Begomovirus Menace and Its Management in Vegetable Crops

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Vidya Sagar, Pradip Karmakar, Jyoti Devi, Nakul Gupta, and Bharat Raj Meena

Abstract

Vegetable is the most emerging sector of the horticultural commodity, which contribute not only to nutritional richness but, also on-farm and off-farm income. The begomoviruses, member of geminiviridae family are the largest contributor in devastation of these crops. Tomato, chilli, cassava, okra, cucurbits, and pulse vegetables suffer greatly due to these viruses. The conducive environment, continuous cropping of one or more host crop throughout the year, emergence of new viruleferoius vectors biotypes, and evolution of new recombinant virus strains are the most important factors in the spread of these diseases. The begomoviruses are either mono or bipartite, can be associated with alpha or betasatellite DNA, which has role in symptom development and virulence. Management of virus vector should be the major strategy to inhibit the contact between host and pathogen. Cultural practices like, removal of alternate hosts, destruction of unwanted weeds, and uprooting and burning of initially infected plants are commonly practiced. Management of sucking pest, mainly whitefly at regular interval with insecticide significantly reduces the chances of transmission of these viruses, however insecticide resistance is frequently observed among these group of pests. The viable and naturally safe method to control these diseases is through host plant resistance, by identification and transfer of resistance governing genes in cultivated backgrounds. Transgenic approaches targeting viral genes are also widely used for development of resistant lines. The most recent technology like genome editing with CRISPR/Cas-9 was also found promising in development of resistant tomato and cassava lines however, its widespread use is limited due to unavailability of information about susceptibility genes in several crops.

Keywords

Stress · Biotic · Vegetables · Begomovirus · Whitefly

V. Sagar (✉) · P. Karmakar · J. Devi · N. Gupta · B. R. Meena
ICAR-Indian Institute of Vegetable Research, Varanasi, Uttar Pradesh, India

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A total of 402 types of vegetables are grown worldwide. Vegetables are important constituents of agriculture for food and nutritional security, their nutritional richness, profitability and ability to generate on-farm and off-farm employment. India is bestowed with huge diversity of vegetables and is the largest contributor (59%) of the total horticultural produce in the country. In terms of global contribution, India is the second largest producer of vegetables across the world. Area under vegetable cultivation is continuously increasing mainly due to higher productivity, shorter maturity cycle, and high value returns that provide greater income leading to improved livelihoods. The Indian vegetable industry has achieved its target for production of vegetables exceeding the daily recommended dose of 250 g of vegetables against the 380 g availability of per capita. However, this growth needs to be sustainable to feed the 1.5 billion people of the country during 2030. It is apparent that the vegetables are infected by a number of diseases and pest. Around 200 viruses are associated with vegetable crops. Among these, the begomoviruses are the largest contributors of economic loss and its management requires a significant amount of time and money (Nagendran et al. 2017). Begomoviruses, a member of family *Geminiviridae,* are the most devastating plant viruses. These viruses spread to every nook and corner of the world, infecting not only cultivated species, but also, the weeds and wild relatives. This virus can be classified into two groups based on the genomic constitution i.e., monopartite and bipartite. Monopartite viruses carry one single stranded circular DNA molecule while bipartite viruses have two single stranded DNA component, namely DNA-A and DNA-B (Table 26.1). It was also observed that most of the new world virus harbors bipartite DNA molecule whereas, the old world begomoviruses are either monopartite or bipartite in nature (Brown and Czosnek 2002) (Fig. 26.1).

The virus is continually evolving through the process of mutation, recombination, and pseudo-recombination aided by satellite viruses (alpha and betasatellite) for symptom development poses a great threat to the vegetable cultivation of the world. The begomoviruses induce different types of symptoms which can be easily recognized by (a) vein yellowing, (b) yellow mosaic, and (c) leaf curl (Table 26.2).

Almost all the begomoviruses are transmitted by the whitefly while feeding on the plant in calculative and persistent manner. The protein encoded by viruses specifically identify and interact with its vector and facilitate virus transmission. In the case of begomoviruses, capsid proteins (CP) are the virus-encoded transmission proteins, which play an important role in establishing virus–vector relationship. In case of circulative, non-propagative transmission starting from the phloem sap of the host where the virus is ingested and travel via the route of the alimentary canal (Gray et al. 2014). After passing the midget, viruses accumulate in the filter chamber region followed by an entry in the insect hemocoel which finally reaches the primary salivary gland. It is also reported that certain endosymbiotic bacteria helps or plays an important role in the transmission of the virus (Gray et al. 2014). In an experiment conducted utilizing the chimeric virus with exchanged ORF between *Beet curly top virus* (leafhopper vector) and *African cassava mosaic virus* (whitefly vector) resulted in vector switching (Briddon et al. 1990). In the competition assay between recombinant CP of Tomato yellow leaf curl virus (TYLCV) and wild type

