MINI-REVIEW

A comprehensive review: persistence, circulative transmission of begomovirus by whitefly vectors

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Abstract

Plant pathogenic viruses rely on insect vectors for transmission. Among insects, hemipterans, including aphids, leafhoppers, plant hoppers, whiteflies, mealybugs, true bugs, and certain treehoppers, are predominant as vectors for plant viruses. Plant viruses contribute to more than 47% of worldwide plant diseases. *Bemisia tabaci* is one of the most threatening pests in agriculture, causing significant losses to many important crops on a global scale. Among the most destructive viruses facilitated by whiteflies are begomoviruses (Geminiviridae), forming an emergent and critical group of plant pathogens solely transmitted by the sweet-potato whitefly *Bemisia tabaci*. In this comprehensive review, we delve into the wealth of data concerning the diverse transmission capacities of various whitefly species, including cryptic members of the *B. tabaci* complex, in their role as vectors for begomovirus and other viruses. We presented a meticulous analysis of the factors influencing viral transmission by whiteflies, shedding light on the intricate interplay of viruse and their insect vectors. Moreover, this review serves as a crucial reference, presenting a profound exploration of the intricate relationships between whitefly vectors and begomoviruses, and providing valuable insights for the scientific community working towards the sustainable management of plant diseases in the face of evolving challenges posed by these complex biological systems.

Keywords Aleyrodidae · Begomovirus · Hemiptera · Propagation · Transmission · Whitefly

Abbreviations

AAP	acquisition access period
AbMV	Abutilon mosaic virus
CdTV	Chino del tomate virus
CuLCrV	cucurbit leaf crumple virus
CypB	cyclophilin B
EACMV	UG-East African cassava mosaic virus-Uganda
ESTs	expressed sequence tags
FISH	Fluorescence in situ hybridization
HSP	70-heat shock protein 70
IAP	immunization access period
MAPK	mitogen activated protein kinase
MEAM1	Middle East-Asia Minor 1
MED	Mediterranean
PGRP	peptidoglycan recognition protein
PSGs	principal salivary glands
SiGMV	sida golden mosaic virus
SLCuV	squash leaf curl virus
SSA1	Sub-Saharan Africa
TEM	Transmission electron microscopy
ToMoV	tobacco mosaic virus
TYLCCNV	tomato yellow leaf curl china virus
TYLCSV	tomato yellow leaf curl Sardinia virus
TYLCV	tomato yellow leaf curl virus
WmCSV	watermelon chlorotic stunt virus

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Introduction

Recent studies reveal that more than 80% of plant pathogenic viruses rely on insect vectors for transmission (Hogenhout et al. 2008; Navas-Castillo et al. 2011b; Gadhave et al. 2020; Naveed et al. 2023). Among insects, hemipterans, including aphids, leafhoppers, plant hoppers, whiteflies, mealybugs, true bugs, and certain treehoppers, are predominant as vectors for plant viruses. The whitefly, *Bemisia tabaci* (Hemiptera: Aleyrodidae) is a widespread pest of agriculture crops in tropical, subtropical and temperate regions worldwide (Navas-Castillo et al. 2011a; Naveed et al. 2023). *B. tabaci* is a globally invasive species that causes serious economic damage to agroecosystems by direct feeding (triggers the physiological symptoms) and by transmitting more than 320 plant viruses belonging to several virus families including Begomovirus, Crinivirus, Carlavirus, Torradovirus and Ipomovirus (Navas-Castillo et al. 2011b; Zerbini et al. 2017; Guo et al. 2021; Li et al. 2023). Additionally, by excreting honeydew that reduces photosynthetic activity and spreading plant viruses, resulted in damage of over 300 million USD dollar annually (Navas-Castillo et al. 2011a). and (loss of 20–100% in vegetable crops). It has an impact on the amount and quality of the crop. Chemicals have been used to control sap sucking insect pests to minimize yield losses (Abbas et al. 2021).According to (Czosnek et al. 2017), *B. tabaci* transmits begomovirus by persistent circulation, which requires the viral particles to pass the midgut barrier and enter the salivary glands through hemolymph. In the midgut of *B. tabaci*, a number of proteins, including heat shock protein 70 (HSP-70), cyclophilin B (CypB), and peptidoglycan recognition protein (PGRP), have been shown to interact with the begomovirus coat protein. The tomato yellow leaf curl virus (TYLCV) is substantially responsible for the present knowledge of the interactions between *B. tabaci* and begomoviruses. On the roles of *B. tabaci* genes in the spread of other common begomoviruses, there is scant data. It is made up of a number of cryptic species with unique phylogeographical ranges (Mugerwa et al. 2021). These cryptic species and their haplotypes are structurally indistinguishable from one another, and some have been identified found to have distinctive biological traits like fecundity, endosymbiont complement, host spectrum, a tendency to acquire insecticide resistance, environmentally friendly modification, and, crucially, spread particularity involving begomoviruses (Chi et al. 2020; Mugerwa et al. 2021).

Begomoviruses have a distinctive morphology that consists of twinned or paired icosahedral particles. Their single-stranded circular DNA genome sizes vary between 2800 (monopartite) to 5200 (bipartite) nt each. They are petite, non-enveloped viruses (Zerbini et al. 2017). Bipartite viruses like sida golden mosaic virus (SiGMV), and cucurbit leaf crumple virus (CuLCrV),contain both DNA-A and DNA-B components, but monopartite viruses like TYLCV only have one DNA component (Zerbini et al. 2017). Whiteflies have to consume viral particles with their stylets when eating in order for begomoviruses to be successfully transmitted. The food canal allows viruses to exit and travel to the oesophagus and midgut, where they enter the hemolymph. The virus is subsequently endocytosed into the primary salivary glands and ingested into the plant phloem along with the saliva (He et al. 2015). According to (Czosnek et al. 2017), interactions between the viral coat protein and potential receptors as well as other whitefly proteins are necessary for the circulatory transmission of begomoviruses in *B. tabaci*. Certain receptors and begomovirus-interacting proteins that were recently identified include the GroEL chaperone protein, heat shock proteins, midgut proteins, peptidyl-prolyl isomerase protein genes, and the peptidoglycan recognition protein gene (Kanakala and Ghanim 2016; Rana et al. 2016). To understand how viruses are transmitted by whiteflies, it is essential to understand that there may be other other factors at play.

