



REVIEW ARTICLE

Global Scenario of Begomovirus Diseases in Vegetable Crops

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Abstract

Whitefly-transmitted begomoviruses are the major threats to the cultivation of vegetable crops worldwide. Begomoviruses infecting vegetables have a broad host range and are distributed among all continents in which vegetables are grown in open fields and protected structures. In most of cases these begomoviruses are commonly found in mixed infections of more than one virus leading to the emergence of new variants/species which is found to be adapted to different hosts in various geographical regions. Mainly the evolution of begomoviruses occurs through point mutation, intra and interspecies recombination and reassortment. The association of satellite molecules such as beta- and alpha-satellites helps in altering the virulence of the helper begomoviruses. Till date there are about 243 begomovirus species are found to be infecting vegetable crops in the global scenario. Further, these vegetable-infecting begomoviruses exhibited diversity in the phylogenetic analysis. They are clustering based on their number of genomic components (monopartite/bipartite), host they are infecting and their geographical origins. The objective of the review is to present the global scenario of the begomoviruses infecting vegetable crops on the aspects of symptomatology, genome organization, taxonomy, diversity, diagnostics, host range and possible management strategies to combat the virus infection.

Keywords: Whiteflies, vegetable virus, diversity, begomovirus, viral disease management, mosaic.

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Introduction

Geminiviruses (family Geminiviridae) have genomes comprised of one or two molecules of circular, single-strand DNA (ssDNA) encapsidated by a single structural protein into twinned quasi-icosahedral particles. This includes the largest number of plant viruses infecting crops of agricultural and horticultural importance. The family contains 14 genera defined based on the type of insect vector, host range, genomic organization and phylogenetic relationships (Fiallo-Olive *et al.*, 2021). On the basis of genome organization, vector, and host range, the family is divided into 14 genera—Becurtovirus, Begomovirus, Capulavirus, Curtovirus, Eragrovirus, Grablovirus, Mastrevirus, Topocuvirus, Turncurtovirus, Citlodavirus, Maldovirus, Mulcrilevirus, Opunvirus, and Topilevirus (Roumagnac *et al.*, 2022). The genus *Begomovirus* includes viruses transmitted by whiteflies of the *Bemisia tabaci* cryptic species complex to dicotyledonous, 445 species accounting to 86% of the total species reported under Geminiviridae. Begomoviruses are widespread in all tropical and subtropical regions of the world, and cause severe diseases in a number of economically relevant crops (Rojas *et al.*, 2018). Begomoviruses are one of the most serious threats to vegetable cultivation in several parts of the globe including North America, South America, the Indian

subcontinent, West Africa, the Middle East, East Asia, and Southeast Asia (Malathi *et al.*, 2017). Till date, begomovirus research were focused on diversity, distribution, and pathogen biology in the various cropping systems. Globally several outbreaks of begomoviruses such as tomato leaf curl New Delhi virus on cucurbits in Spain (Fortes *et al.*, 2016), bean golden mosaic virus in French bean and other leguminous vegetables; tomato yellow leaf curl virus in tomato and French bean; watermelon chlorotic stunt virus in cucurbits as well as tomato; pepper golden mosaic virus on chili and tomato, etc were reported from different parts of the globe during past two decades (Qureshi *et al.*, 2022). Infection of these begomoviruses has caused severe loss up to 90% reduction in the quantity and produces unmarketable poor-quality fruits (Malathi *et al.*, 2017; De Barro *et al.*, 2008). In this review, an attempt has been made to gather information regarding the global scenario of vegetable-infecting begomoviruses their status and future prospects.

Genome Organization

Begomoviruses are major species causing serious diseases among dicotyledonous crop plants. Based on the number of genomic components, begomoviruses are classified into two categories namely bipartite and monopartite. The genome of bipartite begomoviruses consists of two ssDNA genomic components (known as DNA-A and DNA-B) of about equal size (~2.7 kb) whereas monopartite begomoviruses possess a single genomic component (Homologous to the DNA-A component of bipartite viruses) (Rojas *et al.*, 2005; Stanley *et al.*, 2005). Genomic regions of DNA A and DNA B components share no sequence similarity except for the short sequences of ~180 to 200 nts known as common region (CR). The CR contains 9 nucleotide sequence (TAATATTAC) called the nonanucleotide which acts as an origin of replication and is conserved among all the members of Geminiviridae (Eagle *et al.*, 1994; Padidam *et al.*, 1996). Genomic components possess universally 6 ORFs (open reading frames) in both viral (v) sense and viral complementary (vc) sense. The DNA-A component contains one gene (AV1) in viral sense and three genes (AC1, AC2, AC3) in the viral complementary strand among the New World (NW) bipartite begomoviruses (Harrison and Robinson, 1999) and an additional AV2 gene in v sense and AC4 gene in vc sense among the Old World (OW) bipartite begomoviruses (Hanley-Bowdoin *et al.*, 1999). The DNA-B component contains two ORFs, one in sense strand (BV1) and another in complementary strands (BC1) (Sanderfoot *et al.*, 1996).

