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An Overview of Begomoviruses: Structure, Functions, and Interactions

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ABSTRACT

Begomoviruses, which are members of the Geminiviridae family, are among the most economically significant groups of plant viruses, causing substantial losses in a variety of crops across the globe. These viruses are mainly spread by the whitefly (Bemisia tabaci) in a persistent, circulative manner. They have circular single-stranded DNA genomes that are encapsidated in distinctive geminate particles. Begomoviruses are divided into monopartite and bipartite forms based on the organization of their genomes; each type has a different genomic makeup and functional characteristics. Numerous proteins crucial for viral replication, gene expression, intracellular migration, and inhibition of host defense mechanisms are encoded by the begomovirus genome. Many begomoviruses are associated with subviral molecules, such as alphasatellites, betasatellites, and deltasatellites, in addition to their genomic components. These satellites have been shown to affect the onset of symptoms and increase pathogenicity. These satellites are found to affect how symptoms manifest, exacerbate disease, and alter the way the virus and the host plant interact. The way the proteins, the host plants, the vectors and the satellites all work together is very complicated and helps the begomoviruses infect plants, adapt and spread. Begomoviruses infect diverse plant species, evolve rapidly, and are efficiently spread by vectors, thereby posing a serious challenge to sustainable agriculture. This review examines begomoviruses in detail, including how their genes are organized, what their proteins do, how they are transmitted by vectors, the role of satellites, and how they interact with plants and affect plant health. Understanding these aspects is essential for developing effective strategies to control begomoviruses and cultivate resistant plant varieties.

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1. INTRODUCTION

Begomoviruses are an emerging group of plant viruses in the family Geminiviridae, which are responsible for the obliteration of economically significant agricultural crops. Also, being one of the most diverse viruses known globally, to have a wide host range, characterized by circular single- stranded DNA (ssDNA) genomes encapsidated within unique twin- shaped particles. Begomovirus-associated diseases were first recognized in the 20th century, when leaf curl symptoms in cotton were first reported in the Indian subcontinent (Kirkpatrick, 1931). These early observations laid the foundation for subsequent discoveries identifying whitefly-transmitted viruses as the causal agents, ultimately leading to the classification and molecular characterization of begomoviruses. In the past few decades, begomoviruses have been recognized as major limiting factors in the productivity of various crops across the globe. These begomoviruses have been known to infect many important crops, including tomato, cotton, cassava, pepper, and legumes, causing various manifestations of disease, including leaf curling, chlorosis, vein thickening, and severe stunting of the plants. In most of these cases, the disease has been known to cause severe economic losses when the plants become severely affected by

the virus. The rise of begomovirus-related diseases has been largely ascribed to the wide distribution of the vector of begomovirus, *Bemisia tabaci*, as well as the rapid evolution of the virus by mutation and recombination (Rojas et al., 2005; Naveed et al., 2023).

Begomoviruses are mainly found in tropical and subtropical regions, but their distribution is expanding into temperate zones. They have a wide host range, infecting various dicotyledonous plant species, including cultivated plants and wild plants, which serve as reservoirs for the viruses. Their genetic variability and flexibility are major factors for the evolutionary success of these viruses (Hanley-Bowdoin et al., 2013; Sandra & Mandal, 2024). The genetic diversity and flexibility of begomoviruses are two key reasons behind their evolutionary success (Hanley-Bowdoin et al., 2013; Sandra & Mandal, 2024). From a molecular standpoint, begomoviruses are characterized as being either monopartite or bipartite in nature, and these viruses are often associated with subviral agents such as alphasatellites, betasatellites, and deltasatellites, which play a crucial role in the determination of their pathogenicity and symptom expression. The complex association between these viruses, their proteins, host plants, vectors, and subviral agents creates a dynamic system that enables these viruses to successfully infect plants and express diseases. The genetic variability, evolutionary plasticity, and transmissibility of these viruses via their vectors are a serious concern for global food security and sustainable agricultural practices. In addition, advances in molecular biology and high-throughput sequencing technologies have greatly contributed to the understanding of diversity, evolution, and epidemiology of begomoviruses. These techniques have helped in the discovery of novel begomovirus species, detection of recombination, and exploration of virus-host interactions in detail. This information is of prime importance in identifying new strains of the virus and developing innovative techniques for controlling begomovirus-induced diseases in the dynamic environment of modern agriculture. Hence, it is crucial for us to understand the biology of these viruses in order to successfully manage them and improve resistance in their hosts.