Table 26.1 Genomic components and annotated functions of begomoviruses genome

Gene(s)	Predicted ORF size (bases)	Translational product size (amino acids/kDA)	Putative protein	Annotated function of gene(s)
AV1	771 (295–1065)	256/29.62	Coat protein (CP)	Encapsidation
AV2	357 (135–491)	115/13.35	Pre-coat protein	Cell to cell movement protein
AC1	1044 (1559–2602)	361/40.85	Replication initiation protein (Rep)	Replication initiation
AC2	408 (1207–1614)	134/15.13	Transcription activator protein (TrAP)	Transcription activator
AC3	405 (1062–1466)	134/15.88	Replication enhancer protein (Ren)	Replication enhancement
AC4	303 (2143–2445)	85/9.43	–	Suppressor of PTGS
AC5	(733–943)	83/	–	Pathogenicity determinant and RNA silencing suppressor
BV1	770 (419–1189)	–/33.1	Nuclear shuttle protein	Nuclear trafficking
BC1	996 (1221–2117)	–/29.6	Movement protein (MP)	Cell to cell movement and pathogenicity determinant
βC1	–	–	–	Symptom determination and suppressor of host defense mechanism

virus, Wang et al. (2014) found that capsid protein is the viral attachment protein to the viral midgut after virus accusation. Even though the begomoviruses traverses significant amount of time through the body of the whitefly however, no reports of transovarian transmission was found (Stansly and Naranjo 2010). However, recently Wei et al. (2017) reported transovarian transmission of TYLCV often occur, the major factors are developmental stage of whitefly ovary, viral coat protein and whitefly vitellogenin (VG). The younger flies transmit less viruses to the ovary while adult fly transmits more of the viruses to the ovary and to the offspring. The interaction with CP and VG is very specific in determining the interaction of virus with ovary. Knockdown of VG genes inhibits the binding of viruses to the ovary and also reduces the transmission. In the same experiment conducted by Wei et al. (2017) with the other begomovirus of papaya viz. *Papaya leaf curl China virus*, no interaction was found between CP and VG thus, no transovarian transmission was observed. Thus the selective ability of the TYLCV for transovarian transmission may be one of the reasons for global spread of the virus. It was also confirmed that the virus can be transmitted to at least two generations in the absence of virus carrying host.

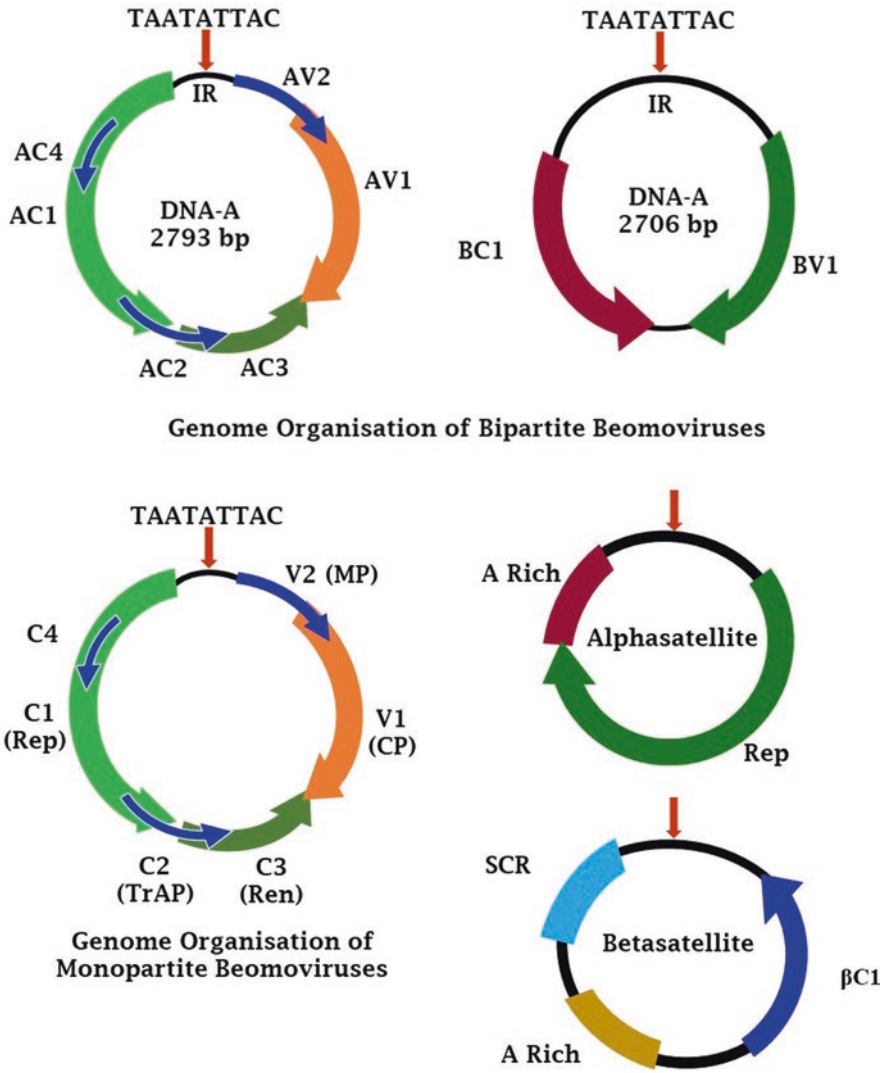

Fig. 26.1 Genome organization of bipartite and monopartite begomoviruses

White flies occur globally and rose to international prominence during 1980s when, the whitefly transmitted viruses created menace to global farming. There are three types of biotypes of whitefly based on its distribution in the different geographical locations and its inability to interbreed. The three biotypes namely New world (biotype A), Middle East-Asia Minor (biotype B), and Mediterranean (biotype Q) are distinct enough to be considered as a species (De Barro et al. 2011). The B biotype is the most predominant, polyphagous, and highly invasive to new areas. This biotype used to occur mainly in the Middle East-Asia Minor region, but through the trade of ornamentals it spread globally and broke havoc during 1980s.