A third type of genomic components (ssDNA) are also associated with the begomoviruses are referred to as satellite-like nucleic acids, several DNA satellites, the well-known beta satellites (Briddon *et al.*, 2003) and alpha satellites (Briddon *et al.*, 2004) and the recently recognized delta satellites (Fiallo-Olivé *et al.*, 2012), have been associated with begomoviruses.

These DNA satellites depend on helper begomoviruses for replication (except alpha satellites), encapsidation, movement in the plant, and transmission by insect vectors (Yang *et al.*, 2019). Alphasatellites, mainly associated with monopartite old-world begomoviruses, possess a genome that encodes a replication-associated protein needed for their replication. Betasatellites, associated with many monopartite old-world begomoviruses, are essential for the induction of typical disease symptoms. The β C1 protein encoded by the beta satellite genome has important roles in symptom induction and suppression of transcriptional and post-transcriptional gene silencing (Li *et al.*, 2018). Unlike beta satellites and alpha satellites, delta satellites lack coding capacity. All delta satellites share several genomic features such as their size, which is about one-quarter of the begomovirus genome component, a stem-loop containing the conserved begomovirus nonanucleotide TAATATTAC, a putative secondary stem-loop structure located close to begomovirus iteron-like sequences, a short region with the sequence identity of the beta satellite conserved region, and an A-rich region (Fiallo-Olivé *et al.*, 2012). In some cases, deltasatellites reduce or increase the accumulation of the helper Begomovirus, but rarely modify the symptoms caused by them.

Taxonomy

Since, Begomoviruses possess small genome size of about 2.7 kb, they become one of the first plant viruses whose complete genomes were characterized. With the increasing large numbers of Begomovirus sequence determination worldwide revealed a significant degree of genetic diversity among the Begomovirus genome. This led an opportunity to the taxonomist to develop a sequence-based taxonomy relying on pairwise nucleotide comparisons. Currently, ICTV proposed 91% cut-off value for begomoviruses to separate the species in the begomovirus genera based on the nucleotide identity of the complete DNA A molecule. If the sequence had <91 % sequence identity to all known begomoviruses, the virus should be considered as a new species under begomovirus genera and should be assigned with a unique name that is not currently in use for any ICTV-recognized species. The naming of the new virus should follow the template of "Host symptom virus" (Eg. Bendi yellow vein mosaic virus). Also, recently ICTV discourages the common practice of using country, city, town, village or province names in naming new begomovirus species to avoid confusion. The Geminivirus study group adopted guidelines of <94 % threshold value as strain demarcation criteria. Nomenclature of strains should reflect biological differences between the members of the same species. For example, Mungbean yellow mosaic virus – Chili will be given for the strain of the mungbean yellow mosaic virus that infects chilli (Brown *et al.*, 2015).

Symptomatology

Begomoviruses cause a wide variety of symptoms in the hosts, including mosaics, mottles, yellowing, yellow vein, enation, leaf curling and/or deformation, reduction in plant growth, and deformation in a decreased number of fruits. In some cases, begomoviruses cause a total loss of production, constituting a limiting factor for the production of open-field vegetable crops in tropical and subtropical regions, as well as in greenhouse production systems worldwide. Begomovirus symptoms in pepper range from symptomless to different degrees of stunting and curling, distortion, mosaic, mottling, and vein yellowing of leaves. In some cases, infected pepper plants show premature leaf or flower drop. BGMV, BGYMV, MYMV and MYMIV cause similar symptoms in most common bean cultivars. Symptoms include varying degrees of yellow and golden mosaic of leaves, flower abortion, and reduced number and size of pods and seeds (Varma and Malathi, 2003; Kwak *et al.*, 2022). Symptoms induced by begomoviruses in cucurbits are similar and include stunting and distorted growth (often severe); leaves with crumpling, upward and downward curling, enations, light green to yellow mosaic or mottle, and vein distortion and swelling; and bumpy, deformed, and discolored fruit (Nagendran *et al.*, 2017a; 2017b; Kumari *et al.*, 2021).

