Barro *et al.*, 2011; Liu *et al.*, 2012; Firdaus *et al.*, 2013). Within this whitefly complex, the putative Middle East-Asia Minor 1 (MEAM1) and Mediterranean species, known formerly as the 'B biotype' and 'Q biotype', respectively, have become economically important pests due to their rapid spread from the Mediterranean regions to the rest of the world and to the serious damage they cause to a wide range of crops (Brown *et al.*, 1995; Liu *et al.*, 2007; De Barro *et al.*, 2011). The *B. tabaci* species complex causes severe crop losses through direct

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feeding and transmission of begomoviruses (*Geminiviridae*, *Begomovirus*) (Brown *et al.*, 1995; Colvin *et al.*, 2006; Jiu *et al.*, 2007; Navas-Castillo *et al.*, 2011), which are the most important group of plant viruses in tropical and sub-tropical regions (Moffat, 1999; Mansoor *et al.*, 2003). Over 200 species of begomoviruses are exclusively transmitted by *B. tabaci* in a persistent-circulative mode (Hogenhout *et al.*, 2008; Nawaz-ul-Rehman & Fauquet, 2009; Navas-Castillo *et al.*, 2011).

Plant-mediated whitefly–begomovirus interactions exert important influences on the abundance of the whitefly and the epidemiology of the virus diseases (Colvin *et al.*, 2006; Jiu *et al.*, 2007). In recent years, several species of begomoviruses, such as *Tomato yellow leaf curl virus* (TYLCV) coupled either with the MEAM1 or Mediterranean species of the *B. tabaci* complex, have spread into many countries and regions (Liu *et al.*, 2007; De Barro *et al.*, 2008; Varma *et al.*, 2011; Péréfarres *et al.*, 2012). In some cases, the invasion of whiteflies and begomoviruses into new territories may have been facilitated by the plant-mediated whitefly–begomovirus interactions (Jiu *et al.*, 2007). The modes of virus transmission by insect vectors can be categorized as non-persistent, where viruses have a transient relationship with their vectors and are only associated with the mouthparts or foregut of vector insects, and persistent transmission, where viruses circulate (and replicate) in the vector body and have developed intimate interactions with more internal components of vectors for longer time periods. In theory, transmission of persistently transmitted (PT) viruses requires that vectors feed on infected host plants for a sustained period to acquire and circulate virions, and then move to a uninfected host plant (Mauck *et al.*, 2012). Thus, PT viruses may tend to enhance vector attraction to infected hosts, improve host quality or decrease host resistance for vectors and promote long-term feeding (Mauck *et al.*, 2012). However, whether plant-mediated whitefly–begomovirus interactions fit this hypothesis is not yet clear.

In this review, we survey and synthesize the case studies on plant-mediated interactions between whiteflies and begomoviruses in an attempt to identify patterns to the interactions; next, we consider investigations into the ecological, biochemical and molecular mechanisms underlying the interactions; and finally, we elaborate on the most interesting issues and suggest some likely fruitful areas for future research.

Patterns of plant-mediated whitefly–begomovirus interactions

Literature survey and synthesis

A literature survey following the method of Mauck *et al.* (2012) was conducted to detect possible patterns of plant-mediated whitefly–begomovirus interactions. The literature search was up to and including the 20th July 2013 and identified 24 papers that reported any aspect of whitefly, *B. tabaci*, attraction, settling and feeding, or comparative performance in relation to uninfected and begomovirus-infected plants (tables 1–3).

For assays to test whitefly performance, results were categorized as positive, neutral or negative effects for virus-infected plants or virus-invasion on vector life-history parameters, i.e. development, survival and reproduction. Where both positive and negative effects were observed in a single experiment, the experiment was categorized as neutral; for example, when whiteflies deposited fewer eggs on virus-infected plants, but developed more rapidly on these plants (Mann *et al.*, 2008). For experiments to measure attraction or settling, probing and feeding behaviour, results were categorized as an indirect effect of the virus on a vector preference (for virus-infected plants, for uninfected plants, or no preference), via plants and a direct effect of virus on whitefly behaviour.

