

Begomovirus-mediated changes in whitefly vectors: implications for viral transmission in response to environmental shifts and vector management strategies

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SUMMARY

Plant viruses are known to cause more than 47% of plant diseases worldwide. Among this motley array, begomoviruses stand out as a prominent genus with a multitude of insect vectors. Whiteflies play a crucial role in the transmission of these viruses. As begomoviruses are transmitted and spread by whiteflies, alterations to the life cycle of these vectors have garnered significant interest. This review paper examines the multifaceted relationship between begomoviruses and their whitefly vectors in the transmission of viral pathogens. The objective of this review is to emphasize recent developments in the field, specifically the molecular and physiological changes that may occur in whitefly vectors when exposed to begomoviruses. It also sheds light on the ecological and evolutionary implications arising from begomovirus-induced changes in whitefly vectors and expands the discussion on vector management strategies. The findings described in this review contribute significantly to the overall understanding of viral transmission dynamics and provide a strong foundation for subsequent research and the development of control measures for diseases caused by begomoviruses and their whitefly vectors.

Keywords: Insect vectors, Viruses, Interactions, Evolution, Environment, Management

Citation: Idrees, M. A., A. K. Khan, G. Deep, M. Rizwan, S. Rukhsar, and B. Ahmed. 2026. Begomovirus-mediated changes in whitefly vectors: implications for viral transmission in response to environmental shifts and vector management strategies. *Journal of Wildlife and Ecology*. 10(3): 204-226.

Received: 04 August, 2026

Revised: 21 August, 2026

Accepted: 19 September, 2026

Published: 30 September, 2026

INTRODUCTION

Insect vectors of plant pathogens, such as fungi, bacteria, phytoplasmas, and viruses, are strongly reliant on the behavioral patterns of their vectors for effective transmission. Consequently, these pathogens have evolved systems to directly or indirectly manipulate their vectors, thus improving the efficiency of transmission. Begomoviruses are the largest group of economically important DNA plant viruses among these pathogens, significantly contributing to the global incidence of crop diseases (Farooq et al., 2022). A study by Luan et al. (2012) on begomoviruses revealed complex relationships between the begomoviruses and their insect vectors. Some

begomoviruses, such as *tomato yellow leaf curl virus (TYLCV)* and *tomato yellow leaf curl China virus (TYLCCNV)*, were found to have adverse impacts on their whitefly vectors. This resemblance to entomopathogenic viruses was also reported in other publications by Czosnek et al. (2017). Another article by Rosen et al. (2015) illuminated how begomoviruses persist in the population of whiteflies. Once infected by the whiteflies, these viruses have a long staying time in the insect vectors, which may extend over the lifetime of the insects. By 2020, the International Committee on Taxonomy of Viruses (ICTV) officially named a total of 445 begomoviruses. They are recognized as the most diverse and destructive type of virus in the world (Mansoor et al., 2003). Infected plants display certain symptoms caused by these viruses, such as curling of leaves, the appearance of a leaf mosaic, yellowing of veins, yellowing of leaves, and slowed plant development (Kwak et al., 2022; Zerbini et al., 2017; Ghosh and Ghanim, 2021). These viruses are unique in that they have their own genomes, which are circular and single-stranded DNA. They have a prominent structure known as twinned particles, in which two half icosahedral capsids are linked together. Because these vector–virus interactions are strongly modulated by prevailing temperature and humidity regimes, and because the practical value of this knowledge lies in guiding vector-management decisions, both dimensions are given dedicated treatment later in this review.

Begomoviruses are classified as monopartite or bipartite based on their genomic organization, with monopartite genomes predominating in the Old World and bipartite genomes in the New World (Brown and Czosnek, 2002; Melgarejo et al., 2013); their circular single-stranded DNA-A component encodes the replication-associated (Rep) and coat proteins that underlie phylogenetic classification into Old World, New World, sweepovirus, and legumovirus lineages (Fiallo-Olivé and Navas-Castillo, 2019). The information presented below focuses on the impact of begomoviruses on whitefly biology, behavior and transmission under varying environmental conditions, which is more relevant to the vector-focused theme of this review, thus leaving the peripheral genomic details to Fiallo-Olivé and Navas-Castillo (2019).

Begomoviruses are causing major economic losses to the global agricultural industry (Arif et al., 2017; Islam et al., 2020). These examples demonstrate the extent and negative effects of begomovirus diseases on crop production in various areas. Qureshi et al. (2022) made a comprehensive list that illuminates the host range and symptoms of many begomoviruses, which are characterized by destructiveness across the globe. Moreover, a study by Kenyon et al. (2014) discovered 36 different species of begomovirus, one of which is TYLCV, in tomatoes and peppers in Southeast and East Asia. Here, at the continental scale, Southeast Asia can be identified as a major begomovirus diversity center, and evidence of the dispersal of species throughout the entire region can be observed. Yellow mosaic disease is a disease caused by begomoviruses that has seen a dramatic rise in Asia, thus further spreading the virus to many different countries (Charoenvilaisiri et al., 2020; Kenyon et al., 2018; Kumar et al., 2019; Subiastuti et al., 2019).

The whiteflies (Hemiptera: Aleyrodidae) are usually phloem sap feeders on the underside of leaves. They are a heterogeneous collection of insects located all over the world and have over 1,550 species and 161 genera (Liu et al., 2015; Hardy, 2018). Some of the most common pest species in the whitefly family are *Aleurocanthus*

woglumi (citrus blackfly), *Aleyrodes proletella* (cabbage whitefly), *Bemisia tabaci* (silverleaf whitefly), and *Trialeurodes vaporariorum* (greenhouse whitefly) (Capinera, 2008). *B. tabaci* has been known to infest over 900 host plants. Over the past twenty years, there has been clear evidence that whiteflies are the leading vectors responsible for the spread of plant viruses among insects (Fiallo-Olivé et al., 2019; Gilbertson et al., 2015). They can feed on different host plants and have a wide repertoire of hosts, which enables them to efficiently transmit plant viruses. Even though it is a common belief that the damage that whiteflies do to crops is mostly due to sap sucking, the indirect damage they cause is of greater concern. An interesting characteristic is their release of a lot of honeydew, which creates a favorable habitat that supports the growth of sooty mold (Polston and Capobianco, 2013). The large population of whiteflies in the agricultural environment does not only play a role in the transmission of plant viruses but also alters the natural population of insects in the ecosystem. This disturbance may bring other pests and predators that threaten healthy insects and pollinators (Gilbertson et al., 2015; Polston and Capobianco 2013). In addition, whiteflies increase the damage to plants by injecting their saliva into the phloem, resulting in the decline of turgor pressure, which is more harmful than fungal growth (Najla et al., 2010). The feeding behavior of the whitefly, which includes feeding on a variety of plant species, offers plenty of chances to obtain and transmit begomoviruses to new host plants (Fiallo-Olivé et al., 2016). Even though the transmission process of begomoviruses is complicated, the mouthparts of the whitefly are used in the acquisition and transfer of the viruses (Moreno-Delafuente et al., 2013). Whiteflies are persistent vectors of begomoviruses that are transmitted through them, typically in the midgut and filter chamber, where the viral genomes can be transcriptionally and replicatively active (Ghanim, 2014; Czosnek et al., 2017).