This review aims to summarize current knowledge on begomoviruses, with special emphasis on their genome organization, protein functions, vector transmission, associated satellites, as well as the intricate interactions underlying their pathogenicity and ecological success, while highlighting emerging insights and knowledge gaps. By providing a comprehensive synthesis of recent research, it aims to guide future studies and inform the development of effective management strategies and resistant crop varieties.

2. BEGOMOVIRUS: FAMILY CONSTRUCTION & GENOME ORGANIZATION

2.1. FAMILY CONSTRUCTION:

The Geminiviridae family includes a large and diverse set of plant-infecting viruses, all with circular single-stranded DNA genomes, as well as unique twinned (geminate) icosahedral particles. The Geminiviridae family, as classified by the International Committee on Taxonomy of Viruses (ICTV), includes viruses with genomes ranging from 2.5 to 5.2 kb in size, which can be monopartite or bipartite in nature. The name 'Geminiviridae' has been derived from the geminate particle morphology, which is a characteristic feature of the family. Geminiviruses are defined as viruses belonging to the family 'Geminiviridae' based on the presence of a circular single-stranded DNA genome. The Geminiviridae family has been shown to infect a wide range of monocot and dicot plant species, with different members being transmitted by various Hemiptera insect species, such as whiteflies, leafhoppers, aphids, and treehoppers (Fiallo-Olivé et al., 2021). According to the genome structure, hosts, vector specificity, and genetic relationship, the family Geminiviridae comprises different genera, which include Begomovirus, Mastrevirus, Curtovirus, Topocuvirus, Turncurtovirus, Becurtovirus, Capulavirus, Grablovirus, Eragrovirus, Maldovirus, Mulcrilevirus, Citlodavirus, Topilevirus, and Opunvirus (Fiallo-Olivé et al., 2021). Out of all the genera of the family Geminiviridae, the largest genus is the Begomovirus genus, which comprises hundreds of species. There are now 133 officially recognized geminivirus species, of which 117 belong to the genus *Begomovirus* (Stanley et al., 2005), and there are almost 400 complete nucleotide sequences deposited in databases (Fauquet and Stanley, 2005), reflecting their economic importance and enormous diversity resulting from their widespread geographic distribution and host adaptation. Other genera of the family differ in the specificity of the hosts and the vector insects. For example, the Mastrevirus genus comprises viruses that mainly infect monocots and are transmitted by leafhoppers, while the Capulavirus genus comprises viruses that are specifically transmitted by aphid insects. Begomoviruses, the largest genus of the family Geminiviridae, are a group of plant viruses first recognized in the late 1970s through electron microscopy, and studies revealed their distinctive twin-shaped, or geminate, particles (Hull, 2014). This classification system represents the

evolutionary history, genetic diversity, complexity of the viruses, as well as the adaptations of the geminiviruses, offering a scientific approach to the study of these viruses.

The major genera within the family *Geminiviridae*, along with their key molecular characteristics, genome organization, and representative features, are summarized in **Table 1**.

Table 1. Genera of the Family *Geminiviridae* and their key characteristics

Genus	Host Range	Genome Organization	Vector Type	Genome Size (kb)	Representative species	Reference
Begomovirus	Infects dicots; highly diverse	Circular ssDNA; monopartite or bipartite	Whiteflies (*Bemisia tabaci*)	2.5–2.8 (each component)	Tomato yellow leaf curl virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014; Hanley-Bowdoin et al., 2013
Mastrevirus	Infects monocots (grasses, cereals)	Circular ssDNA; monopartite	Leafhoppers	2.7–3.0	Maize streak virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014; Hanley-Bowdoin et al., 2013
Curtovirus	Infects dicots	Circular ssDNA; monopartite	Leafhoppers	~3.0	Beet curly top virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014; Hanley-Bowdoin et al., 2013
Topocuvirus	Infects dicots	Circular ssDNA; monopartite	Treehoppers	~3.0	Tomato pseudo-curly top virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014; Hanley-Bowdoin et al., 2013
Turncurtovirus	Infects dicots	Circular ssDNA; monopartite	Leafhoppers	2.7–3.0	Turnip curly top virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014; Hanley-Bowdoin et al., 2013
Becurtovirus	Infects dicots	Circular ssDNA; monopartite	Leafhoppers	~3.0	Beet curly top Iran virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014; Hanley-Bowdoin et al., 2013
Capulavirus	Infects dicots	Circular ssDNA; monopartite	Aphids	~2.7	Euphoria caputmedusae latent virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014; Hanley-Bowdoin et al., 2013
Grablovirus	Infects woody dicots	Circular ssDNA; monopartite	Treehoppers	2.7–3.0	Grapevine and blotch virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014; Hanley-Bowdoin et al., 2013
Eragrovirus	Infects monocots (grasses)	Circular ssDNA; monopartite	Leafhoppers	2.7–2.8	Eragrostis streak virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014; Hanley-Bowdoin et al., 2013
Maldovirus	Infects dicots (woody hosts)	Circular ssDNA; monopartite	Unknown / suspected insect vector	~3.0	Mulberry-associated virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014
Mulcrilevirus	Infects dicots	Circular ssDNA; monopartite	Unknown	~3.0	Mulberry crinkle leaf virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014
Citlodavirus	Infects citrus	Circular ssDNA; monopartite	Unknown	~3.0	Citrus chlorotic dwarf-associated virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014