To examine the pattern of interactions, experiments reported in the 24 papers have been tabulated as individual case studies; each case study involves experiments investigating whitefly performance or behaviour with a given combination of virus isolate, plant cultivar and whitefly species (tables 1–3). When the same combination of virus isolate, plant cultivar and whitefly species was examined by different authors or by the same group of authors repeatedly using different protocols at different times, all the experiments were regarded as one case study. For example, the experiments with *Tomato yellow leaf curl China virus* (TYLCCNV), *Nicotiana tabacum* cv. NC89 and whitefly MEAM1 by Jiu *et al.* (2007), Guo *et al.* (2010, 2012) and Luan *et al.* (2013*c*) to examine whitefly performance on virus-infected and uninfected plants were regarded as one case study (table 1).

Effects of viral infection on whitefly performance

In total, 36 case studies were available for the comparative performance of whiteflies feeding on begomovirus-infected and uninfected plants. These case studies appear evenly distributed among positive, neutral and negative effects (table 1; fig. 1). As these studies involve complex three or four way (if endosymbionts are involved) interactions, it is worth noting that for the same virus isolate, e.g. TYLCCNV-Y10 DNAβ, the effect can vary from positive, neutral to negative, depending on the plant cultivar and/or whitefly species. Although not all publications identified the species within the *B. tabaci* complex involved, there is a strong bias towards the use of the highly invasive MEAM1 (possibly 13 case studies) and Mediterranean (8 case studies) species. This bias may partially help to explain why the effects appear evenly distributed, due to the relatively recent associations of the invasive whitefly with particular begomoviruses and plants.

Only six case studies were available for the comparative performance of viruliferous and non-viruliferous whiteflies feeding on begomovirus-free plants. Of the six case studies, four show a negative effect of begomoviruses on the performance of whiteflies, one shows a positive effect and one shows negative effects (table 2).

Effects of viral infection on whitefly behaviour

Only three case studies were available for the indirect effects of viral infection of plants on whitefly behaviour. One case study reports whitefly preference for virus-infected to uninfected healthy plants, whereas the other two report the reverse. In addition, three case studies report virus modulation of whitefly settling, probing and feeding behaviour in favour of its transmission (table 3).

Mechanisms underlying plant-mediated whitefly–begomovirus interactions

Mechanisms related to changes in plant defence traits

Plant defences have a dynamic impact on the adaptations and interactions of vectors and pathogens (Huot *et al.*, 2013).

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Table 1. Performance of whiteflies on begomovirus-infected or uninfected plants.