In okra, infection of okra enation leaf curl virus produced characteristic symptoms including leaf-curling, vein-thickening, and a reduction of leaf surface area. Further, plants become stunted severely with deformed fruits unfit for marketing (Venkataravanappa *et al.*, 2015). Also, bhendi yellow vein mosaic disease in okra is associated with symptoms such as chlorosis and yellowing of veins and veinlets, smaller leaves, fewer and smaller fruits, and stunting of plant growth (Mishra *et al.*, 2017). In Begomovirus-infected cucurbit crops seen with diverse of symptoms ranging from mild to severe mosaic, chlorosis, curling, mottling, reduction of leaf size, stunting, shoestring appearance of the leaf, leaf distortion, enation and vein clearing have been commonly observed worldwide (Nagendran *et al.*, 2017a; Kumari *et al.*, 2021). In case of legume vegetables, Begomovirus infection produces golden yellow mosaic symptoms on the leaves and plants remain stunted in growth (Nagendran *et al.*, 2022a). On radish infection of radish leaf curl virus causes curling and twisting of leaves, enation on the adaxial side and stunted growth of plants (Singh *et al.*, 2012). Begomovirus infection produces symptoms not only on the vegetative part but also causes malformation of fruits and diminished marketable fruit yield with poor quality.

Transmission

Begomoviruses are exclusively transmitted by whiteflies (*Bemisia tabaci*) in a circulative and persistent manner. Viruses translocate to several important sites within the insect body after ingestion, such as the midgut, filter

chamber, hemolymph, and salivary glands (Ghanim, 2014; Czosnek, *et al.*, 2013). The molecular interactions between virus coat proteins and receptors on the cellular membranes and the hemolymph of the vector is critical for effective translocation through the different tissues and organs therein (Czosnek, *et al.*, 2013). Many Begomoviruses are differentially transmitted by over 40 different cryptic species of *B. tabaci* identified based on the genetic variation in the mitochondrial cytochrome oxidase subunit I (Fiallo-Olivé *et al.*, 2020; Saini *et al.*, 2020). Nine *B. tabaci* cryptic species prevalent in India are Middle East-Asia Minor 1 (MEAM 1), Asia I, Asia I-India, Asia II-1, Asia II-5, Asia II-7, Asia II-8, Asia II-11 and China-3 (Ellango *et al.*, 2015). The two invasive and destructive whitefly biotypes are (i) B or MEAM1 originated from Middle East- Asia Minor, and (ii) Q or MED, which originated in the Mediterranean region they differ among themselves in feeding behavior, virus transmission efficiency, host range, endosymbionts, and insecticide resistance (Nigam, 2021). Upon ingestion of the virus by whiteflies, it translocates inside the insect body and reaches the phloem system. Studies showed 24 hours of acquisition access period is required for the whiteflies to become viruliferous for the rest of their lives (Chen *et al.*, 2011).

In addition to insect transmission, Begomoviruses are experimentally transmissible by mechanical inoculation. So far approximately 20 known Begomovirus species were reported to be mechanically transmissible (Lee *et al.*, 2020). Recently, the agro inoculation method (*Agrobacterium*-mediated transfer) through tandemly repeated cloned genomic DNA or biolistic delivery (gene gun transfer) of cloned genomic DNA of Begomoviruses were found experimentally successful for the transmission in vegetable crops (Rojas *et al.*, 2005; Kushawaha and Dasgupta, 2019).

Begomovirus Seed Transmission

It has long been established that Begomoviruses are not seed transmissible. However, a number of reports have recently demonstrated seed-borne and seed transmission of Begomoviruses. Several reports have raised the possibility of transmission through seeds for some members of this genus (Kim *et al.* 2015; Kothandaraman *et al.* 2016; Suruthi *et al.* 2018; Manivannan *et al.* 2019; Nagendran *et al.*, 2023). No transmission through seeds was demonstrated in other cases (Pe'rez-Padilla *et al.* 2020; Sisodia and Mahatma 2020; Tabein *et al.* 2021). The first Begomovirus reported to be seed-transmitted was sweet potato leaf curl virus in sweet potatoes (Kim *et al.*, 2015), soon after this report, describing seed transmission of other Begomoviruses: TYLCV in tomatoes, soybean, and peppers, ToLCNDV in zucchini, and pepper yellow leaf curl Indonesia virus in chili peppers (Fadhila *et al.*, 2020; Kil *et al.* 2016; 2017; 2018,); tomato leaf curl New Delhi virus (ToLCNDV) in chayote (Sangeetha *et al.*, 2018), zucchini (Kil *et al.* 2020) and sponge gourd (Nagendran