Begomovirus transmission leads to a range of changes in whiteflies, such as changes in feeding behavior, reproduction, a shortened life cycle, and behavioral alterations. All these factors play a role in the spread and survival of begomoviruses, and again demonstrate the significant impact of these viruses on the biology and ecology of whiteflies. The molecular dynamics between the virus and the vector, the long-term effects of begomovirus-induced changes in whitefly vectors, ecology, variations between begomovirus strains and the effects of various environmental factors that may interact with the begomovirus infection are still not well understood. The paper highlights the modification of the whitefly vectors since their association with virus transmission, and the ways to manage these vectors. To unravel the processes of viral transmission, the dynamic changes that occur in whitefly vectors due to begomovirus infection need to be better understood. These changes may have a major impact on vector competence to acquire, maintain and transmit the virus to susceptible plants. It outlines the impact of these changes on the ecology of vectors, expansion of host range, and emergence of new strains of begomovirus. The holistic approach takes into account the broader implications and impacts of the begomovirus-induced changes in the whitefly vectors. Overall, it gives a detailed and comprehensive account of the complexity of interaction between begomoviruses and whitefly vectors including various aspects like molecular, physiological, ecological and evolutionary aspects. In this review also the control of whitefly vectors is discussed in detail.

Although this body of work, the specific knowledge gaps in begomovirus-whitefly interactions are only indirectly addressed in the literature: how much of an impact the direct viral effects have on vector behavior compared to the plant-mediated effects is seldom separated, the impact of other environmental factors such as temperature, humidity etc. on the transmission efficiency spread across studies, and there is no comparative evaluation of the strategies used to manage vectors. Therefore, the primary objectives of this review are to: (1) summarize the molecular, physiological and behavioral changes induced in whitefly vectors by the begomoviruses; (2) elucidate the influence of the environment (specifically temperature and humidity) on the interactions between begomoviruses and whitefly vectors; (3) compare the effectiveness of chemical, biological, cultural, host-resistance and RNAi vector management strategies; and (4) delineate priority areas for future research regarding interactions between begomoviruses and whitefly vectors.

METHODOLOGY

The review has been conducted following structured literature search of peer-reviewed publications that have been published since 2000 and up to 2026 on begomovirus-whitefly interactions. Relevant articles were found by performing searches on Web of Science, Scopus, PubMed and Google Scholar using combinations of keywords in relation to the following terms: “begomovirus,” “whitefly,” “*Bemisia tabaci*,” “vector behavior,” “viral transmission,” “environmental factors,” “temperature,” “humidity,” and “vector management” with the help of Boolean operators (AND/OR) and by screening references from the retrieved articles. Articles were included if they reported on original data or reviewed evidence of whitefly-begomovirus system changes in whitefly biology, behaviour, or physiology, or on the impact of environmental factors on whitefly-begomovirus interactions, or on management strategies for whitefly/begomovirus systems; non-English language publications, conference abstracts without full text, or on studies not related to whitefly-begomovirus systems were excluded. Titles and abstracts were first screened for relevance, followed by full-text assessment of eligible articles, and information extracted from the selected literature was thematically organized into sections corresponding to the review’s stated objectives, covering begomovirus-induced changes in whitefly feeding behavior and biology, the influence of environmental factors, vector-management strategies, and priority directions for future research. Figures 1–3 are original schematic illustrations conceptualized by the authors and created using BioRender (BioRender.com) to visually synthesize findings collated from the reviewed literature; they do not reproduce any previously published figure.

BEGOMOVIRUS-MEDIATED CHANGES IN WHITEFLY VECTORS

Begomovirus-mediated changes in whitefly feeding behavior

Begomoviruses are able to multiply and concentrate in the salivary glands of whiteflies, causing alterations in their behavior (Farooq et al., 2022). Recent research has shown that viruses have the ability to modify the behavior of vectors to enhance transmission (Figure 1) (Ferreles and Raccach, 2015). Whiteflies infected by the virus tend to have a higher probing and plant-feeding frequency, resulting in an increased virus

transmission rate. Thus, it can be concluded that begomoviruses affect the behavior of whiteflies, making virus transmission more efficient. However, plant viruses might have the potential to affect the behavior, health, and life cycle of insect vectors, either directly or indirectly. Moreno-Delafuente et al. (2013) determined that the movement of whiteflies infected with viruses is reduced and that they take longer to salivate when feeding on eggplant leaf discs. The higher the exposure to virus particles, the greater the transmission rates tend to be (Socha et al., 2022). Changes in the behavior of the whitefly can also occur due to an increase in their population and the presence of infected plants in the area (Islam et al., 2020). These behavioral shifts arise through two distinguishable, though often co-occurring, pathways: direct effects, in which the virus itself alters whitefly physiology (e.g., salivary gland titre, probing frequency), and indirect, plant-mediated effects, in which virus infection changes host-plant volatiles, color, or nutritional quality and thereby changes vector preference; disentangling the two remains difficult because most experimental designs cannot fully separate them.

Some of the stories suggest that the plants infected with a virus might eventually affect the fitness of insect vectors and their capacity to transmit the virus when consuming phloem sap (Carmo-Sousa et al., 2016). *B. tabaci* was also found to transmit the cucurbit chlorotic yellow virus (CCYV) in a non-circulative manner on infected plants, and the vector was more inclined to feed on plants with the virus (Islam et al., 2020; Pinheiro-Lima et al., 2020). Host physiology directly influences the feeding pattern of vectors and host preferences. Moreover, the plant pathogenic viruses can change the phenotypic features of plants, which may increase the transmission of the virus to uninfected plants. Reported preferences are not always consistent across studies, and much of this variation likely reflects differences in virus species, whitefly biotype, host-plant species, and the acquisition-versus-inoculation stage tested, rather than a single universal preference rule (Carmo-Sousa et al., 2016).

Viral infection can bring about shifts in the volatile organic compound (VOC) profile emitted by plants, as well as changes in foliage coloration, both of which affect how attractive a plant appears to potential vectors and subsequently drive alterations in vector behavior (Westwood et al., 2013). Evidence indicates that viruses are capable of impacting both insects and plants, disrupting various stages of their interaction and thereby increasing transmission efficiency (Lu et al., 2019; Wang et al., 2020). Nevertheless, the underlying mechanisms driving these shifts in vector preference remain complex and are known to vary considerably across different virus-plant-insect pathosystems, making them difficult to fully disentangle.

Viral interactions with plants and insect vectors are crucial for viral infections and transmission, significantly influencing the spread of viruses and the resulting epidemics. Zhang et al. (2022) suggest that both persistent and non-persistent viruses can alter the behavior and effectiveness of insect vectors. This can occur either through changes in the phenotype of the host or through direct interactions between the insect vectors and the virus, which enhance transmission.