Exotic and prevalent among the *B. tabaci* species complex members include the Middle East-Asia Minor 1 (MEAM1), also known as the North Africa-Middle East mitotype or B biotype, and the Mediterranean (MED), also known as the North Africa-Mediterranean mitotype or Q biotype (de Moya et al. 2019). *B. tabaci* MEAM1 was initially found in the US in the mid-1980s after displacing the native New World 1 species, commonly known as the American Tropics (AMTROP) cryptic species or A biotype. Contrarily, *B. tabaci* MED was only recently discovered in 2004 and is primarily found in ornamentals planted in greenhouses (Dennehy et al. 2005). Recently, agricultural crops in Florida and Georgia were reported to have *B. tabaci* MED (Gautam et al. 2020b). *B. tabaci* MEAM1 is found on cotton and field-cultivated vegetable crops like tomato, eggplant, snap beans and cucurbits in the Southeast of the United States (Gautam et al. 2020b; McKenzie et al. 2020). The viruses that cause illnesses, TYLCV, SiGMV, and CuLCrV, are known to be spread in various cropping systems by *B. tabaci* MEAM1 (Agarwal et al. 2021). According to laboratory investigations, *B. tabaci* MED tissues accumulated less of the two New World begomoviruses than *B. tabaci* MEAM1 tissues and did not transmit SiGMV and CuLCrV, despite being a powerful TYLCV vector (Venkataravanappa et al. 2017). Studies revealing the key determinants of these begomoviruses' differential transmission by the *B. tabaci* MEAM1 and MED are essential since the molecular and cellular processes underpinning by transmit differently including various other begomoviruses have not been fully understood.

Plant viruses have the ability to modify the phenotypic and physiological characteristics of their hosts, which in turn affects vector fitness and preference, occasionally promoting the propagation of the virus (Mauck et al. 2012). Depending on the host plant, Begomovirus infestations were said to have a variety of effects on the fitness and choice of vectors (Gautam et al. 2020b). Although virus-associated macro-effects on whiteflies have been investigated using high throughput sequencing technologies, the mechanisms underlying these begomoviruses' macro-effects on their whitefly vectors are still poorly understood (Catto et al. 2022).

The virus-associated micro-effects of begomoviruses and criniviruses have been investigated for *B. tabaci* (MEAM1 and MED) using a variety of omics platforms, including transcriptomics (Li et al. 2020; Nekkanti et al. 2022). What isn't obvious, though, is whether micro-effects are caused by the virus's direct impact on the vector or by the indirect impacts of the virus's modification of the host plant's physiological changes after infection. To lessen the carrier-modulated downstream impacts of plant viruses on their vectors through feeding on the plant sap of virus-infected hosts, it is crucial to transport viruliferous whiteflies from a virus-infected host plant to a virus non-host plant for gut cleansing before RNA extraction (Ding et al. 2019). By better comprehending the begomovirus transmission mechanisms by *B. tabaci* and the identification of the virus and insect proteins involved in the translocation of the virus in the vector, new strategies for viral control may be developed. We discuss recent developments in this area and outline potential future research avenues to comprehend begomovirus transmission by whiteflies in this review.

B. tabaci acquisition, retention, and transmission of begomovirus

A begomovirus infection cycle begins when an (Fig. 1) insect stylet contacts virus particles in plant phloem (Fig. 2). The reported 10 to 60 min lengths for the acquisition access period (AAP) and immunization access period (IAP) are minimum, when given the same leaf for the same amount of time, different whiteflies pick up varying amounts of virus. After 5 min of AAP, 20% of single insects had TYLCV DNA discovered using PCR; after 10 min of AAP, all insects have TYLCV DNA found (Ghanim et al. 2001). The bipartite
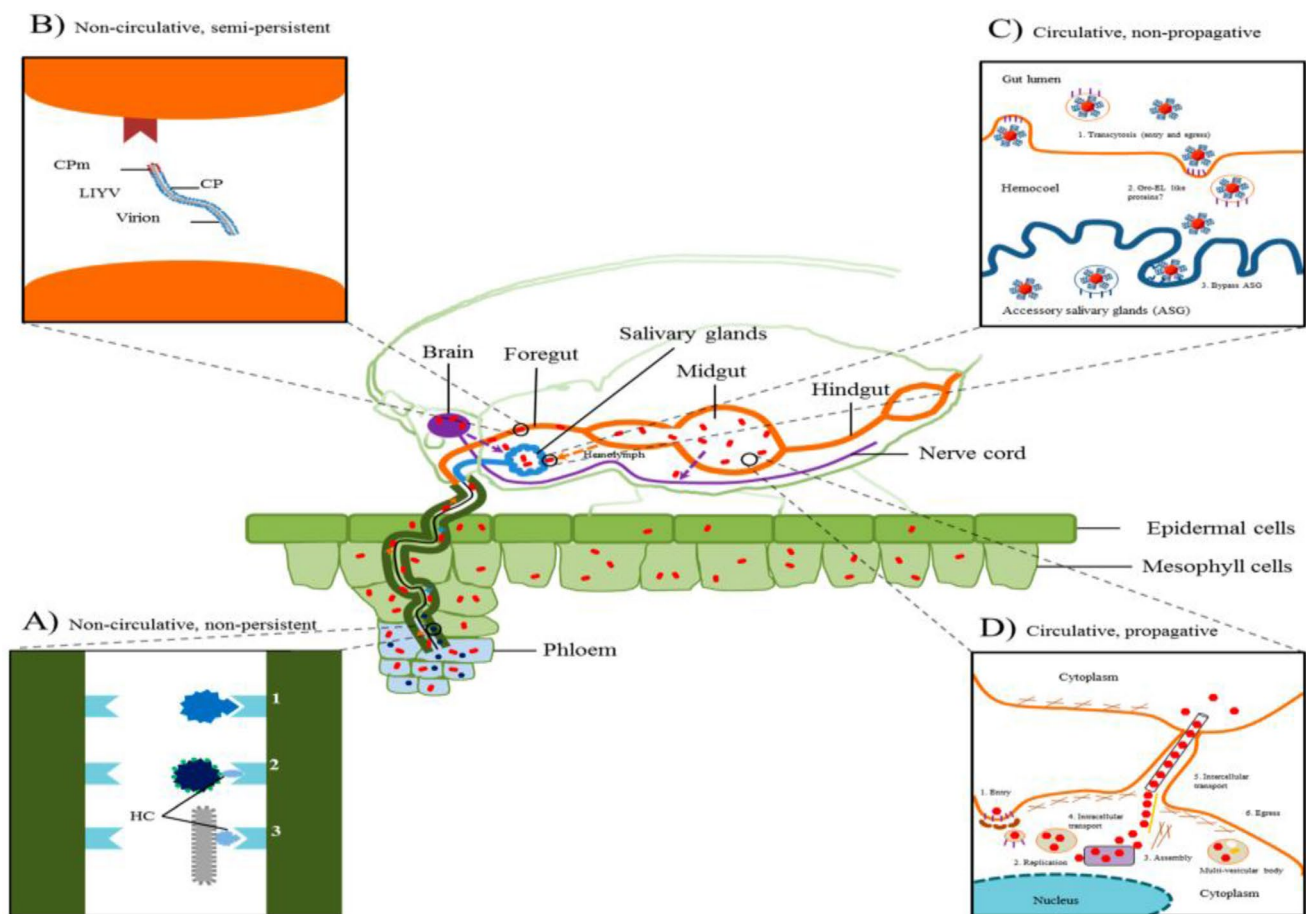
Fig. 1 Techniques used by insect vectors to transmit plant viruses (Dietzgen et al., 2016)

