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Begomovirus Recombination: Mechanisms Driving the Emergence of Novel Strains in Plant Pathogenesis

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ABSTRACT

Begomovirus, a genus of the Geminiviridae family, is one of the most important plant pathogens that spread to many economically significant crops. They are small, ssDNA viruses that harbor circular genomes and are mainly transmitted by whiteflies (*Bemisia tabaci*). Recombination, especially homologous and copy-choice recombination, is a key factor in the evolution of Begomoviruses. Recombination enables the virus to obtain a level of genetic diversity that leads to new strains that may have varying degree of pathogenicity. This process allows Begomoviruses to evade host resistance mechanisms, adapt to new host species, and rapidly respond environmental changes. The need to manage Begomovirus-encoded diseases is often made more difficult by the emergence of rapidly evolving recombinant strains of strain where recombination can potentially generate strains with increased virulence, a broader spectrum of hosts or strains that are resistant to commonly used control measures such as resist ant crop varieties or chemical treatments. Recombination is a major factor influencing the evolution of Begomoviruses and has an important role in plant disease management. This review highlights the importance of recombination in Begomovirus evolution, its implications on plant disease management It identifies increasingly biotechnological modes of eradicating the deleterious effects of viral recombination. Molecular diagnostic tools such as PCR and sequencing deliver a means for early recognition of recombinant strains. Genetic editing technologies like CRISPR/Cas9 will enable development of resistant crops and offer potential for restricting viral recombination. RNA interference (RNAi) is another example of a method used in silencing viral genes and replication. Transgenic crops also have potential for durable resistance against recombinant Begomovirus strains. This knowledge is vital to producing viable integrated virus control initiatives and ensuring a continued food supply worldwide by protecting crops from viral diseases.

Keywords: Begomovirus, recombination, novel strains, plant pathogenesis, biotechnology, viral evolution

1. Introduction

Begomoviruses are members of the family Geminiviridae, a large group of plant viruses that cause serious diseases to many different dicots and other agricultural crop species¹⁻³. The genomic characterization of these viruses is their small circular single stranded DNA genomes⁴. Begomoviruses are one of the most ubiquitous viruses affecting crops in the tropics and subtropics, with high levels of transmission by whiteflies (*Bemisia tabaci*) and productivity losses seen on economically important crops including but not limited to; cotton, tomatoes, peppers, beans and ornamental plants⁵. Begomoviruses pose a serious threat to global agriculture because these infections can

lead to severe yield losses⁶. Begomovirus encompass highly diverse viral species, with all sorts of bipartite and monopartite genomes (depending on the species). Bipartite Begomoviruses have a dual component of DNA, whereas monopartite viruses consist of one single genome, rendering them interesting objects of study to explore their replication, transmission and pathogenesis⁷. These viruses tend to have the greatest economic impact in areas that are dependent upon the agriculture of infected crops, as they significantly decrease crop productivity and increase the expenditure related to disease management⁸. In **(Table 1)** major Key Begomovirus associated diseases, host range and vectors, symptoms and economic damages.

Table 1: Major Begomovirus diseases, hosts, vectors, symptoms and economic impact.

Virus/Disease	Host Crops	Vector	Key Symptoms	Economic Impact	References
Cotton Leaf Curl Kokhran Virus (CLCuKoV)	Cotton, okra, chili, cucumber, papaya, soybean, luffa, and ornamentals Plants	Whiteflies (<i>Bemisia tabaci</i>)	Leaf curling, vein thickening, enations	Up to 100% yield loss	9,10
Cotton Leaf Curl Multan Virus (CLCuMuV)	Cotton, okra, chili, cucumber, papaya, soybean, luffa, and ornamentals	Whiteflies	Leaf curl, vein thickening, stunting	100% crop losses in South Asia mostly	9,11,12
Tomato Leaf Curl New Delhi Virus (ToLCNDV)	Tomato, cucurbits, Cotton	Whiteflies	Leaf curling, stunting, reduced fruit set	50% yield reduction	13,14
Tomato Yellow Leaf Curl Virus (TYLCV)	Tomato, pepper, eggplant, potato, and weeds like datura	Whiteflies	Yellowing, leaf curl, stunted growth	Major global tomato losses	14,15
Cassava Mosaic virus (CMV)	Cassava, Cotton	Whiteflies	Mosaic, distortion, stunted growth	\$1 billion annual losses	8,16
Okra Enation Leaf Curl Virus (OELCuV)	Okra, Cotton	Whiteflies	Leaf curl, enations, reduced yield	Significant yield losses in Asia/Africa	5,17
Chilli Leaf Curl Virus (ChiLCV)	Chilli, pepper, Cotton	Whiteflies	Leaf curl, puckering, stunting	Major yield reduction	5,18