Whitefly feeding habits are very important in the spread of begomoviruses, considering that these insects are vectors of various viral diseases afflicting crops. These effects on the epidemiology of diseases highlight the importance of regulating whitefly feeding behavior (Zhao et al., 2022). Such manipulation has ecological

consequences for the plant, whitefly, and begomovirus. It is possible that whitefly feeding behavior is modulated by direct actions on whitefly physiology or the plant itself. Although a lot of research has been done on the subject, the majority of the research has focused on single infections.

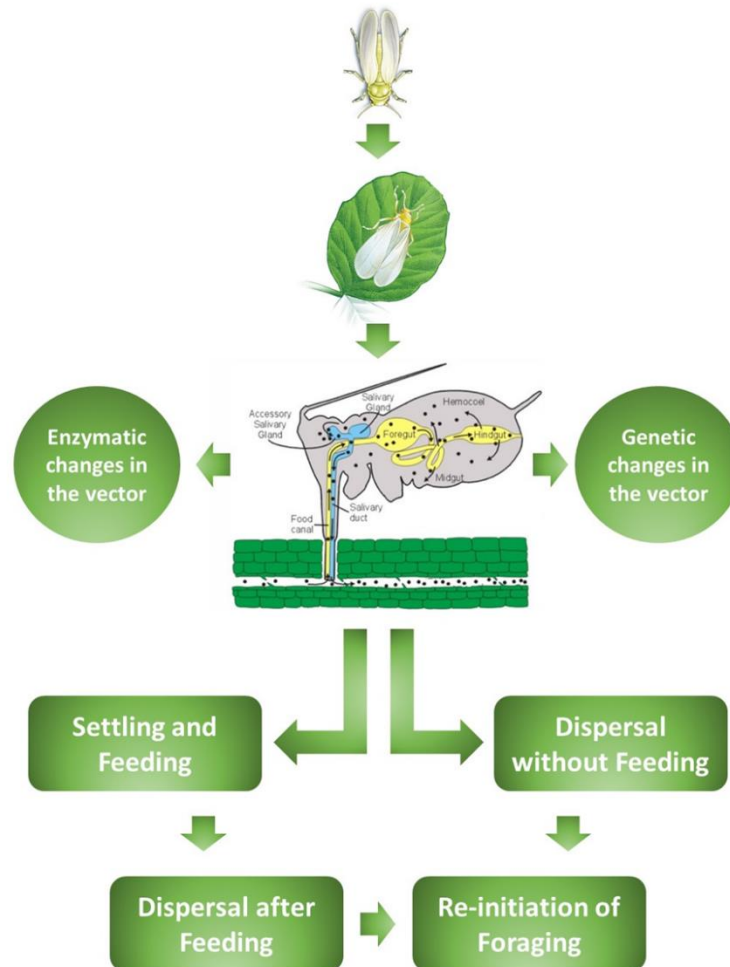


Figure 1: Virus mediated changes in whitefly behavior and biology (Created in BioRender).

The effects of whitefly feeding behavior mediated by plants due to virus infections have been investigated in seven published articles (Zhao et al., 2022). Whitefly sap-feeding is a standard parameter used to unify the results of studies. Out of the research on begomovirus-associated viruses, three were found, and none had significant effects on whitefly feeding behavior (Liu et al., 2013; Maluta et al., 2019). Whitefly feeding behavior can be influenced by plant virus acquisition as well as indirect effects caused by host plants. There are two case studies that have been performed. The first experiment involved a comparison of the feeding behavior of virus-carrying and non-virus-carrying whiteflies, where the feeding behavior of both groups was on healthy host plants. The second study involved the comparison of the feeding behavior of viruliferous and non-viruliferous whiteflies on infected and healthy host plants, as well as the impact of the virus on the host plants and the whiteflies. In

this way, the former is associated with the immediate effects of the infection with the virus, whereas the latter is a combination of the immediate effect of the virus and the effect of the host plant. Although a large number of studies have focused on analyzing the direct effect of virus infection on the feeding behavior of whiteflies (Table 1), few studies have exclusively focused on investigating the complex interaction between direct effects and the plant-induced responses.

Table 1: Direct effects of begomovirus infection on whitefly feeding behavior.

Virus-Isolate	Host Plant	Whitefly	Direct Effects of Virus on Duration of Sap Ingestion by Whiteflies	Reference
TYLCV-unknown	<i>S. lycopersicum</i> cv. Xianke 6	MED	Positive	(Wang et al., 2013)
TYLCV-Israel	<i>S. melongena</i> cv. Black Beauty	MED	Positive	(Moreno-Delafuente et al., 2013)
TYLCV-unknown	<i>S. lycopersicum</i> cv. Unknown	MED	Positive	(Jahan et al., 2014)
TYLCV-SH2	<i>S. lycopersicum</i> cv. Castlemart wildtype	MEAM1	Positive	(Liu et al., 2017)
TYLCV-SH2	<i>S. lycopersicum</i> cv. Castlemart spr2 mutant	MEAM1	Positive	(Liu et al., 2017)
TYLCV-SH2	<i>S. lycopersicum</i> cv. Zhongza 9	MED	No effect	(Liu et al., 2013)
TYLCV-SH2	<i>S. lycopersicum</i> cv. Zhongza 9	MEAM1	No effect	(Liu et al., 2013)
TYLCCNV -Y10	<i>G. hirsutum</i> cv. Zhe-Mian 1793	MEAM1	No effect	(He et al., 2015)
TYLCCNV-Y10	<i>N. tabacum</i> cv. NC89	MEAM1	No effect	(He et al., 2015)
TYLCV-SH2	<i>S. lycopersicum</i> cv. Castlemart 35S::prosys	MEAM1	No effect	(Liu et al., 2017)

Note: Effects vary by virus isolate, host-plant cultivar, and whitefly biotype (see cited studies).

Regarding begomoviruses, five studies have reported a rise in whitefly feeding on infected hosts, but others have reported no effect (Table 1) (Fiallo-Olivé et al., 2019; He et al., 2015; Jahan et al., 2014). Wang et al. (2013) recorded that TYLCV affected the feeding behavior of whiteflies, resulting in higher salivary gland secretions and consistent feeding on healthy tomato plants. Equally, Moreno-Delafuente et al. (2013) noted an increased feeding rate of whiteflies on eggplants infected with TYLCV. Liu et al. (2017) discovered that TYLCV had a direct effect on whitefly behavior, which is determined by the host plant genotype. TYLCV enhanced feeding on JA-deficient mutant spr2 and wild-type castemart tomatoes without affecting the prosys plants with high JA content. Having reported no direct effect of virus infection on whitefly feeding, He et al. (2015) observed a positive reciprocal interaction of TYLCV from a Chinese strain with MEAM1 whiteflies.