begomovirus Squash leaf curl virus (SLCuV) and TYLCV are both effectively transmitted by *B. tabaci*. Following a 24-hours AAP, a single whitefly can infect a tomato plant, and when 5–15 insects are utilised, transmission effectiveness exceeds 100% (Czosnek and Ghanim 2012). Begomoviruses like TYLCV and SLCuV are kept in the whitefly vector for the duration of its life after acquisition, whereas tomato yellow leaf curl Sardinia virus (TYLCSV) becomes undetectable after around 20 days (Czosnek and Ghanim 2012). As whitefly ages the efficacy of TYLCV transmission declines and is inversely connected with the amount of virus that can be found in the vector. However, a fraction of the population can have a virus throughout their entire life (Czosnek and Ghanim 2012).

There are various issues with the biochemical reaction of the virus in insects given that the viral DNA is linked to whiteflies for a much longer period of time than they can transmit the virus. For instance, transmission only continues for eight days following an initial AAP while TYLCSV DNA is traceable for twenty days. Since TYLCV DNA and CP are not preserved in *B. tabaci* for the same period of time, it is likely that virions, rather than viral DNA degradation, are to blame for the decline in transmission. The bipartite begomovirus Abutilon mosaic virus (AbMV) showed comparable outcomes as well (Morin et al. 2000). A begomovirus must first enter a latency period (Fig. 2), during which it travels from the midgut to the blood vessels (insect blood), the salivary glands, and the terminal organ before being discharged with saliva during feeding, before it can be transferred (Ghanim et al. 2001). Additionally, since male whiteflies have been found to be less effective vectors, the sex of the whitefly may potentially have an impact on the virus' ability to spread. The typical latency times for various begomoviruses range from 8 to 17 h for TYLCSV, 19 h for SLCuV, and 17 h for TYLCV (Ghanim et al. 2001). About 8 h after the AAP, SLCuV can be found in the produced saliva, although the minimum latent duration is roughly 19 h. TYLCV, on the other hand, was found in the salivary gland seven hours after the AAP started, and effective injection took place an hour later (Ghanim et al. 2001). These latter findings are consistent with the hypothesis that, for each virus species, a critical but unidentified quantity of a effective infection of a new host plant requires the accumulation of virions in the salivary glands. The majority of the *B. tabaci* species complex members have been found to be capable of transmitting most, if not all, begomoviruses (Polston et al. 2014), but the translocation efficacy varies greatly between the various *B. tabaci* species (Li et al. 2010). Even within the same species' populations, differences in transmission efficiency have been noted (Kollenberg et al. 2014). In contrast, TYLCSV translocation efficacy does not vary amid species (Jiang et al. 2004), despite the fact that the transmitting effectiveness of TYLCV or Chino del tomate virus (CdTV) by MEAM1, MED, and other *B. tabaci* species differs up to 10-fold (Pan et al. 2012). Different life history parameters (Pan et al. 2013), feeding habits, host plant preferences, bacterial endosymbionts harboured by whiteflies (Kliot et al. 2014), and the inherited make-up

a Primary Salivary Glands
b Accessory Salivary Glands
c Fat bodies
d Flight muscles
e Virus particle
f Esophagus
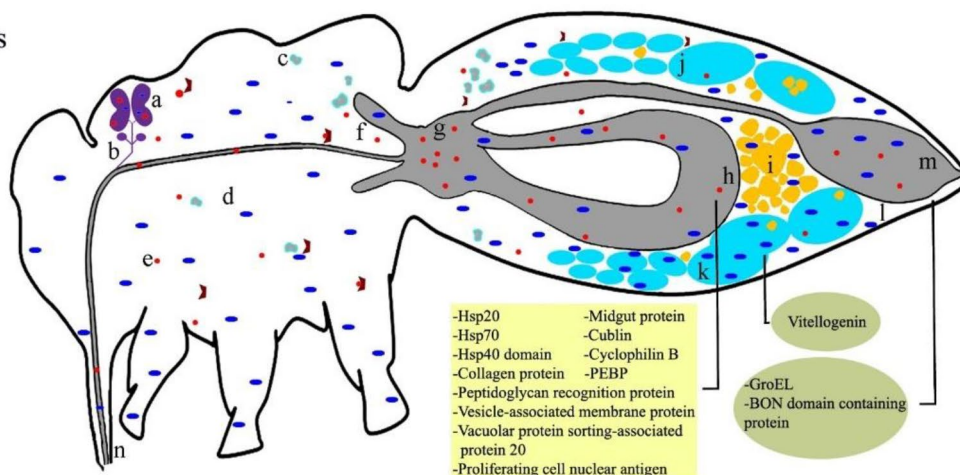g Filter chamber
h midgut
i Bacteriocytes
j Immature egg
k mature egg
l Hemolymph
m Hindgut
n Stylet