et al., 2023); BgYMV in bitter melon (Manivannan *et al.*, 2019); dolichos yellow mosaic virus (DoYMV) in lablab bean (Suruthi *et al.*, 2018); and okra yellow mosaic Mexico virus (OYMMV) (Ortega-Acosta *et al.*, 2019). Grow-out tests with market-procured seeds revealed no transmission for BgYMV compared with 5% transmission for ToLCNDV (Gomathi Devi *et al.*, 2023). Most of the experimental evidence shown was the amplification by PCR of Begomovirus genomes from the seeds of infected plants, and in some cases from the asymptomatic grow-out seedlings. ToLCNDV, ToLCTV, and TYLCTHV can be transmitted *via* seeds or pollens of cucumber and tomato plants to an extent of 70-77% (Chang *et al.*, 2023). Pérez-Padilla *et al.* (2020) reported that TYLCV-IL is seed-borne but is not seed transmitted in tomatoes or *N. benthamiana*, suggesting that transmission through seed is not a general property of TYLCV. Similarly, ToLCNDV is reported to be seed-borne in nature but it is not seed-transmitted in melon (Fortes *et al.*, 2023). Based on previous studies begomovirus seed transmission is not a rule but it is process of adoption. The seed-borne nature and transmission is genotype dependent with the interaction of vector and environmental influence.

Distribution and Host Range

It is evident that begomoviruses are highly adaptive by their wide host range (more than 420 plant species), global distribution, and efficiently transmitted by whitefly vector (Nigam, 2021). Due to its wide host range, many plants serve as primary inoculum sources of begomoviruses leading to the possibility of epidemics. There are reports available for some Begomovirus infecting more than one host and a single crop infected by more than one begomovirus. In case of chili crop, it is reported to be infected by 32 globally distributed distinct species of Begomoviruses (Devendran *et al.*, 2022). Similarly, tomato leaf curl New Delhi virus (ToLCNDV) are reported to be infecting more than 30 different species of vegetable crops belonging to Solanaceae, Cucurbitaceae, Fabaceae and Malvaceae. In India, diverse Begomovirus-beta satellite complexes were identified with tomato leaf curl disease (Nagendran *et al.*, 2019; Kumar *et al.*, 2023). Begomoviruses are hibernate in the weed host present in the vegetable cropping ecosystem during the unavailability of the main host. Some of the weed host acting as a reservoir for the Begomoviruses are *Acalypha indica*, *Calotropis procera*, *Convolvulus arvensis*, *Commelina benghalensis*, *Cyamopsis tetragonoloba*, *Datura stramonium*, *Eclipta prostrata*, *Euphorbia hirta*, *Glycine max*, *Parthenium hysterophorus*, *Phyllanthus niruri*, *Physalis minima*, *Sonchus oleraceus*, etc without even producing prominent symptoms. Begomoviruses are found to be prevalent worldwide in both old world (Europe, Africa, Asia and Australian continent) and new world region (North America and South America) among the different vegetable crops. Till date there are about 243 out of 445 notified begomovirus

species of ICTV classification are documented to be infecting vegetable crops in global scenario.

Detection and Diagnosis

Diagnosis based on symptoms alone is often not sufficient and diagnostic tests must be used to confirm begomovirus infections. For some begomoviruses, such as TYLCV, African cassava mosaic virus (ACMV), SqLCCV and ToLCNDV, antibodies and serological tests, e.g., enzyme-linked immunosorbent assay, were developed, but these are not commonly used (Xie *et al.*, 2013; Seepiban *et al.*, 2017). Initially, dot- and squash-blot hybridization tests with cloned geminivirus DNAs as probes were used (Gilbertson *et al.*, 1991; Alfaro-Fernández *et al.*, 2016). However, it was the application of polymerase chain reaction (PCR) technology, often together with DNA sequencing, that revolutionized the detection and characterization of begomoviruses (Rojas *et al.*, 1993). PCR is currently the method of choice for begomovirus detection, as it is rapid, sensitive, and precise. Furthermore, it can be tailored for detection of a specific virus or all members of a genus. Sequencing of the PCR-amplified geminivirus DNA fragments allows for precise identification of the virus. Universal abutting primers were designed successfully to amplify the complete genome of associated beta satellite and alpha satellite molecules with a number of monopartite begomoviruses and are in use among several researchers (Briddon *et al.*, 2002; Bull *et al.*, 2003). Rolling circle amplification (RCA), which enriches circular DNA molecules in a nonspecific manner, has proved to be a valuable tool for the detection and cloning of uncharacterized and novel begomoviruses (Inoue-Nagata *et al.*, 2004). Indeed, this was the method that led to the identification of several new Begomoviruses. When combined with restriction enzyme digestion, RCA can also be used to identify mixed infections of Geminiviruses (Haible *et al.*, 2006). This method facilitates in cloning whole viral genomes along with its associated satellites and assists in the construction of infectious clones efficiently (Wyant *et al.*, 2012).