When considering plant viruses as a means of controlling whitefly behavior, outcomes tend to vary based on the specific whitefly-virus-plant species, strain, or cultivar combination involved. To illustrate, non-viruliferous MEAM1 whiteflies typically favor healthy tomato plants, whereas the MED biotype tends to be drawn toward virus-infected plants instead (Fang et al., 2013). By contrast, viruliferous MEAM1 whiteflies have been observed to prefer feeding on TYLCV-infected

tomatoes, with a particular inclination toward the Florida-47 cultivar (Legarrea et al., 2015). Altogether, these results point to the complex and context-specific interactions between the effects of viruses and whitefly behavior, and to the need for considering every specific combination of factors.

Also, the experimental materials need to be carefully chosen to study viral epidemics properly. Despite the considerable diversity among begomovirus and whitefly species (Kanakala and Ghanim, 2019; Zerbini et al., 2017), the outcome of a given epidemic often hinges on just a limited number of specific plant-virus-whitefly combinations. Consequently, gaining insight into these tripartite interactions and their role in viral epidemiology requires first clarifying the distinct contributions of each individual whitefly, virus, and plant species involved.

Begomovirus-induced changes in whitefly biology and preference

Begomoviruses usually change the biology of the insect vector, resulting in impacts on the epidemiology of the virus (Zhang et al., 2022). They can also affect the functioning and synthesis of phytohormones, which can subsequently influence the number of insect vectors (Blanc and Michalakakis, 2016; Pan et al., 2021). Vectors that carry viruses have developed to alter their preferences and become more transmissible (Table 2). This change in preference toward plant viruses is confirmed by numerous studies (Eigenbrode et al., 2018). Even though there aren't many studies available, analysis regarding viruliferous and non-viruliferous whiteflies also suggests a similar pattern. Approximately 17 case studies have been documented concerning various begomoviruses, with a total of 12 indicating the host preference of whiteflies for virus-infected plants (Ontiveros et al., 2022; Wang et al., 2020; Yadav et al., 2022), 3 indicating whitefly preference for uninfected plants (Gautam et al., 2020; Maluta et al., 2017), and 2 indicating no preference (Legarrea et al., 2015; Zhao et al., 2022), while 11 out of 19 studies found that viruliferous whiteflies preferred uninfected plants (Feres et al., 2016; Legarrea et al., 2015; Yadav et al., 2022). TYLCV has been a subject of extensive research, especially on its effect on non-viruliferous whitefly feeding preferences among begomoviruses. Numerous studies have shown that in most cases, whiteflies prefer TYLCV infected plants over uninfected plants (Fang et al., 2013; Ontiveros et al., 2022). Studies, however, have not been entirely consistent with respect to the effect of infection on the behavior of whiteflies, and the longevity of the infections do not seem to have as great an impact on preference as the presence or absence of infection. For example, Legarrea et al. (2015) observed that feeding choice was not significantly different between TYLCV-inoculated and control tomato plants at 3 and 12 weeks after-inoculation for MEAM1 whiteflies (no viruliferous stage) but changed significantly at 6 weeks. The same study also indicated that there is a species-specific preference for the virus by whiteflies (Legarrea et al., 2015). In a similar study, Fang et al. (2013) noted that virus-free MED whiteflies attracted to TYLCV-infected tomato plants, but MEAM1 whiteflies preferred uninfected plants. These changes are mechanistically linked to virus-induced changes in the expression of various whitefly genes, such as up-regulation of genes involved in reproduction, including vitellogenin (Huang et al., 2021), modulation of genes involved in immunity (e.g., tolerance) and altered expression of endosymbiont mediated nutritional physiology, all of which contribute to vector fitness, fecundity and pathogen transmission abilities.

Table 2: Begomovirus-induced changes in whitefly vector.

Aspect of whitefly biology	Changes induced by virus	References
Feeding Behavior	Increased probing and feeding behavior	Fiallo-Olivé et al., 2016; Zhao et al., 2022; Lu et al., 2017
Transmission Rate	Enhanced virus transmission	Fiallo-Olivé et al., 2019; Naveed et al., 2023
Feeding Duration	Prolonged feeding periods	Liu et al., 2017
Host Preference	Altered preference for infected vs. healthy plants	Rodríguez-López et al., 2011; Naveed et al., 2023
Physiological Changes	Impact on insect physiology and hormone production	Ingwell et al., 2012

Note: Patterns summarized from cited studies; effects vary by virus species, whitefly biotype, and host plant.

This manipulation, based on preferences, directly promotes viral dissemination (Moreno-Delafuente et al., 2013; Zhao et al., 2022). Although they occur in different modes of transmission and are different in their genomic structure, these viruses seem to have evolved along a similar trajectory - indicating a convergent evolution of these manipulative types. Thus, a detailed study of the interaction between whitefly, plant and virus still needs to be carried out.

Mixed infections are frequently reported (Moreno and López-Moya, 2020) and there is limited research that deals with the influence of mixed infections on feeding preferences of whiteflies, with only a few studies addressing this. Work by Ban et al. (2021) demonstrated that non-viruliferous whiteflies of the MEAM1 biotype showed a feeding preference for TYLCV-infected tomato plants, though no notable difference emerged between plants with single versus partial infections. In a comparable finding, Gautam et al. (2020) reported that both viruliferous and non-viruliferous whitefly populations exhibited a marked preference for healthy plants over those infected with either single or multiple viral strains. Together, these findings suggest that whether plants or whiteflies carry mixed or single infections does not meaningfully alter whitefly feeding preference. Check if the place is right

With regard to the whitefly involvement in such interactions, MEAM1 individuals showed a reduction in the activity of genes associated with the oxidative phosphorylation cascade and detoxification enzymes when feeding on virus-infected plants. This lowering detoxification was probably the cause of energy savings and performance of whiteflies (Luan et al., 2012). Analysis of whitefly honeydew has shown that there is an improvement in nutritional assimilation by whiteflies with respect to plants infected by the virus. This could be attributed to the virus suppressing plant defenses against whiteflies or the decreased detoxification activity needed by whiteflies on infected plants. Currently, the limited availability of case studies makes it difficult to draw firm conclusions regarding how plant-induced viral effects influence whitefly feeding behavior. Even so, based on the evidence currently available, begomoviruses do not appear to substantially disrupt the sap ingestion phase, a stage widely considered central to whitefly feeding activity. However, it is also worth noting

that feeding behaviour may continue to have an impact on whitefly biology and more research is required to fill the remaining knowledge gaps.