Virus	Virus identifier	Host plant	Whitefly vector[1]	Effects on vector performance			References
				Positive	Neutral	Negative	
Chino del tomate virus	CdTV-Sinaloa	*Solanum lycopersicum* cv. Pole Boy	New World			+	Costa *et al.* (1991)
Cotton leaf crumple virus	CLCV-Phoenix	*Gossypium hirsutum* cv. DPL Co. 70	New World			+	Costa *et al.* (1991)
Cotton leaf curl virus	CLCuV	*G. hirsutum* cv. F846	Unknown, likely MEAM1 from Florida		+		Mann *et al.* (2008)
East African cassava mosaic virus	EACMV-Tanzania	*Manihot esculenta* cv. Ebwanateraka	Unknown, collected from Uganda		+		Thompson (2002, 2011)
Squash leaf curl virus	SLCV-WCMoV	*Cucurbita pepo* cv. Fordhook	New World			+	Costa *et al.* (1991)
	SLCV-WCMoV	*Cucurbita maxima* cv. Big Max	New World	+			Costa *et al.* (1991)
Tobacco curly shoot virus	TbCSV-Y35 DNAβ	*Nicotiana tabacum* cv. NC89	MEAM1	+			Jiu *et al.* (2007)
	TbCSV-Y35 DNAβ	*N. tabacum* cv. NC89	Asia II 3		+		Jiu *et al.* (2007)
Tomato leaf curl Bangalore virus	ToLCBV-Ban4	*S. lycopersicum* cv. Arka Vikas	Asia I	+			Colvin *et al.* (2006)
	ToLCBV-Ban4	*Euphorbia geniculata*	Asia I	+			Colvin *et al.* (2006)
	ToLCBV-Ban4	*Parthenium hysterophorus*	Asia I	+			Colvin *et al.* (2006)
	ToLCBV-Ban4	*Acanthospermum hispidum*	Asia I	+			Colvin *et al.* (2006)
	ToLCBV-Ban4	*Ageratum conyzoides*	Asia I	+			Colvin *et al.* (2006)
Tomato Mottle Virus	ToMoV	*S. lycopersicum* cv. Florida Lanai	MEAM1	+			Mckenzie (2002)
Tomato yellow leaf curl China virus	TYLCCNV-Y10 DNAβ	*N. tabacum* cv. NC89	MEAM1	+			Jiu *et al.* (2007); Guo *et al.* (2010, 2012); Luan *et al.* (2013*c*)
	TYLCCNV-Y10 DNAβ	*N. tabacum* cv. NC89	Asia II 3		+		Jiu *et al.* (2007); Guo *et al.* (2010)
	TYLCCNV-Y10 DNAβ	*N. tabacum* cv. NC89	Mediterranean	+			Liu *et al.* (2010)
	TYLCCNV-Y10 DNAβ	*N. tabacum* cv. NC89	Asia II 1	+			Liu *et al.* (2010)
	TYLCCNV-Y10 DNAβ	*S. lycopersicum* cv. Hezuo903	MEAM1		+		Liu *et al.* (2009)
	TYLCCNV-Y10 DNAβ	*S. lycopersicum* cv. Hezuo903	Asia II 3			+	Liu *et al.* (2009)
	TYLCCNV-Y10 DNAβ	*S. lycopersicum* cv. FA-516	MEAM1			+	Liu (2009)
	TYLCCNV-Y10 DNAβ	*S. lycopersicum* cv. FA-516	Asia II 3			+	Liu (2009)
	TYLCCNV-Y10 DNAβ	*S. lycopersicum* cv. FA-189	MEAM1			+	Liu (2009)
	TYLCCNV-Y10 DNAβ	*S. lycopersicum* cv. FA-189	Asia II 3			+	Liu (2009)
Tomato yellow leaf curl virus	TYLCV-Shanghai	*S. lycopersicum* cv. Hezuo903	MEAM1		+		Liu *et al.* (2009)
	TYLCV-Shanghai	*S. lycopersicum* cv. Hezuo903	Asia II 3			+	Liu *et al.* (2009)
	TYLCV-Shanghai	*S. lycopersicum* cv. Zhongza 9	MEAM1			+	Pan *et al.* (2013)
	TYLCV-Shanghai	*S. lycopersicum* cv. Hezuo903	Mediterranean		+		Li *et al.* (2011)
	TYLCV-Shanghai	*S. lycopersicum* cv. Hezuo903	Asia II 1		+		Li *et al.* (2011)
	TYLCV-Shanghai	*S. lycopersicum* cv. Zhongza 9	Mediterranean	+			Pan *et al.* (2013)
	TYLCV-Ng	*S. lycopersicum* cv. House Momotaro	Mediterranean		+		Matsuura & Hoshino (2009)

Table 1. (*Cont.*)

Virus	Virus identifier	Host plant	Whitefly vector[1]	Effects on vector performance			References
				Positive	Neutral	Negative	
	TYLCV-Israel	*S. lycopersicum* cv. 8484	Unknown, likely MEAM1 or Mediterranean from Israel			+	Lapidot *et al.* (2001)
	TYLCV-Israel	*S. lycopersicum* cv. L27	Unknown, likely MEAM1 or Mediterranean from Israel			+	Lapidot *et al.* (2001)
	TYLCV-Israel	*S. lycopersicum* cv. Fiona	Unknown, likely MEAM1 or Mediterranean from Israel		+		Lapidot *et al.* (2001)
	TYLCV-Israel	*S. lycopersicum* cv. TY172	Unknown, likely MEAM1 or Mediterranean from Israel		+		Lapidot *et al.* (2001)
Recombination of *East African cassava mosaic virus* and *African cassava mosaic virus*	EACMV-UG	*M. esculenta* cv. Ebwanateraka	Unknown, collected from Uganda	+			Colvin *et al.* (2006)
Total (=36)				13	11	12	

[1] Names of the putative species of the *Bemisia tabaci* complex were taken from De Barro *et al.* (2011) and Hu *et al.* (2011); 'Unknown' indicates the identity of the whitefly species was unknown.

Fig. 1. Distribution of varying effects of viral infection of host plants on whitefly performance.