In recent years, real-time pathogen detection based on the LAMP technique made it possible to achieve a rapid and accurate diagnosis both in laboratories and in the field (Wilisiani *et al.*, 2019). Loop-mediated isothermal amplification (LAMP) assay is an isothermal reaction employed in the detection of Begomoviruses to overcome some of the disadvantages of PCR. LAMP possesses higher sensitivity and specificity than that of the routine PCR with less time. Many researchers successfully used the LAMP for the detection of begomoviruses infecting vegetable crops (Arutselvan *et al.*, 2017; Fukuta *et al.*, 2003; Herrera-Vasquez *et al.*, 2018; Nagendran *et al.*, 2022b). Another isothermal-based tool, recombinase polymerase amplification (RPA), relies on the extension of primers induced by recombination proteins, is also utilized in Begomovirus diagnosis. RPA could

prove useful for the cost-effective detection of plant viruses by plant diagnostic clinics. It can be performed in one hour or less with a reagent cost similar to that of PCR but with a lower labor cost, and with an acceptable level of sensitivity and specificity of begomoviruses (Londono *et al.*, 2016). The clustered regularly interspaced short palindromic repeats (CRISPR)-based nucleic acid diagnostic method utilizing the CRISPR-Cas12a system for detecting two geminiviruses, tomato yellow leaf curl virus (TYLCV) and tomato leaf curl New Delhi virus (ToLCNDV), which have single-stranded DNA genomes. This assay detected TYLCV and ToLCNDV in infected plants with high sensitivity and specificity (Mahas *et al.*, 2021). High throughput sequencing (HTS) or viral metagenomics (viromics) is a powerful tool for diagnosis, characterization and viral diversity exploration in a wide range of vegetable crops (Aimone *et al.*, 2022; Bornancini *et al.*, 2020; Kavalappara *et al.*, 2021). AlHudaib *et al.* (2022) identified mixed infections of bipartite and monopartite begomoviruses associated with DNA-satellites from tomato and muskmelon in Saudi Arabia.

Genetic Diversity

A broad spectrum of begomoviruses are found to be associated with vegetable crops. Around 55% of known characterized begomoviruses were documented on vegetables. In the phylogeny based on the nucleotide sequences of complete DNA A component, begomoviruses are grouped into different clades based on the crops infecting and a number of genomic components (monopartite and bipartite). Groups of begomoviruses categorized are infecting 1. malvaceous vegetables (monopartite), 2. solanaceous and cucurbits vegetable (monopartite), 3. solanaceous vegetables I (monopartite), 4. solanaceous vegetables II (monopartite), 5. solanaceous and malvaceous vegetables (monopartite), 6. legume vegetables (bipartite), 7. mixed group of vegetables (both bipartite and monopartite); and 8. sweet potato viruses (monopartite) (Figure 1). In some group, both monopartite and bipartite are clustered together, this might be due to the misidentification of some monopartite begomoviruses as bipartite and vice versa. Among the different group of begomoviruses, sweet potato-infecting viruses were found to form a separate cluster from other begomoviruses. Devendran *et al.*, (2022) has reviewed the chili infecting begomoviruses and concluded that phylogenetic relatedness is strongly correlated with geographic regions as a new world (American region - Latin America and North America) and old world (Africa, Asia, Australasia, and Europe). Similarly, the presence and prevalence of begomoviruses virus varied largely according to the geographical location, the host (tomato and pepper), and the production system (greenhouses or open fields) was observed by Barboza *et al.*, (2018). Venkataravanappa *et al.*, (2011) also studied the genetic variability among the begomoviruses infecting okra and derived the conclusion

as they are grouped based on their geographical origin and the evolution of new viruses by interspecific recombination events were identified. Although begomoviruses utilize host DNA polymerase (possessing proofreading activity), they display high levels of genetic variation as that of RNA viruses (Seal *et al.*, 2006). In addition, the co-existence of several begomoviruses together in the same host, the occurrence of recombination and reassortment of the genome become very common which leads to the primary genetic-based mechanisms responsible for rapid evolution of these viruses. This evolution of process ultimately leads to improved adaptation to the host helping to cause severe disease in new host and new geographical horizons.