The plant-mediated effects that pathogenic viruses have on insect vector performance are well established (Ban et al., 2021; Zhao et al., 2022). It is said that this vector performance shift is caused by alteration in phytohormone biosynthesis or perception caused by viruses (Pan et al., 2021; Ray and Casteel, 2022). In light of this, it is important to have a comprehensive knowledge of these complex interactions and their wider implications to help understand the overall whitefly–begomovirus relationship. Since feeding behavior has a direct bearing on insect performance, further research is warranted to clarify whether virus-driven manipulation of whitefly feeding patterns itself contributes to changes in vector performance. This type of study may give information on the processes of manipulation that transform the performance of whiteflies. Direct effects seem to show that begomoviruses are more likely to induce whiteflies to feed on healthy plants. An example is that prior studies have shown that begomoviruses such as TYLCV could possess traits like insect pathogens since their coexistence with whiteflies usually results in lower fertility and survival. To some degree, this claim can be supported with the help of various published reports that indicate that TYLCV is prone to replicate in whiteflies.

Research examining how plant viruses influence whitefly feeding behavior has revealed that non-viruliferous whiteflies show a preference for virus-infected host plants, whereas viruliferous individuals tend to favor uninfected plants instead. This pattern reflects a notable form of behavioral manipulation that facilitates viral propagation under field conditions-enabling non-viruliferous whiteflies to acquire the virus while allowing viruliferous whiteflies to transmit it onward to healthy plants. Changes in vector feeding preference clearly benefit the virus and aid its spread and establishment into new hosts.

In addition, plant viruses have a tendency to exhibit increased genomic diversity, due to the spontaneous nature of their replication process. This natural genetic adaptability enables them to adjust effectively to changing environmental conditions, improving their resilience and ability to withstand the test of time. This variability helps to promote adaptive evolution, since a viral population could carry useful mutations that can allow it to adapt to various selective pressures (Lefevre et al., 2019). Viral strains that can modify the feeding preferences of whitefly in such a way as to be more advantageous to the viral spread may have a significant competitive edge over other viral strains, and over time outcompete them. As whitefly vectors are subjected to a continuous round of selective pressure via viral transmission, the genetic structure of whitefly-transmitted viruses is likely to be continually changing.

Impact of environmental changes on plant-whitefly-Begomovirus interactions

Viral development has a strong relationship with the environmental conditions, which are linked to the factors mentioned above. Viruses typically have properties that are useful in a variable environment, such as a high mutation rate, genetic recombination, structural stability, and fragmented genome composition, which allow them to adapt quickly to changing environments. Host-pathogen interactions are likely to be significantly affected by climate change. Change in environment can lead to a propagation of viruses and their vectors, which can result in increased dispersal,

introduction, colonization and propagation in areas previously not suitable for viruses to survive. Abiotic factors, such as plant physiological status, hormonal regulation, and gene expression in the host plant can also influence plant-virus interactions at the host level (Pandey et al., 2015; Zhang and Sonnewald, 2017). Notably, overlapping signaling pathways are triggered by both abiotic stress and viral infection in plants (Van Munster, 2020). Abiotic stressors like drought, high temperatures, high salinity and CO₂ levels have been seen to affect plant-virus infection dynamics. These stress factors alter the dynamics of plant-virus interactions by reducing plant defense reactions and increasing the probability of infection, frequently leading to the establishment and symptom expression, but sometimes also to the inhibition of plant defense reactions. Abiotic Stress is playing an increasingly important role in plant viral infection dynamics with the continued global warming. Additionally, environmental conditions may shape patterns of virus transmission. Existing research points to differential impacts of environmental variability on viral outbreak dynamics, encompassing shifts in host traits, physiological status, resistance to viruses and vectors, vector behavior, life-cycle patterns, population abundance, diversity, reservoir dynamics, and inoculum sources (Figure 2) (Jones, 2014a). Nonetheless, questions remain regarding the emergence of novel viral pathosystems, the variability of environmental drivers, and the identification of new host species.

Understanding host plant defense mechanisms continues to pose a considerable research challenge, largely owing to gaps in knowledge surrounding emerging and invasive viral pathogens, coupled with ongoing environmental fluctuations that undermine the effectiveness of existing management approaches. Researchers have succeeded in pinpointing particular geographic zones characterized by pronounced climatic variability, conditions that drive shifts among crops, alternative host plants, vectors, and viral populations across differing spatial and temporal contexts. Beyond this, investigators have examined how environmental drivers may accelerate co-evolutionary dynamics among viruses, their hosts, and associated vectors. As extreme weather events grow more prevalent globally, both insect vectors and host plants have shown a capacity to adjust to these shifting conditions. Within the whitefly-begomovirus system specifically, elevated CO₂ and temperature have been linked to faster whitefly development and higher population growth rates, which can translate into greater begomovirus inoculum pressure even without a change in per-insect transmission efficiency (Jones, 2014a).

Nonetheless, considerable ecological changes are capable of reshaping crop distribution and geographic patterns, thereby promoting the emergence of novel weed species and intensifying insect-vector activity (Malmstrom et al., 2011). Emerging evidence suggests that exposure to red light may function as a stimulatory cue that reinforces the mutualistic interaction between whiteflies and begomoviruses. This adaptive response is particularly obvious under modern greenhouse conditions where supplemental red-light illumination is routinely used and, in the end, makes the transmission and spread of viruses more efficient. Such adaptation is a worrying global risk concerning the high rate of spreading plant diseases (Zhao et al., 2021). Also, stronger cyclones will be expected, leading to poleward movements with variations in the pattern of wind, precipitation and temperature that could complicate human

attempts at controlling the plant virus diseases (Jones and Barbetti, 2012; Kossin, 2018).