Recombination is an important evolutionary mechanism for various viruses including the Begomoviruses¹⁹. This is the mechanism by which two viral strains of distinct genetic heritages swap genetic information during infections within the same host plant. In turn, this leads to the formation of chimeric viruses with genetic components from each parental strain²⁰. Because it enables rapid generation of genetic diversity, recombination contributes to viral adaptation in altered environments¹⁸, as well across species barriers (S3) and host resistance mechanisms²¹. With Begomoviruses, recombination can result in the emergence of new strains with modified pathogenicity and virulence, host range or resistance to control methods¹⁸. Recombination is important for the evolution of Begomoviruses because it allows those viruses to rapidly adapt to new environmental conditions and therefore, becomes harder to control with conventional methods²². Understanding recombination is therefore critical to developing management strategies for Begomovirus diseases, particularly in an era where food security and climate change are top global concerns²³.

However, despite the significance of Begomovirus recombination, there are important gaps in knowledge. Although recombination is known as an important mechanism for the evolution of Begomoviruses, the molecular mechanisms involved in these new recombination remains obscure²⁴. The specific genomic regions of Begomoviruses that are prone to recombination have not yet been determined and the host environmental factors affecting recombination remain largely unexplored¹³. Further, how these recombination events drive the emergence of new pathogenic strains is not well understood. Without this knowledge, forecasting new Begomovirus strains that may lead to more devastating diseases or managing them are impossible.

We will primarily focus on the molecular basis of Begomovirus recombination and its contribution to the rapid evolution of new viral genotypes. Here we review the most recent advances in knowledge regarding Begomovirus recombination, with an emphasis on how these viruses evolve and how recombination leads to emergence of new strains, often having different pathogenic potential, as well as discussing applications from this perspective in plant disease management and biotechnology. The molecular basis of Begomovirus recombination has implications for not only basic virology research, but also for applying the knowledge to deploy new biotechnological applications and control strategies such as the use of transgenic plants, viral resistance, and RNA interference technologies against Begomovirus infections. The Review serves to fill in research gaps that are currently left unaddressed while laying out a map for future studies looking at viral evolution and its effects on agriculture and biotechnology.

2. Begomovirus Recombination Mechanisms

2.1. Molecular basis of recombination

Recombination is one of the most important mechanisms through which Begomoviruses evolve, providing genetic diversity that ultimately allows viruses to adapt in new environments. Understanding the molecular basis of recombination in begomoviruses occurs during the replication of viral genomes and when two different strains infect the same host plant. This co-infection enables genetic transfer leading to recombinant viruses that contain dissimilar genomes of both the parent strains. The homologous recombination and copy-choice recombination are the two common types of recombination seen in Begomoviruses²⁵.

Homologous recombination, this occurs when two viral genomes contain regions of sequence identity and are able to align and exchange genetic information during replication. In most cases, this occurs in areas with high sequence homology allowing for the recombination machinery to identify and swap homologous segments of DNA²⁶.

Copy-Choice Recombination, the viral polymerase continues the synthesis of a new genome by switching from one template to another in this case copying genetic material from both an original template and a different strain of virus. Such recombination can produce hybrid viral genomes that contain segments from both parent strains²⁷. This contributes to the generation of genetically diverse populations of virus, which enables the virus to adapt (**Figure 1**).

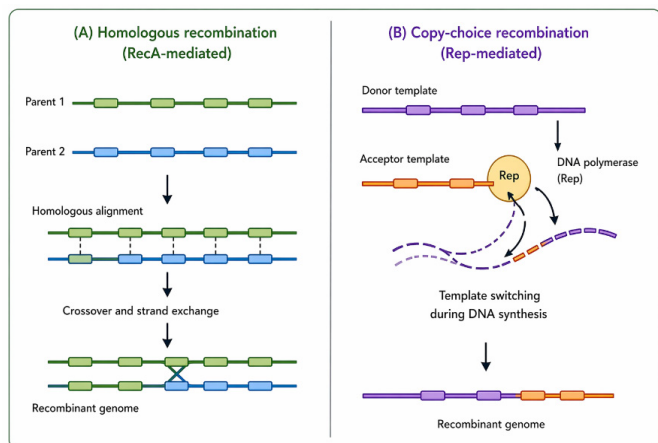


Figure 1: Major recombination mechanisms in begomoviruses (A) Homologous recombination (RecA-mediated) occurs through sequence alignment between related parental genomes, followed by crossover and strand exchange, resulting in recombinant genomes with mixed genetic segments. (B) Copy-choice recombination (Rep-mediated) takes place during rolling-circle DNA replication, where the viral replication-associated protein (Rep) facilitates template switching between donor and acceptor DNA strands, generating recombinant genomes.