-Hsp20   -Midgut protein
-Hsp70   -Cublin
-Hsp40 domain   -Cyclophilin B
-Collagen protein -PEBP
-Peptidoglycan recognition protein
-Vesicle-associated membrane protein
-Vacuolar protein sorting-associated protein 20
-Proliferating cell nuclear antigen

Vitellogenin

-GroEL
-BON domain containing protein

Fig. 2 The intricate inner whitefly structures are pivotal for the *B. tabaci* species to transmit plant viruses in a circulative manner. The virus **e** is acquired when the insect feeds on phloem sap, then traverses through the stylet **n** and esophagus **f** to reach the midgut **h**. In the filter chamber region **g**, the virus particles breach the protective barriers of the midgut, entering the hemolymph **l** by overcoming the midgut plasmalemma and epithelial brush border. Once in the hemolymph, the virus circulates, eventually reaching the primary salivary glands **a**. Within these glands, the virus travels through the basal lamina and secretory cells to reach the central lumen, connecting to the salivary gland duct. During feeding, the virus exits the body through the salivary canal. Notably, the accessory glands **b** are not involved in this transmission process. Some virus particles that do not enter the hemolymph are expelled with the honeydew through the hindgut. Furthermore, the virus can infiltrate developing oocytes **j** and eggs **k**, potentially transmitting to the next generation through transovarial means. Additionally, endosymbionts **i**) significantly contribute in transmission by secreting GroEL into the hemolymph (Naveed et al. 2023)

of the insect population may be responsible for different *B. tabaci* species' transmission capacities (Fig. 3). The majority of the previously listed parameters are likely regulated by the genetic makeup of insects.

Propagation of the begomovirus in *B. tabaci*

During distribution, begomovirus virions migrate from the insect midgut epithelial cells into the hemolymph. Viral particles enter the principal salivary glands (PSGs) while still in the hemolymph and travel there before being ingested into the plant with saliva reviewed in (Ghanim 2014). Although no such receptors have yet been identified, it is hypothesised that the begomovirus virions are transported by receptor-mediated mechanisms from the midgut to the hemolymph and from the hemolymph to the salivary glands (Fig. 4). Using PCR on tissues that had been dissected and separated from viruliferous whiteflies that had picked up the virus during time course studies, the rate of TYLCV circulation in the whitefly was determined. After AAP, TYLCV DNA is found in the brain 10 min later, in the midgut 40 min later, and in the hemolymph 90 min later. For SLCuV, similar findings were seen. Immunolocalization tests using antibodies to the viral CP showed that viable virions of the virus

are present throughout the insect's body. Transmission electron microscopy (TEM) and Fluorescence in situ hybridization (FISH) were utilized to pinpoint the location of the virus within the insect's stylet, midgut, and PSGs (Brown and Czosnek 2002). For TYLCSV, similar outcomes were attained (Caciagli et al. 2009).