Topilevirus	Infects dicots	Circular ssDNA; monopartite	Treehoppers (suspected)	~3.0	Tomato apical leaf curl virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014
Opunvirus	Infects cactus (*Opuntia* spp.)	Circular ssDNA; monopartite	Unknown	~3.0	Opuntia virus	Fiallo-Olivé et al., 2021; Varsani et al., 2014

2.2. GENOME ORGANIZATION:

The genome organization of Begomovirus is highly compact, dynamic, and functionally advanced, which facilitates efficient replication and adaptability in plant hosts. The Begomovirus genus has circular single-stranded DNA (ssDNA) genomes ranging from 2.6 to 2.8 kb in size, which are packaged in geminate particles, a distinctive feature of this genus. The presence of monopartite and bipartite genomes in Begomovirus is one of the major characteristics, which reflects the evolution and adaptability of Begomovirus in host environments (ICTV, 2021; Rojas et al., 2018). An important characteristic of Begomovirus is that it contains two forms: monopartite and bipartite. Monopartite begomoviruses are characterized by having only one DNA component, which contains all necessary information for infection, replication, and movement in the plant. On the other hand, bipartite begomoviruses are composed of two circular DNA components: DNA-A and DNA-B, which work in coordinated manner for the virus to perform its functions. DNA-A is responsible for encoding proteins for replication and regulation, while DNA-B contains movement proteins necessary for intracellular movement and systemic movement in the plant (Rojas et al., 2018; Hanley-Bowdoin et al., 2013).

The DNA-A encoded proteins are involved in replication and regulation, with Replication-associated protein (Rep) initiating rolling circle replication, while Transcriptional activator protein (TrAP) and Replication enhancer protein (REn) are involved in regulating gene expression and enhancing replication efficiency, respectively. The Coat protein (CP), encoded from the virion sense strand, is involved in encapsidation and is critical for vector transmission by the whitefly *Bemisia tabaci* (Hanley-Bowdoin et al., 2013; Fondong, 2019). The DNA-B encoded proteins, unique to bipartite begomoviruses, are involved in movement, with Nuclear Shuttle Protein (BV1) and Movement Protein (BC1) being involved in intracellular movement and facilitating systemic movement through the host plant via plasmodesmata.

A highly conserved common region (CR) exists between the two DNAs, which contains the origin of replication and has a stem-loop structure with the conserved nonanucleotide sequence TAATATTAC, which is essential for the initiation of rolling-circle replication. The genome exists as ambisense, meaning the genes are found on both the virion sense and the complementary sense strands. This maximizes the coding potential for a given genome size. Additionally, the presence of overlapping open reading frames and the frequent recombination events contribute to the genetic diversity and evolutionary adaptability of the begomoviruses. For the case of monopartite begomoviruses, the association with satellite molecules also plays a role in pathogenesis and symptom modulation. This highly efficient and adaptable genome structure is the reason for the ability of begomoviruses to replicate efficiently and adapt to a wide range of hosts, thereby affecting a large number of crops (Ramesh et al., 2022; Kumar et al., 2023).