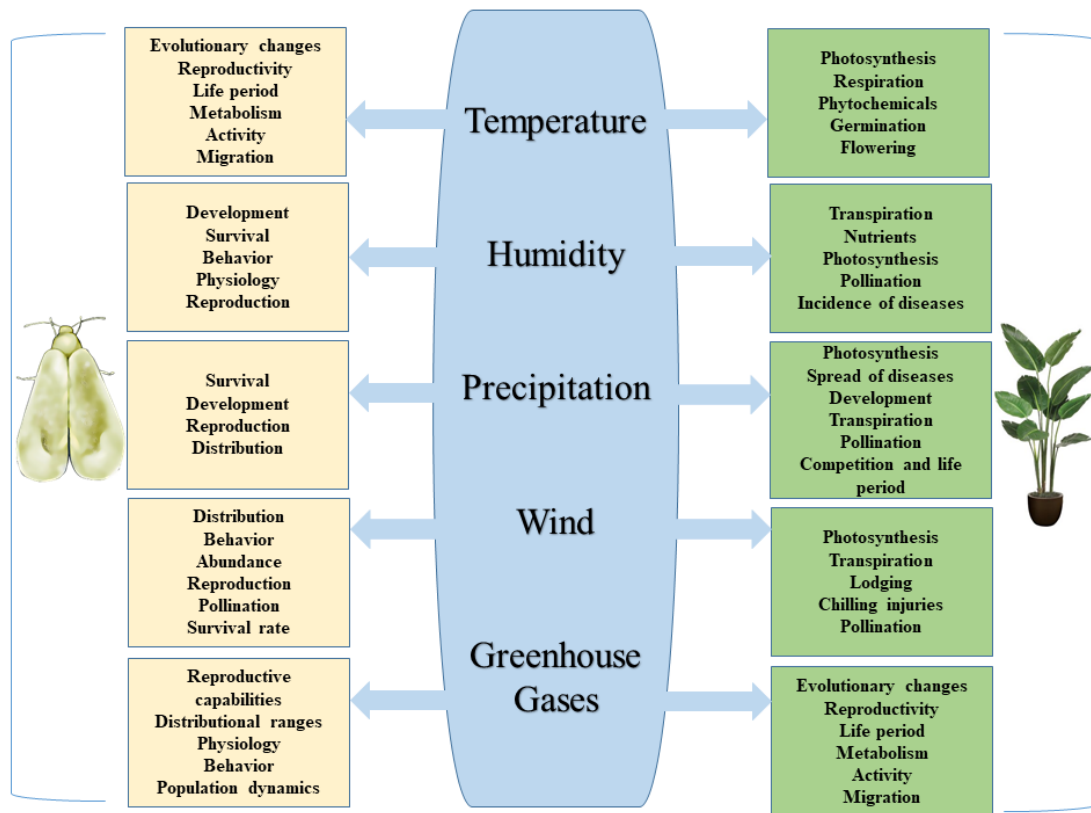


Figure 2: The nature, causes, effects and mitigation of climate change on the environment (Created in BioRender).

Temperature is one of the key environmental influences that may influence such interactions. The population density of whiteflies is likely to increase with the rise in temperatures and this will result in the increase in the transmission of begomoviruses. Also, an increase in temperature can also enhance the virulence of the virus making it harder to contain. These interactions can also be affected by changes in the pattern of precipitation. Plants may be infected by viruses when there is water stress due to drought conditions. On the other hand, the population of whiteflies can be decreased by heavy rainfall, which will wipe off the plants, and therefore control the spread of viruses. These interactions can also be influenced by human actions like use of pesticides. Although the use of pesticides may be effective in reducing the population of the whiteflies, there is the possibility of pesticides inducing pesticide-resistant whiteflies which will in turn be able to transmit viruses more efficiently. The warmer the climate, the more quickly the whitefly population can be built up, the more difficult it becomes to control the whitefly, and the greater amount of begomovirus transmission can occur, which leads to more highly selected insecticide-resistant variegation, and therefore to more whitefly population growth, etc., in one reinforcing cycle, the more insecticide resistance and insecticide use will be selected, the more whitefly populations can be expanded, and the more often begomovirus transmission will

happen (climate change, insecticide resistance, and whitefly population dynamics forming a single reinforcing cycle).

IMPLICATIONS FOR MANAGEMENT AND CONTROL STRATEGIES

Control of begomovirus diseases in agricultural crops is a complex problem due to the interaction between the virus, the host plants and insect vectors. The control strategies should be effective, and that can only be achieved through a multifaceted approach. The disease can be controlled by cultural practices such as crop rotation and clearance of infected plants. It is important to use methods of insect vectors management (chemical or biological control) to minimize the process of begomoviruses spread. One of the strategies in reducing the effects of begomoviruses is breeding resistance. Scientists are coming up with resistant strains capable of withstanding infections and minimizing losses in yields. Knowledge of diversity of begomoviruses and host range is needed to provide customized disease control. To control their spread, their spread requires continuous surveillance and research to provide proactive measures. Different measures, including managing the reservoirs of the virus, resistant rootstock, insecticides (Table 3) and crop destruction techniques, have been examined. A decision support system (DSS) is being designed to support the growers to make informed decisions guided by local virus and vector pressure and weather forecasts. The solution to these issues will allow protecting agricultural productivity and reducing the adverse impact of begomovirus diseases (Adkins et al., 2011). Whiteflies contribute to the spread of viruses, which complicates the process of managing and protecting crops. Amazingly, the fatalities attributed to the viruses that are transmitted by the whiteflies are usually more than the fatalities that are attributed to the whiteflies themselves. This lower limit of virus-carrying whiteflies affects the economic injury rates and strain of control measures. A difficult but important approach to the management of the whitefly is host plant resistance to reduce the impact of the virus. A combination of the use of host plant resistance and other strategies has potential of successfully controlling the whiteflies as well as the viruses they carry. The aim is to have sustainable crop production through the control of the complex relationships between viruses and whiteflies. Such strategies can be host plant resistance, chemical and biological control, RNAi-based control, and other new strategies (Rincon et al., 2019; Riley and Srinivasan, 2019; Simmons and Riley, 2021).

Comparing these approaches directly: cultural and sanitation practices (crop rotation, removal of infected plants, reservoir-host management) are low-cost and broadly applicable but act slowly and cannot contain established outbreaks alone; chemical control gives the fastest population knock-down but is increasingly undermined by widespread insecticide resistance in *B. tabaci* (Table 3) and carries non-target and residue costs; biological control (generalist predators, entomopathogenic fungi) is more sustainable and resistance-resilient but generally slower-acting and more sensitive to abiotic conditions; host-plant resistance (e.g., acylsugar-mediated resistance, resistant bean genotypes) offers durable, low-input protection but requires long breeding timelines and is not yet available for most crop-begomovirus combinations; and RNAi-based control is highly specific and resistance-evasive in principle but remains largely at the proof-of-concept stage, with delivery and regulatory hurdles still unresolved. No single strategy is sufficient on its own, which is why an

integrated pest management approach combining host resistance, targeted chemical or biological inputs, and cultural practices, guided by real-time monitoring such as the decision support system described below, is generally regarded as the most effective and sustainable path forward.