Whitefly–begomovirus interactions are often assumed to be mediated by plant defences (Belliure *et al.*, 2005; Colvin *et al.*, 2006; Stout *et al.*, 2006). However, how plant defence signalling pathways and defensive compounds affect these types of interaction remains poorly understood. By integrating ecological, mechanistic and molecular approaches, however, Zhang *et al.* (2012) recently demonstrated that jasmonic acid-associated defences in tobacco plants were suppressed by infection of TYLCCNV, thereby favouring the performance of the MEAM1 whitefly on virus-infected plants. Working on the same combination of virus, plant and whitefly with essentially the same multidisciplinary approach, Luan *et al.* (2013*c*) further showed that terpenoid synthesis and release were suppressed in the virus-infected plants, which become substantially more favourable to the performance of whitefly compared to uninfected plants. On the vector insect side of the interaction, the genes involved in the oxidative phosphorylation pathway and detoxification enzyme were down-regulated in MEAM1 individuals feeding on virus-infected plants, and reduced detoxification activity likely attenuated the energy costs, thereby enhancing whitefly performance (Luan *et al.*, 2013*b*).

Mechanisms related to changes in plant nutrition

Begomovirus infection may alter plant nutrition and, in turn, its suitability to whiteflies. A population of African cassava *B. tabaci* from Uganda increased more rapidly on *East African cassava mosaic virus*-Uganda (EACMV-UG)-infected than on uninfected cassava plants, and concurrently, the concentrations of four amino acids increased significantly in the phloem sap of the virus-infected compared to uninfected cassava plants (Colvin *et al.*, 2006). It seems that the mutualistic relationship between whiteflies and EACMV-UG may be achieved, at least in part, through improved nutrition in virus-infected plants. It is interesting to note that EACMV-UG is a recombinant virus of EACMV with *African cassava mosaic virus* (ACMV, Zhou *et al.*, 1997), and the improved performance of the African cassava *B. tabaci* on EACMV-UG-infected cassava plants compared to that on uninfected plants was not observed on cassava plants infected with ACMV alone (Thompson, 2002, 2011).

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Table 2. Performance of viruliferous and non-viruliferous whiteflies on begomovirus-free plants.

Virus	Virus identifier	Host plant	Whitefly vector[1]	Effects on vector performance			References
				Positive	Neutral	Negative	
Cotton leaf curl virus	CLCuV	*Gossypium hirsutum* cv. LHH144	MEAM1			+	Sidhu *et al.* (2009)
Tobacco curly shoot virus	TbCSV-Y35 DNAβ	*G. hirsutum* cv. Chuanmian109	MEAM1	+			Jiu *et al.* (2007)
	TbCSV-Y35 DNAβ	*G. hirsutum* cv. Chuanmian109	Asia II 3		+		Jiu *et al.* (2007)
Tomato yellow leaf curl China virus	TYLCCNV-Y10 DNAβ	*G. hirsutum* cv. Chuanmian109	MEAM1			+	Jiu *et al.* (2007)
	TYLCCNV-Y10 DNAβ	*G. hirsutum* cv. Chuanmian109	Asia II 3			+	Jiu *et al.* (2007)
Tomato yellow leaf curl virus	TYLCV-Israel	*Solanum lycopersicum* cv. FA144	MEAM1			+	Rubinstein & Czosnek (1997)
Total (=6)				1	1	4	

[1] Names of the putative species of the *Bemisia. tabaci* complex were taken from De Barro *et al.* (2011) and Hu *et al.* (2011).

Table 3. Manipulation of settling, probing and feeding behaviour of whiteflies directly by begomovirus or indirectly through begomovirus-infected plants.

Virus	Virus identifier	Host plant	Whitefly vector[1]	Indirect effect of virus on vector host preference for plants		Direct effect of virus on whitefly behaviour	References
				Infected plant	Uninfected plant		
Cotton leaf curl virus	CLCuV	*Gossypium hirsutum* cv. F846	Unknown, likely MEAM1 from Florida		+		Mann *et al.* (2009)
Tomato yellow leaf curl China virus	TYLCCNV-Y10 DNAβ	*Solanum lycopersicum* cv. Hezuo903	MEAM1	+			Pan *et al.* (2014)
Tomato yellow leaf curl virus	TYLCV	*S. lycopersicum*	Unknown		+		Berlinger (1986)
	TYLCV-Shanghai	*S. lycopersicum* cv. Zhongza 9	MEAM1			+	Liu *et al.* (2013)
	TYLCV-Shanghai	*S. lycopersicum* cv. Zhongza 9	Mediterranean			+	Liu *et al.* (2013)
	TYLCV-Israel	*Solanum melongena* cv. Black Beauty	Mediterranean			+	Moreno-Delafuente *et al.* (2013)
Total (=6)				1	2	3	

[1] Names of the putative species of the *Bemisia. tabaci* complex were taken from De Barro *et al.* (2011) and Hu *et al.* (2011); 'Unknown' indicates the identity of the whitefly species was unknown.