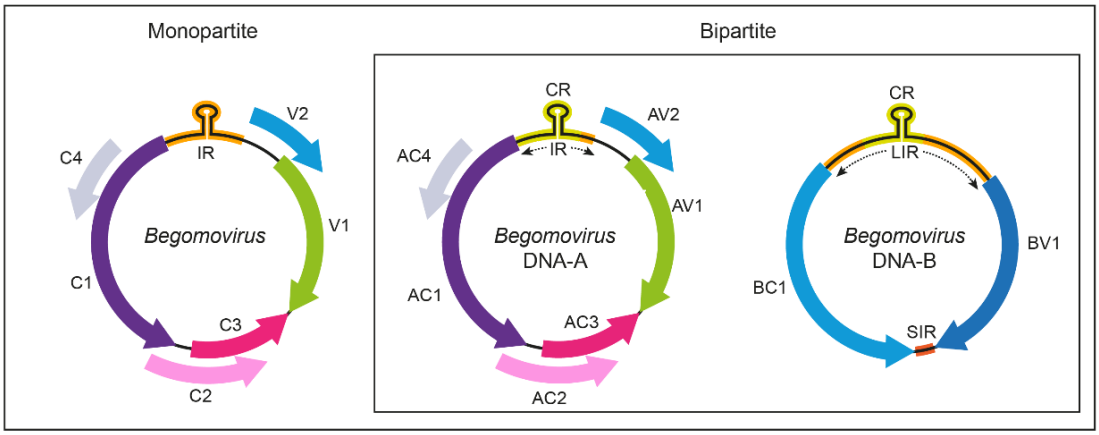

Figure 1. Genome organization of begomoviruses showing monopartite and bipartite genomes (DNA-A and DNA-B), arrangement of open reading frames, and common region (CR). (Fiallo-Olivé et al., 2021)

3. VIRAL PROTEINS AND THEIR FUNCTIONS

Begomovirus has a small but highly efficient set of multifunctional proteins, which play a role in replication, transcription, movement, as well as interactions between the host and the virus. These have resulted from strong evolutionary pressures favouring genome economy. These proteins are present primarily on the DNA-A genome (and DNA-B of bipartite begomoviruses) in ambisense orientation, which ensures compact yet highly coordinated expression of the genes (Hanley-Bowdoin et al., 2013; Fondong, 2019). The Replication-associated protein, or Rep/AC1, is the most critical protein, and its role is to initiate the rolling circle replication process by cleaving the conserved origin of replication found in the intergenic region. The protein also recruits the host replication apparatus and regulates the replication of the virus. The Transcriptional activator protein, or TrAP/AC2, is a critical protein, and its role is to regulate late gene expression, activating it and suppressing the transcriptional gene silencing of the host, thus increasing the accumulation of the virus. The Replication enhancer protein, or REn/AC3, works synergistically with the Rep protein, thus increasing the efficiency of replication and stabilizing the replication intermediates, thus increasing the titers of the virus in the infected tissues.

The Coat protein, or CP/AV1, is a structural protein, and its role is to encapsidate the ssDNA of the virus, forming geminate structures. The CP is critical in the transmission of the virus by the whitefly *Bemisia tabaci*. The CP is also critical in the systemic transmission of the virus and in the specificity of the virus. (Hanley-Bowdoin et al., 2013; Rojas et al., 2018). In many begomoviruses, the C4 protein (AC4) acts as a multifunctional pathogenicity determinant involved in symptom development, modulation of host signalling pathways, and suppression of RNA silencing.

In bipartite begomoviruses, movement functions are encoded by DNA-B. The Nuclear Shuttle Protein (BV1/NSP) mediates transport of viral DNA between the nucleus and cytoplasm, while the Movement Protein (BC1/MP) facilitates cell-to-cell movement through plasmodesmata, ensuring systemic infection throughout the host plant (Rojas et al., 2018; Kumar et al., 2023). Together, these proteins form a coordinated network that enables efficient replication, spread, and survival of the virus within diverse plant hosts. Recent studies also emphasize that some proteins encoded by begomoviruses have overlapping and multifunctional roles, especially in relation to the suppression of host immunity, hormone signalling pathways, and interactions with host transcriptional apparatus, thus emphasizing their high adaptability and success as plant pathogens (Ramesh et al., 2022). The major proteins encoded by begomoviruses and their functional roles are summarized in **Table 2**.