Management

Whitefly-transmitted begomoviruses are one among the most serious threats to vegetable cultivation worldwide. This emergence is due in large part to the movement of plants and plant parts which distribute both vectors and viruses to new locations. Implementation of efficient and sustainable management practices is a highly challenging priority for the successful production of vegetable crops. Whiteflies that transmit viruses are most commonly controlled through the use of host plant resistance or the application of insecticides. Cultural practices often play a secondary role in control regimes, but in many circumstances, their use can be of critical importance in lessening the dependence on the two main tactics. Prevent seedling infestation by whitefly and virus infection—use netting or screening and isolation to maximise protection. Barrier crops (maize, sorghum, pearl millet) are crops grown along the borders of the main field as barrier to the movement of the pest from nearby fields. Both trap crops and barrier crops have shown to be effective in reducing the whitefly populations, consequently reducing the level of virus infection. There are two main approaches to plastic soil mulching—using colored (mainly yellow) plastic that attracts the whiteflies to the mulch instead of to the host, or silver or aluminium-coated plastic mulch that strongly reflects light, which acts as a deterrent to the invading whiteflies (Lapidot *et al.*, 2014). The successful use of reflective plastic mulch to delay the onset of whitefly infestations and infection by whitefly-transmitted viruses in open-field production is well established (Abubakar *et al.*, 2022; Lapidot *et al.*, 2014). Generally, yellow sticky traps or yellow pan traps are used to attract the whiteflies. It helps in both monitoring and mass trapping. These traps (25/acre) are hanged close to the crop canopy or at 30 cm from the ground/or canopy. In addition to these sanitary measures, the removal of weeds around the crop ecosystem and the rouging early infected plants were also provided good amount of control in field conditions (Devendran *et al.*, 2022; Nagendran *et al.*, 2020).

The use of insecticides to reduce vector populations is the most commonly used method for management of