As noted above, the MEAM1 whitefly improved its performance on TYLCCNV-infected tobacco plants compared to uninfected plants (Jiu *et al.*, 2007). However, significant differences were not detected in terms of amino acid profiles, percentage of essential amino acids and sugars to the amino acids ratio between uninfected and TYLCCVN-infected tobacco plants (Wang *et al.*, 2012). Further analysis of the whitefly honeydews indicate that the whitefly improved nutritional assimilation on virus-infected plants compared to that on uninfected plants, and this improved nutritional assimilation of the whitefly on virus-infected plants was speculated to be associated with the suppressed plant defence to the whitefly by the virus (Wang *et al.*, 2012). It may also be related to the attenuation of energy costs associated with reduced detoxification activity required by the whitefly (Luan *et al.*, 2013*b*).

Possible roles of whitefly endosymbionts

Symbiotic bacteria (symbionts) are ubiquitous in hemipteran insects (Akman Gündüz & Douglas, 2009; Douglas, 2009). The endosymbiont '*Candidatus* Portiera aleyrodidarum' (Oceanospirillales), which has evolved with *B. tabaci* and is strictly vertically transmitted through bacteriocytes during reproduction, is called the primary endosymbiont of the whitefly. The primary endosymbiont provides its whitefly hosts with essential amino acids as well as carotenoids (Sloan & Moran, 2012). In addition to '*Candidatus* Portiera aleyrodidarum', seven secondary symbionts have been found in *B. tabaci*, including '*Candidatus* Cardinium hertigii' (Bacteroidales), '*Candidatus* Fritschea bemisiae' (Chlamydiales), '*Candidatus* Hamiltonella defensa' (Enterobacteriales), *Arsenophonus* spp. (Enterobacteriales), *Wolbachia* spp. (Rickettsiales) and '*Candidatus* Hemipteriphilus asiaticus' (Bing *et al.*, 2013). These secondary symbionts may have important effects on whitefly biology (Gottlieb *et al.*, 2010).

Rickettsia can be transferred from the whitefly *B. tabaci* to a plant (Caspi-Fluger *et al.*, 2011). Some types of endosymbionts may regulate the plant defences (Casteel *et al.*, 2012; Frago *et al.*, 2012). Such regulation may influence the transmission of virus and whitefly–begomovirus interactions (Gutiérrez *et al.*, 2013). As *B. tabaci* survival was influenced by an interaction effect between whitefly viruliferous status and amino acid diet type (Douglas, 2009), the variation of symbiont composition in whiteflies may be expected to affect plant mediated whitefly–begomovirus interactions.

Future directions of research

Expand the number and diversity of pathosystems for study

In terms of the influence of begomovirus infection on performance of whitefly vectors, the case studies available so far are distributed evenly among positive, neutral and negative effects (fig. 1). This pattern seems to deviate from those observed in other groups of PT viruses, where proportionally more cases of positive effects have been recorded (Mauck *et al.*, 2012). If the pattern depicted in fig. 1 is real and not due to the biases identified above, one may suggest that it is related to genome structures of viruses, as begomoviruses are DNA viruses whereas all other PT viruses that have been examined belong to RNA viruses (Mauck *et al.*, 2012). Different groups of plant viruses may have differential impact on plant physiology during infection, which probably affects vector–virus interactions.

As discussed above, the number of case studies is currently small considering the possible combinations of interactions in nature (over 200 species of begomoviruses × more than 30 putative cryptic *B. tabaci* species × 100 s of crop species and varieties (Navas-Castillo *et al.*, 2011; Liu *et al.*, 2012). Further, invasions of some begomoviruses and whiteflies into new regions have created new tripartite associations. The diversity of plant-mediated interactions between begomoviruses and whiteflies is apparently enormous and will certainly increase with time, usually driven by human movements of plant material around the globe. We conclude, therefore, that with the limited number of case studies available so far (tables 1–3), any generalization of patterns in the interactions is premature. To proceed towards examination of a general pattern, we must expand the number and diversity of pathosystems for investigation with regard to all aspects of the virus–host–vector interactions. In particular, studies involving longstanding tripartite associations, where evolution has had a chance to operate for a significant period, will be particularly instructive.