Table 2: Viral proteins of Begomovirus and their functions:

Protein	Gene	Genomic component	Major functions	References
Replication-associated protein (Rep)	AC1 / C1	DNA-A	Initiates rolling-circle replication by nicking the origin (TAATATTAC); recruits host DNA replication machinery; regulates viral DNA synthesis	Hanley-Bowdoin et al., 2013; Fondong, 2019
Transcriptional activator protein (TrAP)	AC2 / C2	DNA-A	Activates late viral gene expression; suppresses host RNA silencing and defense responses	Fondong, 2019; Rojas et al., 2018
Replication enhancer protein (REn)	AC3 / C3	DNA-A	Enhances efficiency of viral DNA replication; stabilizes replication complexes	Hanley-Bowdoin et al., 2013; Fondong, 2019
Coat protein (CP)	AV1 / V1	DNA-A	Encapsidation of viral ssDNA; required for whitefly transmission; involved in systemic movement and host interactions	Rojas et al., 2018; Hanley-Bowdoin et al., 2013
C4 protein	AC4	DNA-A	Symptom development; alters host signaling pathways; suppresses RNA silencing	Fondong, 2019; Ramesh et al., 2022
Nuclear shuttle protein (NSP)	BV1	DNA-B	Transports viral DNA between nucleus and cytoplasm; essential for intracellular trafficking	Rojas et al., 2018
Movement protein (MP)	BC1	DNA-B	Facilitates cell-to-cell movement through plasmodesmata; ensures systemic infection	Rojas et al., 2018; Kumar et al., 2023

4. REPLICATION AND INFECTION CYCLE

The replication and infection process of Begomovirus is tightly regulated, occurring almost exclusively in the nucleus of the infected cell. This process mirrors the dependence of Begomovirus on the replication machinery of the host cell. After the virus has successfully entered the host cell, usually through the whitefly vector *Bemisia tabaci*, the viral genome of the single-stranded DNA (ssDNA) is transported into the nucleus, where it undergoes conversion into double-stranded DNA (dsDNA), which acts as the transcriptional and replicative genome (Hanley-Bowdoin et al., 2013; Fondong, 2019). The replication process of Begomovirus occurs via the rolling-circle replication (RCR) process, which begins with the interaction of the viral protein, the Replication-associated protein (Rep), with the conserved intergenic region (IR), specifically the stem-loop structure containing the nonanucleotide sequence TAATATTAC, where the virus introduces a site-specific nick. DNA polymerases of the host cell then interact with the virus, synthesizing the viral genome, which takes the forms of both single-stranded genomes and replicative intermediates. The Replication enhancer protein (REn) assists the replication process of Begomovirus, stabilizing the replication complexes and optimizing the interactions of the virus with the host cell (Rojas et al., 2018).

Subsequently, expression of viral genes is regulated in time. Early genes, such as Rep, TrAP, and REn, are first expressed to facilitate replication and suppress host responses to infection. After this, structural genes, such as the Coat protein, are expressed for encapsidation and transmission. In bipartite begomovirus, DNA-B replication is coordinated with DNA-A replication to ensure equal expression of movement and replication functions. Intracellular movement is another significant phase in the infection cycle. The Nuclear Shuttle Protein, BV1, moves DNA from the nucleus to the cytoplasm, while the Movement Protein, BC1, moves viruses from one plant cell to another through plasmodesmata, facilitating systemic infection in vascular tissues, which eventually leads to systemic symptoms in infected plants (Rojas et al., 2018; Kumar et al., 2023). The systemic infection process is further facilitated by the inhibition of host RNA silencing, which is suppressed by TrAP and C4 proteins, thus evading host immune responses and ensuring optimal replication. This ensures the production of mature viruses in the nucleus, which are then transmitted to new host plants via the whitefly vector, thus completing the infection process.

Overall, the begomovirus replication and infection cycle is a highly coordinated process involving nuclear replication, regulated gene expression, and efficient intracellular and intercellular movement, ensuring successful infection and rapid spread within host plants.

5. VECTOR TRANSMISSION OF BEGOMOVIRUS

The transmission of *Begomovirus* is uniquely and obligatorily mediated by the whitefly *Bemisia tabaci*, making vector biology a central determinant of begomovirus epidemiology and emergence. Transmission occurs in a persistent, circulative, non-propagative manner, in which the virus is acquired during feeding on infected phloem tissue, circulates through the insect body, and is retained for extended periods without replicating within the vector (Navas-Castillo et al., 2011; Wei & Zhou, 2016). This mode of transmission enables even low whitefly populations to initiate widespread epidemics under favourable environmental conditions. At the molecular level, begomovirus acquisition begins in the midgut, followed by passage through the gut barrier into the hemolymph and eventual accumulation in the salivary glands. Successful transmission requires specific interactions between viral particles and insect cellular components, where the coat protein (CP) is a key determinant of vector recognition, internalization, and retention (Fondong, 2019; Rosell et al., 1999). The first stage in the infection cycle involves the injection of viral ssDNA into a plant cell by an insect vector. Geminiviruses replicate through a double-stranded (ds)DNA intermediate in the nucleus of the infected cells. Upon initial entry of a geminivirus into a host cell, there are no viral proteins present other than CP. Recent studies further indicate that additional viral factors beyond CP, including non-structural proteins and viral DNA forms, may contribute to vector competence and transmission efficiency (Ghanim, 2014).