Begomoviruses as they replicate inside *B. tabaci*

The classification of begomoviruses as circulative, non-replicative viruses disseminated by *B. tabaci*, however earlier research raises the possibility that viral transcriptional activity may take place inside the insect. The probability of TYLCV and TYLCSV as infectious agents for a longer time than the latent stage, which is frequently for the entire insect, increases the likelihood of virus propagation within the host (Czosnek and Ghanim 2012; Fang et al. 2013b). A buildup of viral DNA in *B. tabaci* after it had consumed TYLCV-infected plants before moving on to TYLCV-unaffected plants has been interpreted as TYLCV replication in its vector (Czosnek et al. 2001). For TYLCSV, however, no comparable buildup was seen. In whiteflies that had contracted and hold the virus, a qRT-PCR method was utilized to measure
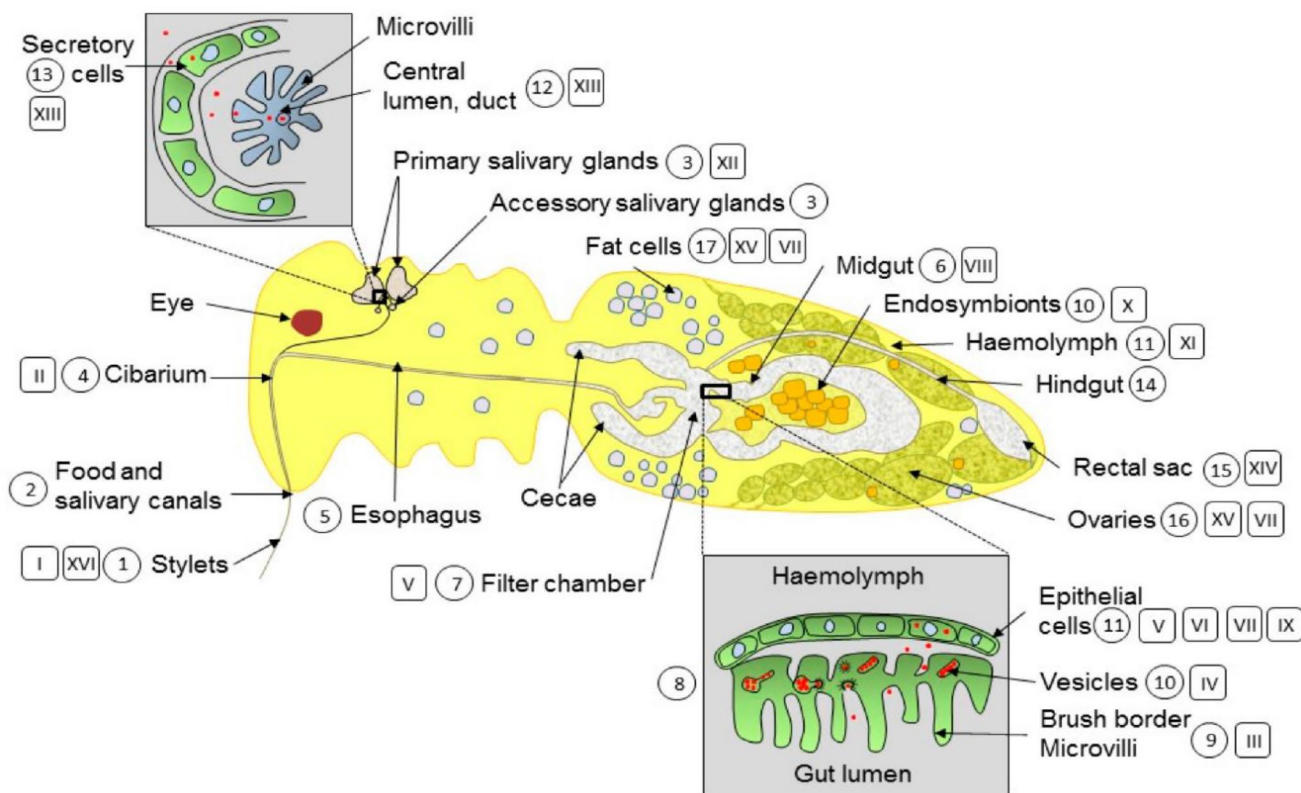
Fig. 3 A female whitefly longitudinal cross-sectional drawing showing the incredible journey of begomovirus in their specific vector (Czosnek et al. 2017)
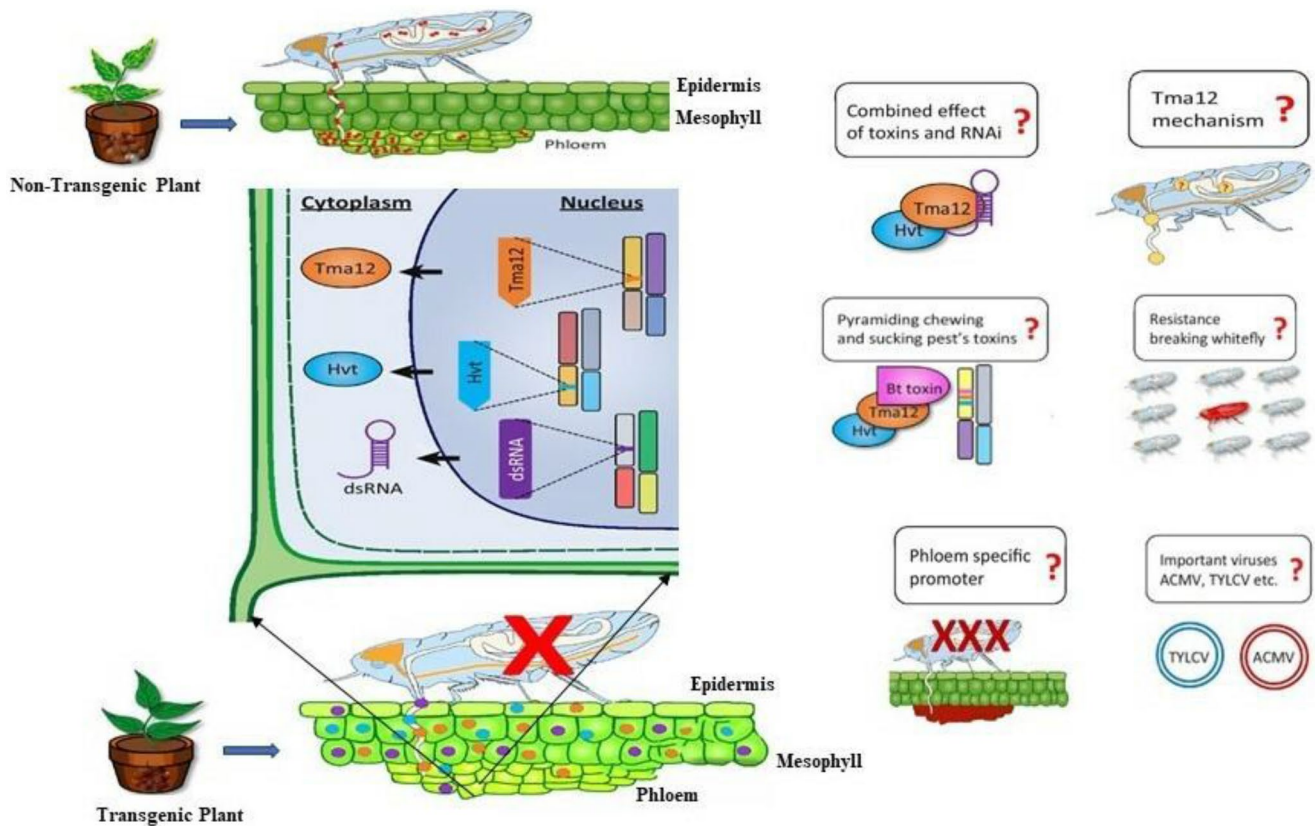
Fig. 4 Diagrammatic illustration of dual resistance to begeomovirus and *B. tabaci*. By sucking the sap from non-transgenic (NT) plants' phloem, *B. tabaci* spreads begomoviruses, or red geminate particles. The resulting NT plants show classic signs of begomovirus infection, such as curling of the leaves, vein yellowing, and foliar yellow mosaics. On the other hand, the transgenic plants (T) express toxins that target essential *B. tabaci* osmotic regulators or actins, such as Tma12 (orange) and Hvt (blue), or double-stranded RNA (dsRNA; purple). The transgenic plants show no symptoms and are poisonous to *B. tabaci* when fed, which eventually results in *B. tabaci* death and protects it from begomoviruses. The following are some unanswered concerns and potential paths forward, indicated by red question marks: (i) Is it possible to create broad-spectrum resistance by pyramiding several toxins against insects that chew and sap? (ii) How is *B. tabaci* killed by Tma12? (iii) If expressed from promoters unique to the phloem, will dsRNA and Tma12 function better? (iv) Will *B. tabaci* become resistant as a result of the toxins?

transcripts from specific viral genes of TYLCV and ToMoV (Sinisterra et al. 2005). After being transferred from tomato plants, the virus' host, to cotton plants, the virus' non-host, the levels of ToMoV transcripts speedily drop, whereas TYLCV transcript levels rise and are easily recognized after 7 days. These findings confirm that the TYLCV gene is actively being transcribed and that ToMoV does not have this activity (Ghanim et al. 2009). Although the reproduction of AbMV, a different begomovirus, was hypothesized, no evidence of replication in the vector was found.