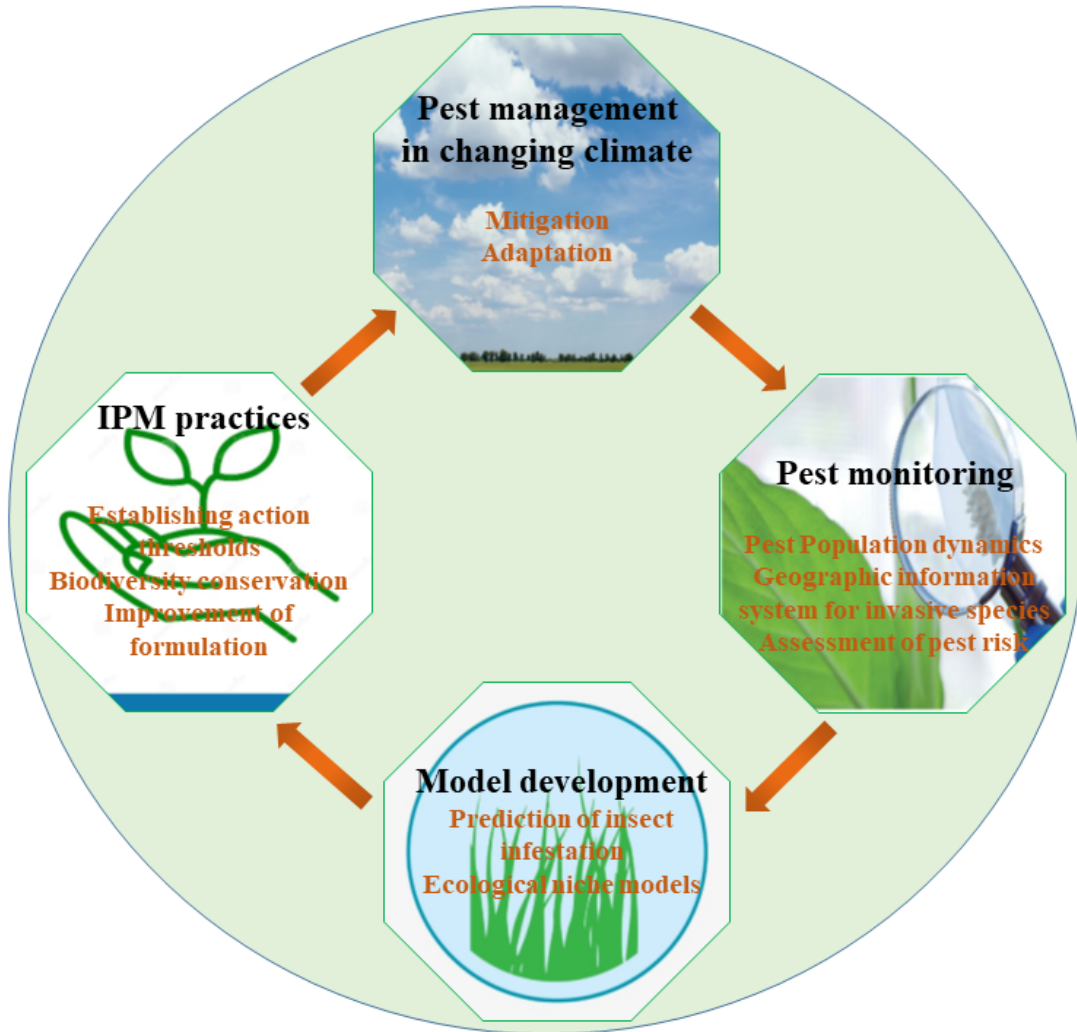


Figure 3: Potential pest management strategies for mitigation and adaption to new environmental conditions (Created in BioRender).

Challenges

The key findings and insights that are crucial for addressing the challenges associated with whiteflies and promoting sustainable crop production are highlighted:

Crossley and Snyder (2020) conducted a study that offers a global outlook on comprehending the whitefly problem. Their study particularly explores the study of spatial dispersal of genetic variants of *B. tabaci* species. By showing how they have conducted their findings, they introduce state of the art genetic analysis tools that can transform the numerous areas of whitefly management. This is a precious resource that can offer researchers with the latest techniques and knowledge so that the challenges of whiteflies could be addressed in a more effective way.

Gautam et al. (2020) conducted an experiment to examine genetic variation of *B. tabaci* MEAM1 in the Georgia farmscapes of the USA. The findings of their study showed that there was a relative lack of genetic variation between these populations. This study provides valuable background data, which is also area-specific and could be applicable in the future management initiatives aimed at solving the issue of whiteflies in the area. By leveraging the insights gained from this study, it will be possible to develop effective strategies and approaches to address and minimize the impact of whiteflies in Georgia's farmscapes.

Table 3: Widely used insecticides against whiteflies.

Insecticide	Resistance Development in <i>B. tabaci</i>	Approval for Use
Endosulfan	Yes	Not approved
DTT	Yes	Not approved
Lindane	No	Not approved
Fipronil	Yes	Approved
Malathione	Yes	Approved
Acephate	Yes	Not approved
Aldicarb	Yes	Not approved
Carbosulfan	Yes	Not approved
Bifenthrin	Yes	Approved
Fenpropathrin	Yes	Not approved
Acetamiprid	Yes	Approved
Imidacloprid	Yes	Approved
Sufoxaflor	No	Approved
Diafenthiuron	No	Not listed
Pymetrozine	Yes	Approved
Flonicamid	Data Not Available	Approved
Pyridaben	Yes	Approved
Tolfenpyrad	Data Not Available	Not listed
Spiromesifen	Yes	Approved
Spirotetramat	No	Approved
Cyantraniliprol	Data Not Available	Pending
Chlorantraniliprol	Data Not Available	Approved
Pyriproxyfen	Data Not Available	Not listed
Fenoxycarb	No	Approved
Pyriproxyfen	Yes	Approved
Kinoprene	No	Not approved
Novaluron	No	Approved
Teflubenzuron	No	Approved
Buprofezin	Yes	Approved

Abamectin	Yes	Approved
Spinosad	Data Not Available	Approved
Rotenone	Data Not Available	Data Not Available
Azadirachtin	Yes	Approved
Pyrethrum	Data Not Available	Approved

Note: Resistance and regulatory-approval status are compiled from multiple national and regional sources and are illustrative rather than exhaustive; because approval status varies by country and is revised over time, readers should verify current registration and resistance status for their target region with the relevant national regulatory authority (e.g., US EPA, EU Pesticides Database) before use.

The regulatory gene networks of whiteflies need to be studied in detail to identify potential targets that can be used to regulate them using RNAi. Hasegawa et al. (2020) in a recent study conducted a study with the aim of unravelling the complicated microRNA regulatory process of the whitefly species *B. tabaci*. Their research results provided useful information on the intricacy nature of this regulatory system and its possible role in acquisition and the transmission of viruses by whiteflies. The research serves as a pre-test to other research in the future, which can help create new RNAi-based systems that can be useful in managing the infestation of whiteflies and the spread of the viral pathogens they carry.

Whiteflies can be affected by the presence of plant viruses significantly in behavior and biology. Huang et al. (2021) carried out an experiment to examine how tomato chlorosis virus affects the reproductive ability of *B. tabaci*. Their findings revealed that the effect of the virus on the reproduction of whiteflies was very strong by up-regulating the expression of one protein called vitellogenin that is a significant factor in the process of reproduction. These findings have significance in the study of the complicated interactions between plant viruses and the biology of whiteflies that helps to formulate the knowledge of how viruses can disrupt the reproductive ability of whitefly groups.

It is important to have a holistic understanding of the population dynamics of the pests in the development of effective management strategies. In a large-scale survey, Krause-Sakate et al. (2020) investigated the distribution patterns and distribution of the most used whitefly species which has become a threat to crops in South America. The viruses that these whiteflies carry and the steps that have been implemented to keep the viruses at bay were also discussed. The study offers valuable information and facts about the dynamics of the whitefly population in the region which could be used to come up with certain measures to control the whitefly efficiently and avoid the spread of the virus.

B. tabaci is a serious threat to the soybean crops in Brazil. A recent study by Barros et al. (2021) was successful in demonstrating that proximal sensing is a promising method to estimate the level of infestation of *B. tabaci* populations in the field as well. The new technology will also allow closer monitoring and evaluation of the whitefly populations, which will allow more effectively and efficiently applying pest control measures.