Recombination is a very intricate process that includes several kinetic factors: some of them are enzymes, others are host proteins. Central to the recombination is the Begomovirus replicase, which synthesizes new DNA copies of viral genome information. This enzyme can also contribute to homologous recombination or copy-choice recombination, depending upon replication dynamics and the template present²⁸. Furthermore, host cellular proteins that play a role in DNA repair and replication processes, such as DNA polymerases and recombinase enzymes, also play a crucial role in repairing and restructuring the viral genome during homologous recombination. These host factors involved in replication, such as RNA polymerases and other regulatory proteins might also modulate the recombination process by supplying the conditions that allow for the exchange of genetic material²⁹.

2.2. Role of recombination in viral evolution

Recombination is important in viral evolution as it creates genetic diversity, especially within begomoviruses³⁰. Such diversity gives the virus the capacity to quickly evolve in response to selective pressures, including host resistance mechanisms, environmental pressures or changes and new vectors. In contrast to point mutations, recombination can

trigger the quick emergence of new viral variants that may have beneficial attributes, including higher virulence, an expanded host range or escape from control measures³¹.

Recombination allows Begomoviruses, on the other hand, to be more rapid tractor toward the new characters than mutations ever could. Exchanging genetic material between strains also allows a virus to gain genes that help it cope with host immunity or persist in new ecological niches³². The fast adaptability has made Begomoviruses a major threat to crops because new strains with new pathogenicity appear in short time, and disease management becomes very complicated^{18,20}.

As an example, mutant strains of Begomoviruses recombinants have been revealed that display transformed host specificity and quality with the ability to contaminate resistant plant species. Recombination, for example, can generate strains that are more virulent, damaging crops and giving rise to more diseases that matter. With the evolution of these recombinants, they could also escape resistance control, such as resistant crops or chemical treatment leading to higher management complexity³³.

2.3. Recombination hotspots

Although recombination does occur throughout the genomes of Begomovirus, some regions are more predisposed to such events due to their genomic architecture and functionality. Recombination hotspots are usually located in genome regions that are important for virus replication and host interactions. An example of this region is the intergenic region (IR) that is situated between both elements of the bipartite genome organizations found in many Begomoviruses^{2,34}. The IR is common to replication and transcription of the virus and harbors conserved features that enable recombination to occur among closely related viral strains. Another recombination hotspot is the C4 gene, which encodes a protein associated with pathogenesis and manipulation of host cellular processes. Mutations or recombination on that gene may cause major alteration of the virus possible to reach a number of plant's species³⁵.

These recombination hotspots are important because they signify the parts of the genome that are most engaged in the virus's infection and proliferation ability within host plants. Such recombination can result in the generation of viral strains with modified pathogenicity, potentially allowing for a wider range of plant species to be infected and/or their virulence. A deep understanding of these hotspots is needed to predict evolutionary behavior of Begomovirus strains, and to devise counterstrategies for the impact of recombinant emerging strains¹⁷.

Homologous recombination and copy-choice recombination, the molecular mechanism of Begomovirus recombination, play a key role in the emergence of new viral types. The underlying mechanisms allow Begomoviruses to create genetic variance, which allows new strains with different pathogenicity to emerge. This knowledge of the distribution and nature of hot spots for recombination across the viral genome can also assist researchers in tracking how strategies have evolved with evolutionary adaptation as well, providing new approaches to controlling risks posed by these emerging Begomovirus strains³⁶.

3. Emergence of Novel Strains

3.1. Mechanisms driving novel strain emergence

Genetic material can be exchanged during co-infection by two different strains of the virus within one host, resulting in

new viral variants. It is the reason that more virulent strains arise by bringing across useful characteristics from both parent strains during this recombination process. The new strains may better evade plant defense or have greater adaptability to environmental changes, making them more fit in wild populations³⁷. Recombination has important consequence, which is that new strains escape host resistance. Over the course of time, host plants gain resistance either naturally or through breeding. But in recombinant viruses, these resistance mechanisms are overcome because the new genetic traits allow it to infect species that were previously resistant. Strains that evolve through recombination could also change their replication machinery or coat protein structure to decrease susceptibility to plant immune responses (**Figure 2**). This allows the virus to infect pl. species across from a wider spectrum of host plant or escaping pre-existing R-genes that were previously effective against earlier strains³⁸.