Whitefly-begomovirus associations include specific mechanisms and proteins

Regardless of substantial attempts, little progress has been made in identifying the insect proteins implicated in begomovirus transmission. The accessibility of vector and non-vector *B. tabaci* populations may be very helpful in identifying receptors and other proteins concerned in begomovirus transmission in the insect. When TYLCV and watermelon chlorotic stunt virus (WmCSV) distribution patterns in vector and non-vector populations of MEAM1 species were compared, (Kollenberg et al. 2014) discovered that the vector strain had significantly higher uptake and concentrations of both viruses than the non-vector strain, in which only minute amounts of virus were found in the midgut and salivary glands. According to (Kollenberg et al. 2014), these findings point to the lack or alteration of a receptor or receptors implicated in begomovirus translocation. Bt HSP-16, a 16 kDa small heat shock protein from the HSP-20 family, was found to be associated with the TYLCSV CP in a different study, but its function in virus transmission was not confirmed (Ohnesorge and Bejarano 2009). To examine more extensive transcriptional response of *B. tabaci* to begomovirus acquirement or preservation,

an initial step in this manner was the development of an enormous scale expressed sequence tags (ESTs) sequencing analysis of *B. tabaci* from different phases of life of the insect, including insect adults that had picked up TYLCV and ToMoV (Liu et al. 2013). A spotted DNA microarray with 6000 distinct *B. tabaci* ESTs was able to be designed as a result of this study, which produced more than 20,000 ESTs (Leshkowitz et al. 2006). The reaction of *B. tabaci* to the acquirement and preservation of begomoviruses was investigated using DNA microarrays (Götz et al. 2012). Using this method, another heat shock protein (HSP-70) was discovered that interacts both in vitro and in vivo with the TYLCV and SLCuV CPs (Götz et al. 2012). Anti-HSP70 antibodies artificially fed to viruliferous whiteflies increased the transmission of TYLCV, indicating an inhibitory role for HSP-70 in begomovirus transmission (Götz et al. 2012). Further research into the whitefly response to the TYLCCNV was conducted utilising next-generation sequencing on the Illumina platform (Luan et al. 2011). Using this method, 1606 *B. tabaci* genes participating in 157 metabolic pathways were found to have distinct expression patterns in response to the acquisition and retention of TYLCCNV. According to those findings, a begomovirus can alter the cell cycle and basic metabolism while also inducing an immunological response in whiteflies. This study also showed that TYLCCNV invades ovaries and fat body tissues and triggers mechanisms connected to autophagy. By reducing the expression of genes involved in the Toll signalling and mitogen activated protein kinase (MAPK) pathways, those molecular modifications also suppressed immunological responses in the whitefly (Luan et al. 2011). To find putative receptors or proteins associated in begomovirus transmission, the transcriptome of the PSGs of MED *B. tabaci* was analysed (Su et al. 2012). According to (Wei et al. 2014), B. *tabaci* PSGs play a crucial role in the spread of begomoviruses. 13,615 unigenes were found including numerous highly expressed genes that code for secretory proteins or have other functions that may be related to viral transmission or passing (Su et al. 2012). Some cells in the PSGs, particularly those near the secretory areas, are a key location that regulates the specificity of TYLCV and TYLCCNV transmission (Wei et al. 2014).

Differential transmission determinants

Whitefly factors

Most of the data on potential variables that might be at work has come from studies on the differential spreading of plant viruses by diverse whitefly species. For instance, in this context, the geographic origin of populations of begomovirus and *B. tabaci* has been examined. Thus, the first proof that the begomoviruses' whitefly transmission efficiency were higher when the virus and the vector utilized for transmission, either Western Africa or the Indian Subcontinent, were from the same geographic origin than when their origins did not overlap (McGRATH and Harrison 1995). Later, it was discovered that NW whiteflies, which are endemic to the Americas, are more effective transmitters of a New World begomovirus than MEAM1, which is indigenous to the Middle East and Asia Minor (Idris et al. 2001). When researching *B. tabaci* populations from Africa and the Indian Subcontinent and cassava mosaic begomoviruses, a similar conclusion was drawn (Maruthi et al. 2002). Additional evidence for this finding came from reports on numerous viruses, including TYLCV, EuMV, CLCuMuV, and TbCSV (Li et al. 2010; Chen et al. 2016; De Marchi et al. 2017; Pan et al. 2018a, b). There are several exceptions to this rule, though; it was discovered that various begomoviruses, including ToLCBaV, PaLCuCNV, and TYLCCNV, are spread more effectively by the invasive MEAM1 than by native whiteflies (Guo et al. 2015).

Instead of consumption from the plant, the whitefly's persistence by the host seems to be key in the propagation of the chronic begomovirus (Czosnek et al. 2017; Pan et al. 2018a, b). Whiteflies typically exhibit a strong positive correlation between the amount of virus they contain and their capacity to spread the disease (Jiu et al. 2006). For instance, when using PaLCuCNV, more virus was discovered in MEAM1 than in MED, mirroring the pattern of variance in transmission effectiveness (Guo et al. 2015, 2018).

The virus's ability to travel via primary salivary glands is the same as this. For instance, TYLCCNV was unable to concentrate in the cells surrounding the primary salivary glands of MED whiteflies, which prevented the virus from entering saliva and causing a virus transmission (Wei et al. 2014). Additionally, it has been observed that the virus movement scenario in some begomovirus-whitefly combinations is always consistent with the virus retention scenario. This suggests that when more viruses are retained, they are able to pass through the primary salivary glands and cross the midgut wall (Guo et al. 2015, 2018; Pan et al. 2018a, b).

Some endosymbiotic bacteria are also a participant in *B. tabaci* ongoing transmission of begomoviruses. For instance, it has been established that the chaperonin GroEL homologs produced by endosymbiotic bacteria (live inside other organisms, forming a mutually beneficial relationship by providing essential functions in exchange for a protected environment and nutrients), which were thought to shield the virus from erasure during its journey through the hemolymph, are necessary for TYLCV transmission (Baumann 2005). Additionally, the ability of populations of whiteflies

from the same species to spread begomoviruses can differ depending on whether they have an endosymbiont species present or not. Because Hamiltonella's GroEL protein interacts with the virus coat protein to facilitate transmission, it was discovered that the transmission effectiveness of TYLCV by different MEAM1 and MED whitefly populations obtained from Israel was associated with the presence of Hamiltonella (Gottlieb et al. 2010). Additionally, Rickettsia infection has been demonstrated to enhance TYLCV transmission in MEAM1 whiteflies (Kliot et al. 2014). Whiteflies belonging to the Sub-Saharan Africa 1-subgroup 3 (SSA1-SG3), with or without the endosymbiotic bacteria Arsenophonus and Rickettsia, exhibited various level of uptake and retention of the East African cassava mosaic virus-Uganda variant (EACMV-UG)(Ghosh et al. 2018).