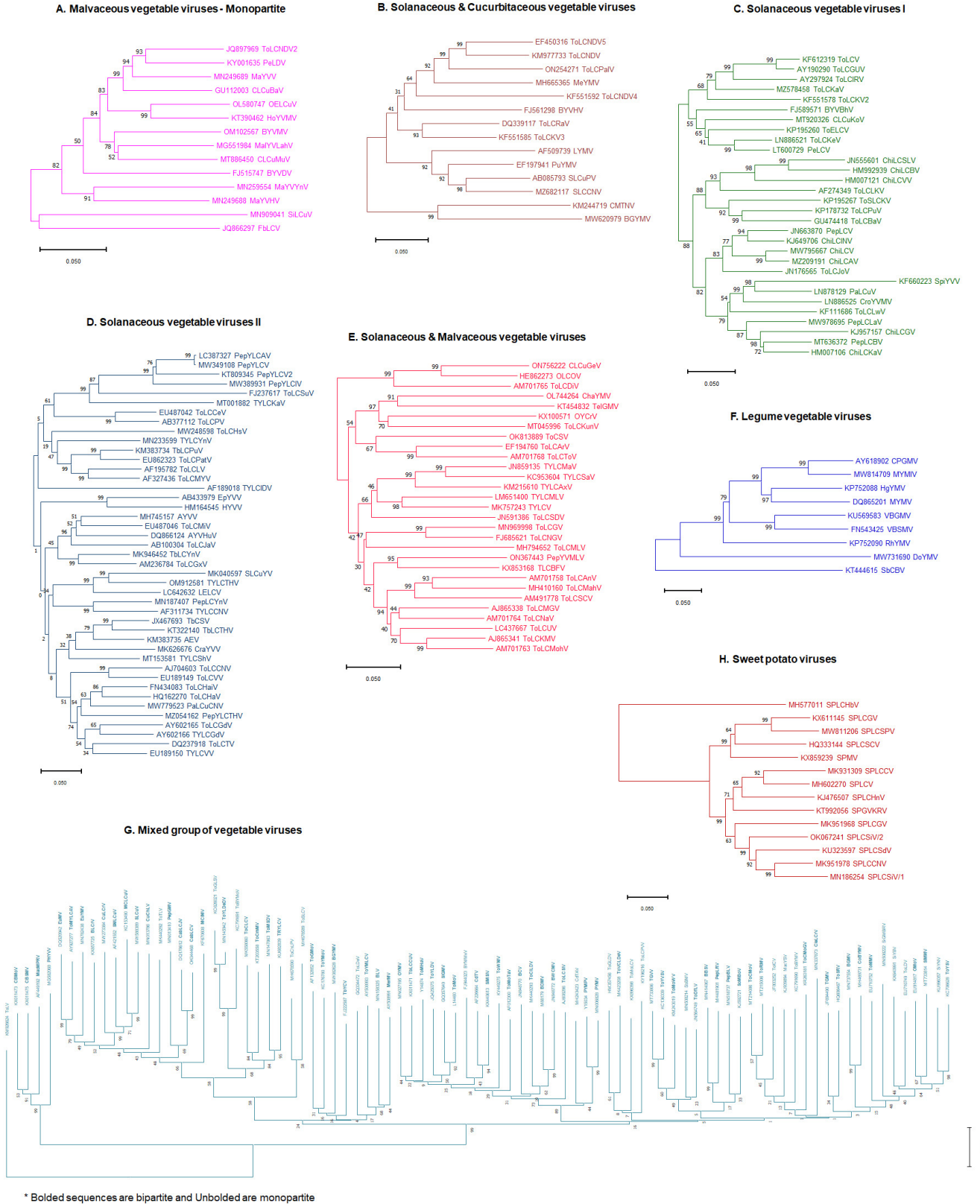


Figure 1: Phylogeography of known begomoviruses infecting vegetable crops globally

begomovirus diseases. It is common for seeds or transplants in greenhouses or seedbeds to be treated with systemic insecticides such as neonicotinoids (e.g., acetamiprid, dinotefuran, imidacloprid, and thiamethoxam) or the more recently available cyazypyr to manage vector populations, especially whiteflies. Yellow sticky cards can be used to monitor vector populations (whiteflies) in protected culture and in open fields. Though whitefly management was depending on synthetic pyrethroids until mid-1990s, the introduction novel insecticides such as afidopyopen, buprofezin, clothianidin, cyantraniliprole, diafenthiuron, dimethoate, fenpropathrin, flupyradifurine, oxydemeton-methyl, pyriproxyfen, spiromesifen, spirotetramat, thiamethoxam, tolfenpyrad, etc were recommended on vegetable crops (Nagendran *et al.*, 2017c). Several biocontrol agents, including entopathogenic fungi (*Beauveria bassiana*, *Verticillium lecanii*, and *Paecilomyces fumosoroseus*), predators (*Amblyseius swirskii*, *Macrolophus caliginosus*, and *Nesidiocoris tenuis*), and parasitoids (*Encarsia formosa* and *Eretmocerus eremicus*) were also reported to be effective in controlling whiteflies. However, due to concerns about the effect of insecticides on pollinators, consumer demand for reduced pesticide use, and the ability of the whitefly vectors to develop insecticide resistance, there is a growing need to develop and deploy strategies that do not rely on insecticides.

While host resistance has proven to be the most cost-effective management solution, few examples of host resistance have been developed to date. The best crop protection method is host resistance against viruses and/or whiteflies. In tomato breeding for Begomovirus resistance, the most prominent approach is transferring virus-resistance genes from wild tomato relatives into cultivated tomatoes. So far, six resistance genes (Ty-1, Ty-2, Ty-3, Ty-4, ty-5 and Ty-6) were identified from a few tomato wild species, including *S. habrochaites* and *S. chilense* (Anbinder *et al.*, 2009; Yan *et al.*, 2021). Four of these TYLCV resistance genes (Ty-1/Ty-3, Ty-2 and ty-5) have been cloned and characterized, representing three classes of antiviral defense mechanisms (Verlaan *et al.*, 2013; Yan *et al.*, 2021). At present, the introgression of Ty-1 or Ty-3 into cultivated tomatoes has been the major focus in breeding programs worldwide. However, Ty-1-mediated resistance has been observed not to be effective in the field and during mixed infection (Koeda and Kitawaki, 2023). Further, the breakdown of Ty-2-based resistance was reported by TYLCSV (Barbieri *et al.*, 2010). Therefore, efforts have been made to pyramid the Ty-genes (Yan *et al.*, 2018). Pyramiding of Ty-2 and Ty-3 genes conferred resistance to monopartite and bipartite begomoviruses causing leaf curl viruses of tomatoes in India (Prasanna *et al.*, 2014). Additionally, there is an urgent need to further exploit wild tomato relatives for novel genes against tomato leaf curl disease caused by begomoviruses.

To produce durable and broad-spectrum resistance, an essential approach would be to use multiple genes, a process known as pyramiding/stacking. Desirably, the stacked genes should confer different types of resistance.