A key factor that influences the spread of begomoviruses is the genetic composition of *Bemisia tabaci*, which comprises various cryptic species with unique biological characteristics. For example, the invasive species MEAM1 and MED have a high fecundity rate, a rapid ability to switch hosts, and a strong resistance to insecticides. These characteristics enable them to thrive and dominate the agroecosystems, thereby facilitating the rapid spread of the virus across the regions (Fiallo-Olivé et al., 2021; De Barro et al., 2011). These cryptic species of *Bemisia tabaci* have unique efficiencies for the transmission of specific begomoviruses. These unique efficiencies contribute to the differential disease outbreaks observed in various regions of the globe.

Environmental and agronomic conditions also play a crucial role in influencing the population of the vector and the transmission of the virus. For example, an increase in temperature, the practice of intensive monoculture, and the year-round cultivation of crops contribute to the buildup of the vector population. Furthermore, the plant–virus–vector interaction is now recognized to be a tripartite interaction. For example, the plant can influence the behaviour of the vector and enhance the spread of the virus through changes in the emission of volatile organic compounds and nutrient composition (Wei & Zhou, 2016). Overall, begomovirus transmission is governed by a complex interplay of molecular interactions, vector population biology, and environmental conditions. This intricate relationship between virus and *Bemisia tabaci* underpins the rapid emergence and global distribution of begomovirus-associated diseases in agricultural ecosystems (De Barro et al., 2011; Ghanim, 2014).

6. BEGOMOVIRUS ASSOCIATED SATELLITES

Begomoviruses are frequently associated with small, circular, single-stranded DNA molecules known as satellites, which are dependent on the helper virus for replication, encapsidation, and movement within the host plant. Satellites are defined as viruses or nucleic acids that depend on a helper virus for their replication but lack extensive nucleotide sequence homology to the helper virus and are dispensable for its proliferation (Mayo et al., 2005). These satellite molecules do not encode all functions required for independent infection but play a crucial role in modulating disease severity, host–virus interactions, and epidemiological outcomes. The major types of begomovirus-associated satellites include betasatellites, alphasatellites, and occasionally deltasatellites, each differing in structure, coding capacity, and functional roles (Fiallo-Olivé et al., 2021; Nawaz-ul-Rehman & Fauquet, 2009).

Betasatellites are the most well-characterized satellite molecules, which are approximately 1.3 kb in length. They contain a single protein-coding region, βC1, which plays a critical role as a pathogenicity determinant, causing symptoms, suppressing host RNA silencing, and modulating the plant defense system. Betasatellites are primarily associated with Old World monopartite begomoviruses. These satellite molecules are essential for the development of severe disease symptoms in various economically important crops. (Gnanasekaran et al., 2019; Zhou, 2013)

The begomovirus/betasatellite complexes are often associated with a second type of circular ssDNA satellite, initially referred to as DNA-1 (Mansoor et al., 1999; 2001; Saunders and Stanley, 1999; Briddon et al., 2004), but now called alphasatellites (Mubin et al., 2009b, Tiendrebeogo et al., 2010). They are approximately 1.3 kb in length. These satellite molecules contain a protein-coding region, replication-associated protein (Rep), which allows the satellite molecules to replicate autonomously in the host cell. However, the replication of these satellite molecules depends on the helper begomovirus. Alphasatellites, like betasatellites, do not cause symptoms. However, these satellite molecules modulate the severity of the disease. (Fiallo-Olivé et al., 2021)

Deltasatellites are small, less well-characterized satellite molecules. These satellite molecules contain no protein-coding regions. These satellite molecules totally depend on the helper begomovirus. However, the role of these satellite molecules has not been clearly elucidated. These satellite molecules are believed to modulate the virus concentration, causing symptoms during begomovirus infections. Overall, begomovirus-associated satellites significantly enhance pathogenic complexity by acting as molecular amplifiers or modulators of infection. Their interactions with helper viruses and host plants contribute to increased virulence, symptom diversity, and epidemiological unpredictability, making them critical determinants in begomovirus disease complexes and a major challenge for sustainable crop protection strategies (Zhou, 2013; Gnanasekaran et al., 2019; Fiallo-Olivé et al., 2021).