We also propose that the diversity and identities of each of the three partners in the interactions needs to be considered and accurately documented in future studies. (1) Virus diversity: groups by genome structure, i.e. monopartite, monopartite with satellite DNA and bipartite; and different isolates or strains of viruses to examine the genetic basis for the viral effects. For example, cassava plants infected with EACMV does not benefit *B. tabaci*; in contrast, cassava plants infected with the recombinant virus EACMV-UG involving genomic components of both EACMV and ACMV promotes population increase of the vector whitefly (table 1; Thompson 2002; Colvin *et al.*, 2006). (2) Whitefly diversity: different genetic groups or cryptic species, invasive and indigenous species, different biotypes of the same cryptic species to investigate the genetic basis for the vector effects. For instance, the invasive MEAM1 benefits from TYLCCNV-infected tobacco plants, whereas the indigenous Asia II 3 does not (table 1; Jiu *et al.*, 2007). Due to the distorted history of *B. tabaci* taxonomy and the enormous genetic diversity within this whitefly species complex, it is extremely important to know exactly the phylogenetic group and sub-clade of *B. tabaci* that is being used in each study (Gill & Brown, 2010; Liu *et al.*, 2012). It is increasingly apparent, for example, that within the Sub-Saharan Africa 1 there is a lot of biological variation that we did not recognize previously and this probably affects the outcome of the interactions when different populations/virus species are used (Boykin *et al.*, 2012; Mugerwa *et al.*, 2012). For future interaction studies, we may need to 'type' the *B. tabaci* populations much more rigorously by sequencing more than just their mtCO1 gene, perhaps some nuclear genes as well (Boykin *et al.*, 2012). (3) Plant diversity: different families, species, varieties/cultivars of the same species, and different levels of constitutive suitability to whitefly and/or virus to reveal the genetic basis for the plant effects. For example, MEAM1 performed better on TYLCCNV-infected tobacco plants compared to uninfected plants, whereas such a positive association between MEAM1 and TYLCCNV was not observed with TYLCCNV-infected tomato plants (table 1; Jiu *et al.*, 2007; Liu *et al.*, 2009). (4) Novel vector–virus–plant systems brought about by biological invasions: invasion events of both whiteflies and begomoviruses have been increasing in recent years to create novel tripartite associations, which impose new challenges to world agriculture, but

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provide unique opportunities to study novel interactions in nature (De Barro *et al*., 2008; Mauck *et al*., 2012; Péréfarres *et al*., 2012).

Investigate molecular and biochemical mechanisms

The recent progress of research on molecular and biochemical mechanisms of plant-mediated whitefly–begomovirus interactions demonstrates the complexity as well as the tractability of the subject when adopting a multidisciplinary approach and the latest technology (e.g. Zhang *et al*., 2012; Luan *et al*., 2013*b*, *c*). To understand the underlying mechanisms of the tripartite interactions, each of the three bipartite interactions of virus–vector, plant–vector and virus–plant needs to be examined in detail and integrated for further analysis to reveal both direct and indirect effects (Blanc *et al*., 2011; Luan *et al*., 2011, 2013*b*, *c*). In many cases, particular effort may be required to separate the direct from the indirect effects, e.g. direct effect of virus on vector and indirect effect of virus on vector via plants. Here, we elaborate briefly on a strategy to explore the molecular and biochemical mechanisms.