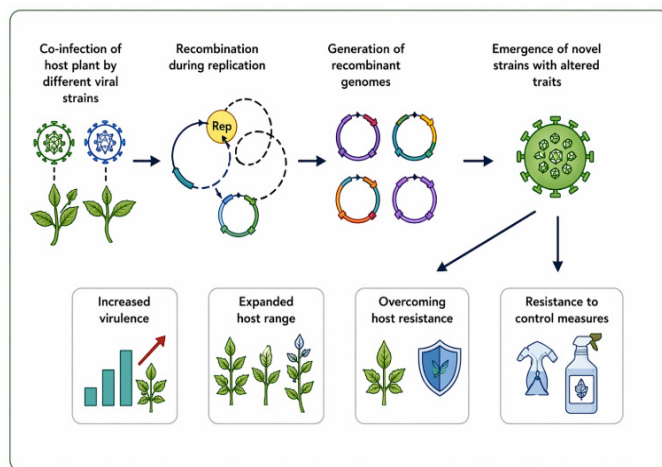


Figure 2: Recombination-driven emergence of novel begomovirus strains. It shows how co-infection of a host plant by different viral strains can lead to recombination during replication, generating recombinant genomes and resulting in novel strains with altered traits such as increased virulence, expanded host range, overcoming host resistance, and resistance to control measures.

In addition, recombination can have a substantial impact on virus-host interactions and enable Begomoviruses to alter their interaction with plant defence systems. In this way, recombined strains may adopt new strategies to hijack host cellular machinery and ultimately increase their ability to replicate and spread within the plant. This results important changes in the plant and could lead to a more aggressive version of disease, as pathogen utilizes resources from host plant at higher rates also influencing infection levels and symptoms severity³⁹.

3.2. Examples of novel begomovirus strains

A notable instance of Begomovirus recombination giving rise to new, more virulent strains is the Cotton leaf curl Multan virus (CLCuMV). Recombination among different CLCuMV strains has been associated with higher virulence and wider host ranges. At the beginning, CLCuMV was only to cause infection in cotton but via recombination the virus has started remixing and being able to infect a range of other crop species including tomato, pepper and several vegetable species. As a result of this recombination event, cotton and many other crops have been subject to major losses due to the economic importance of Begomoviruses¹¹.

Apart from cotton, these novel strains of CLCuMV have now spread to a number of crops in several regions such as Pakistan, India, China and also the Philippines and Thailand. In these areas, the virus has evolved to infect other plant species which adds a layer of difficulty for management of the two diseases. Recombination events increasing the ability of CLCuMV to infect a wider range of hosts are one of the best examples demonstrating how recombination produces strains with enhanced virulence and adaptability, which results in an increased threat to agriculture. This poses important economic significance, especially for cotton producing countries where cotton is a very important cash crop, as well as areas with large acreage of tomatoes and peppers¹².

Likewise, recombination among other Begomovirus species have produced strains with changed pathogenicity. One notable case is the recombination of Tomato yellow leaf curl virus (TYLCV) strains followed by emergence of new virulent viral variants that infect crops in previously TYLCV-uninfected areas. The emergence of such new strains renders existing control measures ineffective in managing agricultural Begomovirus diseases, thereby complicating its management. The emergence and dissemination of recombinant strains pose considerable challenges to the global agriculture community in controlling viral infections effectively, underscoring an urgent need for novel strategies for viral management and surveillance¹⁵.

3.3. Geographic distribution of novel strains

Recombinant Begomovirus strains have spread globally and have been associated with severe outbreaks in areas where susceptible crops are grown⁴⁰. This proliferation of new strains is evident in South Asia where the identification of new Begomovirus genotypes due to either strain recombination or movement of whitefly vectors, has been reported^{41,5} specifically from Pakistan and India. More virulent strains such as those causing Cotton leaf curl disease; have spread rapidly in these regions. High density of host plants, multiple infections of diverse viral strains and appropriate conditions that favor whitefly dispersal are responsible for the increased proportion of recombinant strains⁴².