The use of generalist predators has been largely recognized as an effective and recommended biological control measure to control whitefly infestations. This method will entail increasing the number of natural predators or preserving the already existing

predator populations in the area. Kheirodin et al. (2020) also investigated the efficacy of predators in controlling *B. tabaci* as a part of the entire world survey. The research paper highly underscores the importance of biological control as a key ingredient of integrated pest management (IPM) program against this pest (Figure 3). The results highlight the importance of giving priority to biological control strategies in establishing effective control strategies against *B. tabaci*.

Biological control is an environmentally friendly control method that can be affected by different abiotic and biotic factors. A study by Wu et al. (2020) notes the potential of a new strain of entomopathogenic fungi, *Cordyceps javanica* to be used as a biopesticide. The researchers showed that this fungus was effective in a variety of temperatures and in high-ultraviolet radiation (UV). The results indicate that *C. javanica*, a product of whitefly infestation, has high potential in being a practical alternative to be utilized as a biopesticide.

Another factor that contributes to minimization of the threat of whiteflies is plant resistance. They showed that the wild species *Solanum pennellii*, which they introduced into the tomato plants (*S. lycopersicum*), had acylsugar-mediated resistance, which was effective in a study by Marchant et al. (2020). The impact of this resistance mechanism on whiteflies was found to have grim consequences as it led to reduction in the population of whiteflies and impaired their ability to access and spread the TYLCV. These results demonstrate the relevance of including plant resistance mechanisms, including acylsugar-mediated resistance, as an efficient method in the fight against whitefly infestations and reduce the prevalence of viral diseases in tomato plants.

In their study, Agarwal et al. (2021) determined several genotypes of snap bean (*Phaseolus vulgaris*) and lima bean (*P. lunatus*) with resistance to two whitefly-borne begomoviruses: cucurbit leaf crumple virus and sida golden mosaic Florida virus. This paper brings out the fact that some genotypes of beans are resistant to natural forces and therefore, there is a high possibility of developing whitefly resistant bean varieties. By identifying and making use of these resistant genotypes it is possible to increase the resistance of snap bean and lima bean crops to begomoviruses carried by the whiteflies and minimize adverse effects of the viral diseases on bean crops.

Inhibition technology of gene expression has become a promising technology in the control of crop pests, especially insects. Shelby et al. (2020) has conducted a comprehensive review to understand the potential benefits, drawbacks, and other necessary considerations of the RNAi application into silencing whitefly *B. tabaci* genes and controlling them. The review provides a good source of information about short-term and long-term effects of RNAi-mediated control, and sheds light on the merits and gaps of the method. The review has practical information through a keen observation of the complex considerations related to gene silencing through the application of RNAi that can be instrumental in the development and implementation of effective control measures that can be used to contain whiteflies.

Whiteflies are dependent on endosymbionts, both primary and secondary, in their life cycle in agroecosystems. Andreason et al. (2020) conducted an extensive review, with a keen eye to the biological, evolutionary, and plant interaction functions of these endosymbionts in the cryptic species of *B. tabaci*. The main objective of the review is to shed light on the significance of such endosymbionts and offer some helpful information about the multifacetedness of interactions between them and whiteflies and

the influence of these interactions on the interactions between plants. The review contributes to the current information on the complexity of interactions happening within the system of whiteflies and their endosymbionts by investigating the different functions of the latter.

The number of economically important whitefly species overall in the framework of integrated pest management was surveyed, and the number of more than 50 species explored. The review was centered on the application of advanced control mechanisms which included nanotechnology, RNAi and genetic modifications of plants. The new methods will be integrated to induce some proteins into the plants which can ruin whiteflies. The article by Saurabh et al. (2021) offers valuable insights into how this state of art strategies could be useful in the effective management of whitefly populations and gives hopeful prospects to improve pest management in agricultural settings.

Whiteflies are quite a challenge to control relative to infected fresh produce especially bearing in mind that export of such products is done worldwide. Cho et al. (2020) have come up with an interesting study which provides good evidence of the usefulness of electron beam and X-ray radiation in decontaminating fresh strawberries which are to be exported. Their study substantiates the effective use of these radiating processes as effective methods of guaranteeing the quality and safety of fresh products and consequently mitigates the chances of whitefly attacks on international trade. The findings have implications that are critical to the safety of agriculture products and the general food safety standard in the world.

CONCLUSION AND FUTURE DIRECTIONS

The Begomoviruses greatly contribute to the whiteflies leading to molecular, physiological and behavioural changes that increase the virus transmission. It is important to ensure that begomoviruses are able to induce molecular changes, physiological changes, and behavioral changes to be able to come up with specific ways of control. Future studies ought to be based on the need to understand the mechanism of action behind the begomovirus-induced alterations of whitefly vectors, both viral and host. These ecological and evolutionary interactions will be a helpful step towards understanding how viruses spread. Practical applications should be channelled towards sustainable approaches like resistant varieties of plants and new strategies to control vectors to safeguard food production systems and food security. To mitigate the economic losses and burdens of the begomovirus infections, our knowledge can be enhanced and proper control measures taken to ensure that in the long run, agricultural productivity is not lost. Research, collaboration and innovation around this is required to address the impact of the Begomovirus diseases. They are also supposed to be more practical in their applications and development of sustainable and effective management strategies towards begomovirus diseases is of utmost significance. Research should aim at developing and adopting new control measures which involve use of resistant varieties of plants, biological control agents and novel ways of controlling the vectors. These, in conjunction with existing agricultural technologies, may prove to be effective in minimising the economic impact of begomovirus infections. The following research directions are suggested to further the understanding of changes that occur in whitefly vectors as a result of begomovirus infection and their

implications: Molecular Mechanisms, Host Factors, Ecological Dynamics, Vector Dispersal and Colonization, Management Strategies and Climate Change Impact and Collaborative Efforts. These research directions will enable us to better understand the begomovirus-induced changes in the whitefly vectors which will translate to better crop protection, food security and reduced economic loss in incidences of begomovirus diseases.

Across the evidence reviewed above, the clearest recurring gaps are: (i) direct virus effects on whitefly physiology are rarely separated experimentally from plant-mediated effects; (ii) the combined influence of temperature, humidity, CO₂, and insecticide selection pressure on transmission efficiency is studied piecemeal rather than in combination; and (iii) management strategies are mostly evaluated individually rather than compared or integrated. Closing these three gaps, rather than generating further isolated case studies, should be the priority for the next phase of research in this system.

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Competing interests: Authors have declared that no competing interests exist.
Funding This research was funded by the National Natural Science Foundation of China (31861143051, 31872425).
Authors' contributions: Idrees: conceptualization, writing (original draft), formal analysis, data handling, variable construction and methodology, supervision, funding acquisition. writing (review and editing). Everyone from the authors has studied and approved the document's final version.