7. EVOLUTION AND DIVERSITY

The evolutionary success of Begomoviruses has been attributed to the exceptional ability of these viruses to undergo genetic diversification, thus adapting easily to new hosts, environments, and ecological conditions. Begomoviruses have the highest evolutionary rates compared to other DNA viruses, attributed to the use of host polymerases, coinfection, and ecological pressures from interactions with the vector, virus, and plants (Fondong, 2019; Ramesh et al., 2022). An essential evolutionary process of begomoviruses has been homologous recombination, which has been widely accepted as the principal process of genetic innovation. In the case of the coinfection of a host plant with various begomovirus isolates, genetic fragments are exchanged, thus forming a mosaic genome. These genetic fragments have unique combinations of replication, movement, and pathogenicity genes. The process of homologous recombination has been shown to frequently take place at the intergenic region, the replicase gene, and the coat protein gene, which are essential regions of

the begomovirus genome. These regions are essential in the initiation of replication and the transmission of the virus from the vector. Such processes have resulted in the unpredictable nature of begomoviruses, thus affecting the host plants (Varsani et al., 2014; Rojas et al., 2018).

One of the major mechanisms of begomovirus evolution is homologous recombination, which is considered the most important mechanism of genetic innovation in begomoviruses. The process of recombination occurs when a plant is co-infected with multiple begomovirus isolates, and as a result, segments of the viral genome are swapped, producing a new genome or a mosaicism of begomoviral genome segments, which may have new combinations of replication, movement, and pathogenicity determinants. Recombination is most frequently found in the intergenic region, the Rep gene, and the coat protein gene, which are essential for the initiation of replication and transmission of the virus by the vector. Recombination in begomoviruses is considered a major mechanism of abrupt evolution, making begomoviruses the most unpredictable viruses in the field (Varsani et al., 2014; Rojas et al., 2018). In begomoviruses, the tendency for recombination and acquisition of extra DNA components has resulted in emergence of new viruses that infect new hosts and cause new diseases (Varma and Malathi, 2003; Chakraborty et al., 2003).

Another mechanism of begomovirus evolution is mutation, which is considered a major mechanism of gradual evolution, particularly in the face of host immune responses and environmental pressures. Although DNA viruses have a low mutation rate compared to RNA viruses, the huge population size and the fast replication rate of begomoviruses play a significant role in the evolution of the virus, making it easy for the virus to adapt and diversify its lineage.

A major evolutionary bifurcation is observed between Old World (OW) and New World (NW) begomoviruses, reflecting historical geographic isolation and independent evolutionary trajectories. OW begomoviruses are frequently monopartite and commonly associated with betasatellites that enhance pathogenicity. In contrast, NW begomoviruses are predominantly bipartite and generally lack betasatellite associations, indicating distinct evolutionary constraints and genome organization strategies (Fiallo-Olivé et al., 2021; Rojas et al., 2018). Moreover, satellite molecules play important roles as modulators of evolution, especially betasatellites that increase disease severity and put additional selection pressure on helper viruses to evolve to more virulent recombined viruses. Similar to the evolution of viruses at the molecular level, the global dissemination of *Bemisia tabaci* cryptic species complexes has accelerated the dissemination of viruses through multiple instances of introduction, interregional recombination, and rapid epidemic evolution in new agroecosystems (De Barro et al., 2011; Ghanim, 2014).

8. DISEASE SYSTEM AND HOST RANGE

Begomoviruses infect a wide range of economically important dicotyledonous crops, causing severe disease symptoms that significantly reduce agricultural productivity. The symptom expression varies depending on the viral strain, host species, environmental conditions, and presence of satellite molecules. Common symptoms include leaf curling, leaf crumpling, vein thickening, chlorosis, interveinal yellowing, stunted growth, and reduced fruit or flower development (Rojas et al., 2018; Fondong, 2019). In many crops, such as tomato, cotton, chilli, and cassava, begomovirus infections lead to severe yield losses due to disruption of normal plant growth and development. The βC1 protein of betasatellites often intensifies symptom severity by interfering with host defense mechanisms and hormonal signaling pathways, resulting in more pronounced morphological abnormalities (Gnanasekaran et al., 2019). The host range of begomoviruses is highly diverse and continues to expand due to recombination and vector-mediated spread. While many begomoviruses exhibit host specificity, others demonstrate the ability to infect multiple plant species, contributing to cross-crop transmission and epidemic outbreaks in agricultural landscapes.