Private sector-mediated global trade and agricultural practices, including the movement of infected plant material as well as extensive production of susceptible crops, further facilitate the transboundary movement of such novel strains⁴³. The migration of the whitefly vectors has been increased due to climate changes and near agricultural area¹⁷. The understanding of factors influencing the geographical distribution of newly dispersed strains is critical to limit the spread and manage their detrimental effects on global agriculture⁴⁴.

Recombination, which leads to the emergence of new Begomovirus strains, mainly allows viruses to escape host resistance and adapt to new environments, thereby increasing virulence⁴⁵. The dynamic nature of the Begomovirus evolution is reflected in the case of Cotton leaf curl Multan virus and other recombinant strains. An added concern is that the widespread geographic distribution of the new strains makes the case for a global surveillance and co-ordinated control strategy for plant disease to be put in place first, if the threat they pose to agricultural production and food security is to be mitigated.

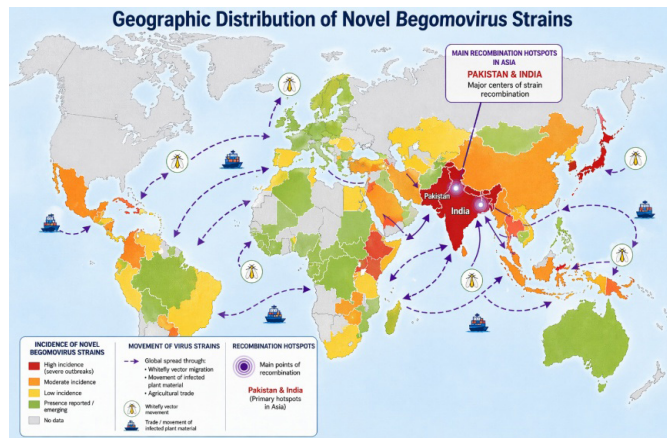


Figure 3: Global geographic distribution and movement of recombinant Begomovirus strains.

4. Implications for Plant Pathogenesis

4.1. Disease dynamics

The impact of recombination on plant disease dynamics is massive as new Begomovirus strains occur through this mechanism. Recombinant strains, which consist of a mixture of genetic material from multiple viral strains, more virulent, causing more severe disease manifestations and rapid progression. Recombination may allow Begomoviruses to circumvent host immune defenses, particularly in the case of new viral variants that escape resistance mechanisms acquired by selective breeding³⁰ or those acquired through natural plant defense systems³⁸. Specifically, recombination can alter coat proteins or machinery involved with virus replication; these mutations allow the virus to infect new host species, or evade plant defense responses¹⁰. This dynamic responsiveness to environmental and host alterations is crucial in the propagation and manifestation of viral diseases, particularly when novel strains possess increased infectivity and pathogenicity.

4.2. Impact on crop yields

In agriculture, recombinant Begomovirus strains and their economic impact are significant. These strains act more aggressively and result in substantial crop yield losses. Begomovirus-induced diseases like the ones occurred from Cotton leaf curl Multan virus (CLCuMuV) which can severely adversely affect cotton by reducing fiber quality and causing yield loss. This demonstrates the potential for recombination of the virus to infect a broad variety of host plants, which in turn represents an ongoing food security challenge⁴⁶. The increased cost of disease management is attributed to the emergence of strain diversity through recombination that enables the virus to adapt to new conditions or evade resistance. Farmers may therefore have to undertake more frequent pesticide application, purchase of genetically resistant crops or changing the crop management practices, each of which adds up to greater costs. This situation is aggravated by the diffusion of these recombinant strains via trade and agricultural practices across regions around the world, which translates into economic losses globally⁴⁷.

4.3. Host-pathogen co-evolution

Recombination influences not just the virus but also provokes host-pathogen co-evolution. Plants also have constantly adapted their defense systems to resist virulent infections, and viruses, mainly Begomoviruses evolve quickly in order to overcome those

defenses⁴⁸. This promotes co-evolution because recombination allows for viral evolution of new immune evasive strategies. For instance, Begomoviruses can change the conformation of their coat proteins or adjust their replication mechanisms to evade host defense⁴⁹. This might prompt host plants to evolve new resistance genes to defend against new viral strains such as BSMV-F. Similar to other evolutionary arms races, this conflict between the virus and its host ultimately shapes the potential persistence of Begomoviruses in agricultural systems. Due to the emergence of new strains, plant breeders are challenged to develop more sophisticated resistance strategies⁴⁹, which makes the management of viral diseases even more complex.