Impact of environmental changes on plant-whitefly-*begomovirus* interactions

The environment plays a critical role in the evolution of viruses and influences the factors mentioned earlier. In dynamic environments, viruses show a preference for specific traits such as high mutation rates, recombination, robustness, and segmented genomes, enabling them to adapt rapidly to changing conditions. Climate change is expected to have a profound impact on the complex relationship between pathogens and their hosts. As environmental conditions shift, it is likely that the movement, introduction, establishment, and subsequent spread of viruses or their vectors could increase significantly in regions where they were previously unable to thrive. Abiotic factors at the host level, including plant physiology, hormones, and gene expression (Pandey et al. 2015; Zhang and Sonnewald 2017), have implications for the interaction between plants and viruses. Abiotic stressors and viral infections often activate the same signaling pathways in plants, leading to interference (Van Munster 2020). Consequently, various abiotic

conditions such as drought, high temperatures, elevated salinity, and increased CO_2 levels have been observed to impact the progression of plant virus infections (Varela et al. 2019). These stressors modify the plant-virus interaction by impeding plant defense responses and increasing susceptibility to viruses. This facilitates viral infection and symptom development, although conflicting effects have also been reported. As climate change, particularly rising temperatures, continues to unfold, the influence of abiotic stressors on plant virus infections becomes increasingly significant. Furthermore, environmental conditions can also impact virus transmission. Analyses suggest that diverse environmental changes yield distinct impacts on virus outbreaks. These changes encompass alterations in host traits, physiology, resistance to viruses and vectors, vector behavior, virus life cycles, abundance, diversity, reservoirs, and inoculum (Jones 2014b). However, there is still much to discover about the emergence of new virus pathosystems, variability in environmental factors, and newly discovered hosts. Investigating host plant defense mechanisms is challenging due to limited knowledge of emerging and invasive viruses, as well as ongoing environmental changes that reduce the effectiveness of management strategies. Researchers can pinpoint particular areas where frequent climate fluctuations lead to changes in crops, alternative hosts, vectors, and viruses across different times and locations. Additionally, they can delve into the environmental elements that may speed up the evolution of viruses, hosts, and vectors. Extreme weather events have become more frequent worldwide, and insect vectors and host plants have adapted to changing conditions. For instance, virus-infected plants in Yellowstone National Park's geothermal soils have exhibited adaptability towards fungal endophytes (Jones 2014a).

However, notable changes within an ecosystem can modify cropping patterns and geographic areas, promoting the emergence of new weed species and increased activity of insect vectors (Malmstrom et al. 2011). Emerging research suggests that red-light exposure can act as a stimulant, promoting a mutually beneficial relationship between whiteflies and begomoviruses Table 1. Particularly in the context of modern greenhouse agriculture, where supplemental red lighting is employed, these viruses have demonstrated an ability to adapt, leading to an increased efficiency in transmission and spread. This adaptation poses a concerning global threat in terms of the rapid dissemination of plant diseases (Zhao et al. 2021). Additionally, more severe cyclones are anticipated, causing poleward projections with changes in wind, precipitation, and temperature patterns that may challenge human efforts to manage plant virus diseases (Jones and Barbetti 2012; Kossin 2018). One of the main environmental factors that can impact these interactions is temperature Table 2. As temperatures rise, the population

Table 1 In two different investigations, the tobacco curly shoot virus (TbCSV) signals in the primary salivary glands (PSGs) of MEAM 1 and Asia II 1 were examined at 48 and 168 h after virion administration (Pan et al. 2018b)

No. of experiments	Time post injection	Whitefly species	No. of PSGs observed	No. of PSGs with virus signal
Exp. 1	48 h	MEAM1	26	4
		Asia II 1	22	8
	168 h	MEAM1	32	1
		Asia II 1	36	15
Exp. 2	48 h	MEAM1	18	1
		Asia II 1	10	4
	168 h	MEAM1	26	7
		Asia II 1	17	12

density of whiteflies tends to increase, leading to an increase in the transmission of begomoviruses. Additionally, higher temperatures can also increase the virulence of the virus, which can make it more difficult to control. Changes in precipitation patterns can also impact these interactions. Drought conditions can lead to water stress in plants, making them more susceptible to infection by viruses. Conversely, heavy rainfall can reduce the population density of whiteflies by washing them off plants, which can limit the spread of viruses. Human activities, such as the use of pesticides, can also impact these interactions Table 3. While pesticides can be effective in controlling whitefly populations, their use can lead to the development of pesticide-resistant whiteflies, which can then transmit viruses more effectively.

Conclusion and future perspective

Begomoviruses significantly influence whiteflies, triggering molecular, physiological, and behavioral shifts that amplify viral transmission Table 3. Understanding these viral-induced molecular mechanisms, physiological changes, and behavioral adaptations is pivotal for crafting precise control strategies. Despite extensive documentation regarding begomovirus diversity, emergence, acquisition, preservation, and propagation within the *B. tabaci* species complex, there remains limited knowledge about the biological processes governing the

Table 2 Different viruses and modes of transmission by whiteflies

Viruses	Mode of Transmission	Location	No. of Species	References
Begomovirus	Circulative, Non-Propagative	Salivary glands	424	(Ghosh and Ghanim 2021)
Carlavirus	Non-Persistent	Salivary glands	55	(Brown and Czosnek 2002)
Crinivirus	Semi- Persistent	Forgut	14	(Agranovsky 2021)
Cytrohabdovirus	Unknown		1	(Pinheiro-Lima et al. 2020)
Ipomovirus	Semi- Persistent	Unknown	7	(Dombrovsky et al. 2014)
Polerovirus	Circulative, Non-propagative		2	(Patton 2018)
Torradovirus	Semi-Persistent	Stylet	5	(Verbeek et al. 2014)

circulative spread of these viruses by *B. tabaci*. This is evident as only a handful of insect proteins have been associated with begomovirus spread, and none show particular likelihood of serving as begomovirus receptors. Novel synthetic insecticides at lethal and sublethal concentration remain a crucial tool in combating sucking insect pest (Abbas et al. 2021, 2023). However, due to their minimal toxicity risks and negligible residual