On the plant side of the interactions, crosstalk roles between individual defence signalling pathways and various classes of metabolites or toxic proteins involved in tripartite interactions should be determined. Moreover, other plant properties such as size, shape, colour, odour and development stage and disease severity must also be considered in the investigations (Wang *et al*., 2012; Zhang *et al*., 2012; Gutiérrez *et al*., 2013). On the insect side of the interactions, the role of the correctly identified putative *B. tabaci* species and its endosymbionts should be considered, since endosymbionts constitute an essential part of the insect in its structure and functions (Dale& Moran, 2006; Frago *et al*., 2012; Bing *et al*., 2013). Specifically, efforts are warranted to investigate: (1) effects of insect proteins or endosymbionts on efficiency of virus transmission (Gottlieb *et al*., 2010; Götz *et al*., 2012); (2) roles of salivary proteins or endosymbionts in manipulating plant physiology and in turn virus transmission, virus evolution and vector–virus interactions (Blanc *et al*., 2011; Casteel *et al*., 2012; Gutiérrez *et al*., 2013); and (3) effects of the insect itself or endosymbionts on nutritional assimilation and other metabolic regulation of vectors in response to changes in the physiology of virus-infected plants and to invasion by plant viruses (Luan *et al*., 2011, 2013*b*; Thompson, 2011; Wang *et al*., 2012; Zhang *et al*., 2012). On the begomovirus side of the interactions, the pathogenicity factors and other proteins regulating plant physiology or whitefly behaviour require further identification (Czosnek & Ghanim, 2012; Ingwell *et al*., 2012). Ultimately, examination on many of the effects from bipartite interactions must be taken one step further to decipher their influence via other partners in the associations.

Examine virus–host–vector interactions in the field

For the agricultural entomologist, ecologist or evolutionary biologist, the necessity of investigating the interactions between begomoviruses, whiteflies and plants in the field is self-evident, because the tripartite interactions are often important determinants of the vector population dynamics and virus disease epidemiology (Colvin *et al*., 2004, 2006). In this regard, the diversity of begomoviruses and their mode of infection again must be considered, which include alien and indigenous viruses, cryptic viruses that do not cause symptoms, and new viruses via mutation and/or combination, as well co-infection of multiple geminiviruses that produces synergistic effects on transmission (da Silva *et al*., 2011; Renteria-Canett *et al*., 2011; Varma *et al*., 2011). Apart from studies on pathosystems in agriculturally relevant ecosystems, research on virus–host–vector interactions in natural plant communities will be particularly instructive (see above), especially in the context of gaining insight into the evolution of these interactions.

Field studies are always challenging, because so many important variables are not controllable. Studies using a correlative approach in this context may be more feasible in many circumstances than those using a manipulative approach. Correlative field studies may help to show significant associations between incidences, abundance and/or severities of whiteflies and viruses (e.g. Colvin *et al*., 2004) and provide a useful background for manipulative studies in the laboratory and field. Where feasible, manipulative field studies should also be pursued, because compared to correlative studies, they can yield stronger evidence for causality in the real world.

Ramification of community effects of the tripartite interactions

The ramification of community effects of the plant–virus–vector interactions has seldom been tested (Stout *et al*., 2006). In nature, other pathogens, herbivores and natural enemies may co-occur with whiteflies in begomovirus-infected plants (Mayer *et al*., 2002; Inbar & Gerling, 2008). These microbes and herbivores may interfere with or be affected by plant-mediated whitefly–begomovirus interactions. In addition, abiotic factors and environmental heterogeneity also influence these tripartite interactions (Rodelo-Urrego *et al*., 2013). Thus, in a broader perspective, how begomovirus-induced changes in host phenotype influence (and are influenced by) other pathogens and non-vector organisms cannot be ignored. Equally important, the effects of major abiotic factors such as temperature, humidity, fertilizer and soil type must be considered in field-based investigations of begomovirus–whitefly–plant interactions.

In summary, this review reveals that we are just starting to understand the tripartite interactions between whiteflies, begomoviruses and plants. As both whiteflies and begomoviruses are two groups of the most important and invasive pests of world agriculture, major effort to reveal the patterns and underlying mechanisms of the plant-mediated, vector–virus interactions is warranted in the years to come. Research in this area will likely produce breakthroughs not only in understanding vector–virus–plant interactions but also the development of urgently needed new strategies for the management of whiteflies and begomoviruses. Unravelling the role of plant defence traits in virus–vector interactions, for example, will likely promote development of new strategies for virus control through interference of vector transmission or of vector control through interference of whitefly development (Rodríguez-López *et al*., 2011; Bragard *et al*., 2013; Luan *et al*., 2013*a*). As such, future research in this field has the clear potential to create novel applied solutions for some of the greatest pest and crop-disease problems currently facing farmers in tropical and sub-tropical regions of the globe.

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