Recombinants between Begomovirus strains cause serious threats to plant pathogenesis. Agriculture and Disease management In addition to the improved virus propagation capacity, these strains also provided additional challenges in managing viral diseases. It has widespread economic implications, imposing higher costs on farmers and greater risks to yields¹⁶. Additionally, the co-evolutionary dynamics between Begomoviruses and their host plants indicate that without proper management approaches this cycle of virus adaptation and resistance in host will continue, possibly resulting in more virulent strains with an ever-increasing epidemic potential that can lead to polycyclic diseases. Most importantly, insights into the mechanisms governing recombination will better inform virus-host interactions that are necessary for sustainable management of Begomovirus diseases in future.

5. Biotechnology Approaches to Understanding and Controlling Begomovirus Recombination

5.1. Diagnostic tools

Molecular diagnostics are critical in the detection of recombinant Begomovirus strains that enable early diagnosis and management of viral diseases. Recombinant strains are uniquely fielded using techniques such as polymerase chain reaction (PCR) and next-generation sequencing (NGS) statistics⁵⁰. PCR-based approaches can certainly confirm the presence of Begomovirus DNA in plant tissues, whilst sequencing enables detailed analysis of viral genomes that allows identification of recombination events and on-going emergence of novel strains. Such PCR assays that can target specific genomic regions susceptible to recombinant such as the intergenic region (IR) and the C4 gene have been used successfully to differentiate recombinant from parental strains⁵¹. Furthermore, sequencing techniques allow us to capture the entire scenes of recombination hotspots on viral genomes and provide insights into how genetic transmissions happen and what regions are more susceptible to such events⁵².

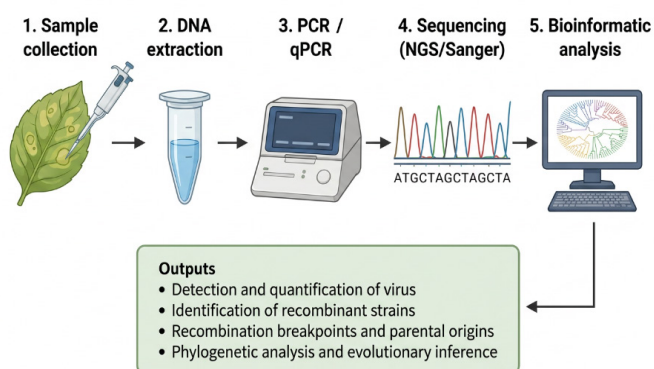


Figure 4: Workflow for detection and characterization of begomovirus recombinants using molecular diagnostics and bioinformatic analysis.

5.2. CRISPR/Cas9 and gene editing

The development of new gene editing technologies, especially CRISPR/Cas9 (clustered regularly interspaced short palindromic repeats/CRISPR-associated protein 9) have opened exciting possibilities for controlling the high frequency of Begomovirus recombination and improving plant resistance against these genotypes. CRISPR/Cas9 systems may be used for targeted cleavage of a site in the Begomovirus genome, which could derail the recombination events that confer virulence. Appropriate editing of viral genomes could also restrict the ability to undergo recombination, which in turn could limit the emergence of novel pathogenic strains⁵³. In addition, CRISPR/Cas9 can be applied to plants by modifying plant genes behind the host-pathogen relationship, avoiding infection. For instance, editing plant genes encoding susceptibility factors⁵⁴ or increasing the expression of resistance-activating genes⁵⁵ would endow crops with capabilities to resist viral infections driven by recombination events.

5.3. Viral resistance through transgenics

One of the most relevant biotechnological methods for curtailing the emergence of new recombinant Begomovirus strains is through the use of transgenic crops⁵⁵. Introduction of particular genes into plant genomes has, to some extent, produced Begomovirus-resistant genetically-modified crops. For one, the C4 gene from Tomato yellow leaf curl virus (TYLCV) has been introduced into cotton and other crop plants which gave them resistance against Begomovirus-related diseases. This would mean that transgenic plants are either preventing the viral replication cycle or they are increasing the plant's immune reaction, limiting the efficiency of infection and spread by Begomovirus. An important tool in the management of these

ever-changing viruses is the use of transgenic crops tolerance to recombinant Begomovirus strains¹⁴.