Table 3 Whitefly preference influenced by virus infection transmitted via plants

Scientific Name	Virus-isolate	Whitefly	Preference of Virus-Infected (+) Versus Uninfected (–) Plants by Non-Viruliferous Whiteflies	References
Nicotiana tabacum cv. NC89	TYLCCNV -YIO	MEAMI	+	(Shi et al. 2018)
Datura stramonium cv. Unknown	TYLCV -SH2	MED	+	(Chen et al. 2013)
Solanum lycopersicum cv. Zhongza9	TYLCV-SH2	MED	+	(Fang et al. 2013a)
S. lycopersicum cv. Florida 47	TYLCV -unknown	MEAMI	+	(Legarrea et al. 2015)
S. lycopersicum cv. Security	TYLCV -unknown	MEAMI	+	(Legarrea et al. 2015)
S. lycopersicum cv. Santa Clara	TSRV-unknown	MEAMI	+	(Fereres et al. 2016)
S. lycopersicum cv. Florida 47 R	TYLCV -unknown	MEAMI	+	(Johnston and Martini 2020)
S. lycopersicum cv. Florida 47	TYLCV -unknown	MEAMI	+	(Gautam et al. 2020a)
S. lycopersicum cv. Moneymaker	TYLCV -SH2	MED	+	(Wang et al. 2020)
N. benthamiana cv. unknown	TYLCV -SH2	MED	+	(Wang et al. 2020)
Capsicum annum cv. IIHR 3909	CLCV-unknown	MEAMI	+	(Yadav et al. 2022)
S. lycopersicum cv. Moneymaker	TYLCV -Israel	MED	+	(Ontiveros et al. 2022)
S. lycopersicum cv. Zhongza9	TYLCV -SH2	MEAMI	–	(Fang et al. 2013a)
S. lycopersicum cv. Santa Clara	TSRV-unknown	MEAMI	–	(Fereres et al. 2016; Maluta et al. 2017)
Cucurbita pepo cv. Goldstar	CLCV -unknown	MEAMI	–	(Gautam et al. 2020a)
S. lycopersicum cv. Florida 47	TYLCV -unknown	MEAMI	0	(Legarrea et al. 2015; Gautam et al. 2020a)
S. lycopersicum cv. Security	TYLCV -unknown	MEAMI	0	(Legarrea et al. 2015)

+ Represents Virus-infected plants; – represents Uninfected plants; 0 represents no preference, MEAM1 (Middle East-Asia Minor 1); MED (Mediterranean)

Table 4 Viral infection directly influencing whitefly preference behavior

Scientific Name	Virus-isolate	Whitefly	Preference of Virus-Infected (+) Versus Uninfected (−) Plants by Viruliferous Whiteflies	References
S. lycopersicum cv. Florida 47	TYLCV -unknown	MEAM1	+	(Shi et al. 2018)
S. lycopersicum cv. Moneymaker	TYLCV -Israel	MED	+	(Chen et al. 2013)
Gossypium hirsutum cv. F846	CLCV -unknown	Unknown	−	(Fang et al. 2013a)
G. hirsutum cv. F846	CLCV-unknown	Unknown	−	(Fang et al. 2013a)
S. lycopersicum cv. Florida 47	TYLCV -unknown	MEAM1	−	(Legarrea et al. 2015)
S. lycopersicum cv. Florida 47	TYLCV -unknown	MEAM1	−	(Legarrea et al. 2015)
S. lycopersicum cv. Security	TYLCV -unknown	MEAM1	−	(Legarrea et al. 2015)
S. lycopersicum cv. Security	TYLCV -unknown	MEAM1	−	(Legarrea et al. 2015)
S. lycopersicum cv. Santa Clara	TYLCV -unknown	MEAM1	−	(Fereres et al. 2016)
S. lycopersicum cv. Santa Clara	TYLCV -unknown	MEAM1	−	(Fereres et al. 2016)
C. pepo cv. Goldstar	CLCV -unknown	MEAM1	−	(Johnston and Martini 2020)
S. lycopersicum cv. Florida 47	TYLCV -unknown	MEAM1	−	(Johnston and Martini 2020)
C. annum cv. IlHR 3909	CLCV -unknown	MEAM1	−	(Gautam et al. 2020a)
G. hirsutum cv. F846	CLCV -unknown	Unknown	0	(Wang et al. 2020)
S. lycopersicum cv. Zhongza 9	TYLCV -SH2	MEAM1	0	(Wang et al. 2020)
S. lycopersicum cv. Zhongza 9	TYLCV -SH2	MED	0	(Wang et al. 2020)
S. lycopersicum cv. Security	TYLCV -unknown	MEAM1	0	(Ontiveros et al. 2022)
S. lycopersicum cv. Moneymaker	TYLCV -SH2	MED	0	(Fang et al. 2013a)
N. benthamiana cv. unknown	TYLCV -SH2	MED	−	(Fereres et al. 2016; Maluta et al. 2017)

+ Represents Virus-infected plants; − represents Uninfected plants; 0 represents no preference, MEAM1 (Middle East-Asia Minor 1); MED (Mediterranean)

effects, the research focus is shifting towards developing safer biopesticides, including botanical insecticides and biocontrol agents (Abbas et al. 2022). Living mulches present sustainable pest management by fostering natural predator habitats and disrupting pest life cycles (Gul et al. 2022), while genome editing in crops offers precise methods to control insect pests through targeted genetic modifications (Ullah et al. 2023). Advanced technologies (Plant virus epidemic prediction models), like proteomic and next-generation sequencing methods have identified potential proteins involved in the circulative distribution of begomoviruses, further investigation is necessary to ascertain their specific roles in viral dissemination. Research endeavors should prioritize the development and implementation of novel control methods, such as using resistant plant varieties, biological control agents, and innovative vector management approaches Table 4. These include transgenics, efficient gene silencing in whiteflies, establishing effective methods to verify protein functionalities, and selectively mutating or targeting the development of transmitting and non-transmitting insects. These targeted efforts will help us to understand the spread of begomoviruses and their whitefly vectors.

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Declarations

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