9. MANAGEMENT STRATEGIES

Managing begomovirus diseases is challenging due to their rapid evolution, wide host range, and efficient whitefly transmission. Therefore, effective management requires an integrated disease management (IDM) approach combining multiple strategies.

One of the most important control measures is vector management, targeting *Bemisia tabaci* populations through insecticides, biological control agents, reflective mulches, and barrier cropping. Reflective mulches, for example, reduce whitefly landing rates by altering light reflection patterns, thereby lowering virus transmission in crops like tomato and pepper (Rojas et al., 2018; Nouri et al., 2022). However, insecticide resistance in whitefly populations has reduced the long-term effectiveness of chemical control methods (De Barro et al., 2011; Ghanim, 2014). Field studies (2022–2024) show that fungal biocontrol agents combined with reduced pesticide use significantly suppress *Bemisia tabaci* populations

while maintaining ecological balance (Sharma et al., 2023). The use of resistant crop varieties is another key strategy. Host plant resistance can be achieved through conventional breeding or modern biotechnological approaches such as RNA interference (RNAi) and CRISPR-based genome editing. These approaches aim to disrupt key viral processes such as replication or movement. Cas9 or Cas12 systems can be engineered to recognize conserved viral sequences, especially in the intergenic region (IR) or Rep gene, leading to cleavage and degradation of viral DNA. For example, CRISPR/Cas9 targeting of Tomato leaf curl New Delhi virus (ToLCNDV) has shown a significant reduction in viral load and symptom severity in experimental plants. However, viral escape mutants due to repair mechanisms remain a challenge, leading to ongoing research into multiplex CRISPR targeting strategies (Ali et al., 2016; Kumar et al., 2019). A major breakthrough is Spray-Induced Gene Silencing (SIGS), where externally applied dsRNA molecules trigger transient antiviral responses without genetic modification. SIGS has shown promising protection against DNA viruses, including begomoviruses, under greenhouse conditions (Dalakouras et al., 2022; Koch et al., 2023). Some recent work shows that combining HIGS with RNAi significantly enhances resistance durability and reduces viral load more effectively than single-gene approaches (Kumar et al., 2022; Singh et al., 2024). This approach is gaining attention due to its non-transgenic, environmentally safe nature.

Also, modern genomic breeding tools such as genomic selection (GS) and high-throughput phenotyping are now increasingly used to identify durable resistance sources against Tomato leaf curl and Cassava mosaic begomoviruses (Legg et al., 2022; Patil et al., 2023). Recent studies have explored the use of nanoparticles (Ag, ZnO, SiO_2) as antiviral agents or delivery systems for RNAi molecules. These approaches represent a next-generation delivery system for RNAi and antiviral compounds (Khan et al., 2022; Prasad et al., 2024). These nanoparticles can enhance stability, uptake, and systemic movement of antiviral compounds in plants, representing a promising frontier in plant virology research. Cultural practices, including crop rotation, removal of infected plant debris, use of virus-free planting material, and adjustment of planting time, also play a critical role in reducing disease incidence. Additionally, the use of biotechnological tools, such as transgenic resistance and gene silencing technologies, has shown promising results in limiting begomovirus infection and spread. Despite these strategies, the high genetic variability of begomoviruses and the adaptability of their vector continue to pose significant challenges, necessitating continuous development of innovative control approaches.

10. CONCLUSION AND FUTURE PERSPECTIVES

Begomoviruses represent one of the most economically significant and evolutionarily dynamic groups of plant DNA viruses, causing widespread damage to global agriculture. Their success is driven by compact genome organization, multifunctional viral proteins, efficient whitefly-mediated transmission, and strong interactions with satellite molecules. The continuous emergence of new recombinant strains, expansion of host range, and global spread of *Bemisia tabaci* cryptic species complexes highlight the increasing complexity of begomovirus disease systems. Moreover, satellite molecules further amplify pathogenicity and contribute to unpredictable disease outcomes.

Future research should focus on understanding virus–vector–host molecular interactions, identifying durable resistance genes, and developing advanced genome-editing approaches for crop protection. Additionally, improved surveillance and genomic monitoring of begomovirus populations will be essential for early detection and management of emerging strains. Ultimately, addressing begomovirus-associated diseases will require sustained interdisciplinary efforts that integrate molecular virology, vector ecology, and advanced crop biotechnology to achieve durable and long-term disease management.

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