5.4. RNA interference

An additional strong biotechnology-based tool against Begomovirus recombination is RNA interference (RNAi) that could help to minimize its effects on crop health⁵⁶. RNAi silences selected genes of a virus to stop it multiplying in a host plant. This method consists of a form of RNAs, double-stranded RNA (dsRNA) that is introduced into the plant and these strands activate and stimulate the plant RNAi tools to degrade viral RNA. RNAi can reduce viral load by silencing essential genes for replication, such as those related to the replicase or C4 gene⁵⁷. Moreover, RNAi can silence specific recombination-prone zones in the Begomovirus genome, preventing virus emergence of new more virulent strains⁵⁸.

5.5. Synthetic biology approaches

Synthetic biology is a new technology that integrates aspects of engineering, genomics and biochemistry to construct biological systems in novel ways⁵⁹. For Begomovirus recombination, a synthetic biology approach could allow for the creation of new combinations of viral genetics either coded into modified viral systems or be constructed as engineered genomes together with designed built-in controls to prevent any further potential recombination events. As an example, this could result in the synthesis of engineered viral systems that contain stable and non-recombinant genomes such that, within a controlled system, evolution into a new strain is avoided⁶⁰. Synthetic biology could also be used to design crops with boosted immune responses or even synthetic viral “decoys” that lure and destroy the virus, preventing infection of healthy crops. These strategies could be powerful not only for regulating viral evolution, but also establishing robust agricultural ecosystems and safeguarding against new viral challenges⁶¹.

Intriguingly, there are a number of interesting and potentially useful biotechnology tools which could aid in elucidating the recombination occurrence and/or control this organism. These approaches, ranging from molecular diagnostics and CRISPR/Cas9 gene editing to RNAi and synthetic biology, are paving the way for novel strategies that will allow us to tackle viral evolution and enhance plant resistance. Our findings provide a foundation for future work and important biotechnological interventions to show their value in the emergence of Begomovirus that evolve through recombination (**Table 2**), and will be critical for maintaining the sustainability of global agriculture while reducing economic losses caused by viral diseases⁶².

Table 2: Biotechnological approaches for detection and control of Begomoviruses.

Approach	Principle	Application	Advantages	Limitations	References
PCR / qPCR	DNA amplification	Detection and quantification	High sensitivity	Lab setup required	50,63
NGS	Genome sequencing	Recombination detection	High resolution	Expensive	51,53
CRISPR/Cas9	Genome editing	Virus-resistant crops	Precise	Regulatory issues	53,54,64
RNAi	Gene silencing	Virus suppression	Specific	Variable efficiency	56,57
Transgenic crops	Gene insertion	Resistance development	Long-term	Regulatory barriers	55,65
Synthetic biology	Engineered systems	Virus control	Innovative	Early-stage tech	59,61

6. Challenges in Begomovirus Management and Future Directions

6.1. Recombination control challenges

Frequent recombination is a feature of Begomoviruses rendering that difficult to control, especially in farming systems. Recombination facilitates rapid adaptation of Begomoviruses to new hosts, environments and resistance mechanisms, it is nearly impossible to predict the emergence of novel strains. In contrast to the more gradual mutations, recombination may give rise to strains with increased virulence or host adaptation all at once⁶⁶. This is particularly problematic for the management of disease because recombination can break down durable resistance in crops⁶⁷, and thus requires ongoing new control strategies. The ability of Begomoviruses to rapidly evolve makes traditional approaches such as the development of resistant cultivars or chemical control ineffective upon the emergence of a new recombinant strain⁶⁷. This means that successful manipulation of recombination in Begomoviruses relies on knowledge of the molecular basis of this process but also, at the same time, new adaptive and flexible strategies to control it based on rapidly evolving targets.

6.2. Barriers to biotech solutions

Though biotechnology looks promising in terms of tools for the management of Begomovirus, several hurdles limit its scope. These still poses a major barrier due to regulatory hurdles, especially in the domain of GMOs and transgenic crop approval. The legislative buffers in different countries that oversee GMOs differ, with the strict testing and safety assessments that are required delaying resistant crops⁶⁵. In addition, there are worries about the environmental consequences of the introduction of genetically modified crops into ecosystems, especially unintentional effects on biodiversity or that wild virus populations can develop resistance. There are also persistent technical hurdles, especially for site-specific targeting of viral genes or stable genetic engineering of resistance traits across the target crop genomes. And, despite CRISPR/Cas9 and other advanced tools, the attainment of effective, stable and large-scale expression of resistance in crops remains an enormous challenge that will require substantial research and development. Such barriers highlight the relevance of work forums to ensure cooperation between researchers, policy-makers and agriculture stakeholders in order to overcome hurdles and facilitate the implementation of biotech solutions⁶⁸.