The recessive resistance gene ty-5 identified from *Solanum peruvianum* encodes *Pelota*, which is the homolog of pepy-1 (Lapidot *et al.* 2015) and other genes such as *SISnRK 1*, *LeHT1*, *SIVSRLip*, *NIK* and *WRKY* in tomato; *Pepy-2* gene in chili; *CchGLP* gene in *Capsicum chinense*; and *Permease-1 like* gene in *Solanum habrochites* introgressed *S. lycopersicum* were identified to offer resistance against begomoviruses in vegetable crops (Beam and Ascencio-Ibáñez, 2020; Koeda *et al.*, 2022). Utilizing these genes upon developing varieties through classical breeding programs will generate crops resistance to either begomovirus or/and their vector. Alternative to the traditional breeding programs, through transgenic technologies several vegetable crops were developed resistant to begomoviruses. Strategies such as overexpression of plant defense gene (e.g., *CchGLP*) and silencing of genes targeting viral genome (AC1, AC2 and β C1) or whitefly genome (*v-ATPase*, *Aquaporins*, and *P450 CYP6M1*) through siRNA and miRNA were explored (Devendran *et al.*, 2022). Each and every component discussed so far renders viral disease control to a certain extent. In order to obtain a durable and sustainable solution for the management of begomoviruses in vegetable crops, an amalgamation of traditional and modern methods in the integrated pest and disease management program (IPDM) should be ensured.

To overcome begomovirus resistance challenges, conventional transgenic approaches such as pathogen-derived resistance (PDR) has been utilized for improved begomovirus resistance. Expression of a truncated Rep/C1 gene from TYLCV-Mld confers resistance in tomato but not to the TYLCV-IL strain. Transgenic common bean (*Phaseolus vulgaris*) cultivar Embrapa 5.1 was developed using RNA silencing via the expression of an intron-containing hairpin RNA corresponding to a portion of the Rep (AC1) gene of BGMV (Bonfim *et al.*, 2007). Recent research indicates that durable and broad-spectrum resistance can be achieved using the CRISPR/Cas9 system to target viral genes (Ji *et al.*, 2018). First, given the recombination ability of the TYLCV complex in the coding region, the CRISPR/Cas9 system targeting the non-coding intergenic region (IR) reduces the chance of non-homologous end-joining repair (NHEJ)-induced viral variants and enables durable virus interference (Ali *et al.*, 2016). CRISPR/Cas9 has been used to edit the genome of Bean yellow dwarf virus, BCTV, TYLCV, and ChLCV (Ali *et al.*, 2015; Ji *et al.*, 2015; Roy *et al.*, 2019).

IPM is the most desirable and effective approach for managing begomovirus diseases. This approach can be broken down into measures used before, during, and after the growing season. The combination of measures used in IPM programs depends on the crop and cropping system,

geographical region, knowledge of the virus-vector biology and disease epidemiology.

Future Prospective

This review highlights the global importance of begomovirus diseases, which continue to spread worldwide, and efforts to manage these diseases. Furthermore, new begomovirus species and genera continue to be described, further expanding the geographic distribution and host range of these viruses. Extensive efforts to understand the biology of these viruses and the epidemiology of begomovirus diseases have allowed for considerable progress in managing begomovirus diseases. The most desirable measure entails the breeding and deployment of begomovirus-resistant cultivars. Clearly, no single measure will provide long-term sustainable management. Hence, an IPM approach will help to sustainable and eco-friendly management is required.

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सारांश

सफ़ेद मक्खी द्वारा प्रसारित बेगोमोवाइरस दुनिया भर में सब्जी फसलों की खेती के लिए एक गंभीर समस्या बन चुका है | अधिकांश मामले में यह विषाणु आमतौर पर मिश्रित संक्रमण में पाए जाते हैं, जिसकी वजह से एक नए वाइरस प्रजाति की उत्पत्ति होती है | ये प्रजाति विभिन्न भौगोलिक क्षेत्रों में लगायी जाने वाली भिन्न-भिन्न फसलों के लिए अनुकूलित पाए जाते हैं | अभी तक लगभग बेगोमोवाइरस की कुल 243 प्रजातियाँ पायी जाती हैं, जो पुरे विश्व में उगाई जाने वाली सब्जी फसलों को संक्रमित करती हैं | सब्जी फसलों को संक्रमित करने वाला ये विषाणु फायलीोजेनेटिक विश्लेषण में विविधता प्रदर्शित करते हैं | इस समीक्षा का उद्देश्य बेगोमोवाइरस द्वारा कुल सब्जी फसलों का वैश्विक परिदृश्य, संक्रमण का लक्षण, जीनोम संगठन, वर्गीकरण एवं विविधता, रोग को पहचानने का तरीका, एवं उनके नियंत्रण के लिए विभिन्न तरीके को प्रस्तुत करना है |