6.3. Future research directions

Several gaps remain that have hitherto inhibited the effective management of Begomovirus', even given recent advances in our understanding of this group of viruses. Better tools for diagnosis are essential to identify recombinant strains in early stages, especially in areas where Begomovirus is endemic⁶⁹. More sensitive and rapid diagnostic techniques would enable enhanced surveillance and significantly quicker responses to emerging strains. Resistance breeding is another component that need further studies⁷⁰. Although transgenic approaches hold promise, the need for durable resistance against Begomoviruses still relies on conventional breeding for novel sources of resistance. A focus on new methods for breeding crops with novel germplasm to bring these genetic traits into commercially cultivable plants will be beneficial, and many knowledge gaps exist regarding how resistance can be obtained from wild

relatives of crop species⁷¹. Also, how recombinant viruses are characterized is an area still under investigation.

Greater resolution genome mapping of begomovirus strains, especially recombinants, will help localize potential recombinogenic hotspots and reassess the role of these regions in the evolution of novel virulent variants⁷². Future research should also investigate vector control strategies, as whiteflies are the primary vectors of begomoviruses and play a central role in the spread of these diseases. Information on whitefly population dynamics and their interactions with begomoviruses is essential to understand how to effectively limit the spread of the virus across different geographic regions.

Despite the potential of biotechnology to/for control Begomovirus diseases, regulation, environmental concerns and technical aspects will require further multidisciplinary effort to be overcome. Advancing diagnostic techniques, resistance breeding and the characterization of recombinant viruses will be key to designing more effective control strategies for these rapidly diversifying plant pathogens.

7. Conclusion

7.1. Summary of key insights

Recombination underpins Begomovirus evolution through its ability to rapidly generate molecular diversity^{2,19}. This process is responsible for the generation of new viral strains that can bypass host resistance, be incorporated into new climatic and environmental conditions, and become impervious to control strategies. Since the majority of Begomoviruses are bipartite or multipartite, recombination enables faster evolution than mutations alone and promotes viral property changes to be disseminated rapidly. Consequently, the role of Begomovirus evolution by recombination can have a profound impact on plant virology⁷³, making it more difficult for effective disease management and increasing the threat to world agriculture. The rapid evolution and adaptation potential of Begomoviruses highlights the importance of AV analysis to aid continuous monitoring, deployment of new management strategies and development of agri-policies that consider viral diversity and recombination⁷⁴.

7.2. Biotechnological promise

Biotechnology could have an important role in the reduction of adverse effects of viral recombination on Begomovirus disease control. Molecular diagnostics, gene editing using CRISPR/Cas9, RNA interference (RNAi), and the development of transgenic crops are some major biotechnological tools that can be used against Begomovirus⁷⁵. CRISPR/Cas9 is for altering viral resistance genes; RNAi technology silences any virus genes giving rise to recombinant strains. In addition to the health benefits, genetically modified crops that are intrinsically resistant to specific strains of Begomovirus would also minimize the economic impact of these viral diseases. These biotechnological solutions remain subjected to regulatory and technical hurdles, but they could provide fundamentally new approaches to the management of Begomovirus infections by providing tools that can slow viral evolution and their agronomic impact^{64,76}.

7.3. Final thoughts

Management of Begomovirus strains, therefore, must adopt a multi-disciplinary approach in combining virology,

plant breeding and biotechnology with pest management practices. This suggests that these viruses are facing substantial evolutionary pressures via recombination; therefore, scientists need to adopt flexible and adaptive approaches. This will include the generation of new diagnostic tool and resistance breeding technologies, as well as employing novel biotechnologies to limit spread recombinant strains and develop durable resilient crops. International collaboration and cross-border knowledge sharing will be fundamental to addressing the challenges posed by Begomovirus infections, given their complexity, the global scale of their impacts, and need for sustainable solutions towards this issue. Begomovirus management of the future will rely on a more integrated method that uses advances in science and agricultural practices to protect crops worldwide, keeping food secure.

8. Declarations

8.1. Ethics approval and consent to participate

N/A

8.2. Consent for publication

All authors are agreed for publication of the article.

8.3. Availability of data and materials

All data is available and provided upon request to corresponding author.

8.5. Conflicts of interest

There is no conflict of interest.

8.6. Funding

N/A

8.7. Authors' contributions

FA ER, MYM and MS idea and wrote this manuscript. MBA, EY, AM, MA review and format the manuscript.

8.8. Acknowledgements

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