Table 26.2 Diseases produced on different crops by begomoviruses

Name of the crop affected	Name of the virus species	Nature of genome	Disease	Symptoms	References
Lycopersicon esculentum	*Tomato leaf curl virus*	Mono/ bipartite	Leaf curl	Curling and puckering of the leaves, sterility, and stunting of plants	Padidam et al. (1995)
Capsicum annum	*Chilli leaf curl virus*	Monopartite	Leaf curl	Upward leaf curl	Khan et al. (2006)
Capsicum frutescens	*Tomato yellow leaf curl virus*	–	Leaf curl	Leaf curl, chlorosis, and stunting	Shih et al. (2007)
Abelmoschus esculentus	*Bhendi yellow vein mosaic virus*	Bipartite/ monopartite	Yellow vein mosaic	Yellowing of leaves and fruits	Harrison et al. (1991)
Abelmoschus esculentus	*Okra enation leaf curl virus*	Bipartite	Enation leaf curl	Vein thickening and upward curling of leaves. Sterility observed at latter stage.	Singh (1996)
Sechium edule	*Tomato leaf curl virus*		Mosaic	Yellow spot, mosaic and upward curling	Mandal et al. (2002)
Momordica charantia	*Bitter gourd yellow mosaic virus*	Monopartite	Mosaic	Yellow mosaic and chlorosis	Raj et al. (2005a)
Manihot esculenta	*Indian cassava mosaic virus/ Sri Lankan cassava mosaic virus*	Bipartite	Mosaic	Chloratic mosaic, leaf distortion, and stunted growth	Berrie et al. (1998)
Solanum melongena		Bipartite	Yellow mosaic	Yellow mosaic and mottling symptom	Pratap et al. (2011)
Glycine max	*Mung bean yellow mosaic India virus*	Bipartite	Yellow mosaic	Yellow mosaic on leaves and stunting	Girish and Usha (2005)
Vigna unguiculata	*Mung bean yellow mosaic India virus*	Bipartite	Yellow mosaic	Stunting, sterility, reduced growth, and leaf curling	Kumar et al. (2017)
Mucuna pruriens	*Velvet bean severe mosaic virus*	Bipartite	Mosaic	Mosaic on leaves, stunting, and sterility	Zaim et al. (2011)

(continued)

Table 26.2 (continued)

Name of the crop affected	Name of the virus species	Nature of genome	Disease	Symptoms	References
Lycopersicon esculentum	*Tomato leaf curl New Delhi virus*	Bipartite	Leaf curl	Leaf curling, vein clearing, and stunting	Padidam et al. (1995)
Solanum tuberosum	*Potato apical leaf curl virus*	Bipartite	Leaf curl	Apical leaf curl	Venkatasalam et al. (2011)
Benincasa hispida	*Tomato leaf curl New Delhi virus*	Bipartite	Yellow stunt	Stunted growth and yellowing of leaves	Roy et al. (2013)
Lagenaria siceraria	*Tomato leaf curl New Delhi virus*	Bipartite	Chlorotic stunt	Small chlorotic and curled leaf and stunted growth	Sohrab et al. (2003)
	Tomato leaf curl New Delhi virus	Bipartite	Yellow leaf curl	Yellowing of leaves and curling of leaves	Ito et al. (2008)
Cucumber	*Tomato leaf curl New Delhi virus*	Bipartite	Yellow mosaic	Yellowing of leaves and mosaic	Raj and Singh (1996)
Cucurbita moschata	*Tomato leaf curl New Delhi virus*	Bipartite	Leaf curl	Leaf curl along with chlorotic patches	Phaneendra et al. (2012)
Cucurbita moschata	*Squash leaf curl China virus*	Bipartite	Leaf curl	Upward curling and yellowing of leaves	Ito et al. (2008)
Luffa cylindrica	*Tomato leaf curl New Delhi virus*	Bipartite	Yellow mosaic	Mosaic and yellowing of leaves	Sohrab et al. (2003)

Currently, this biotype is reported to occur in at least 52 countries of the world. In the recent times, the Q biotype is also taking a global position with respect to *Bamesia* dynamics. This biotype other than the Mediterranean region was reported from 10 countries (Legg et al. 1994; Sseruwagi et al. 2006).

Vegetables are highly season specific crops which require a specific set of climatic conditions to complete the life cycle. With the release of more and more hybrid vegetables and continuous cultivation throughout the year helps in survival of the viral vectors. The yield loss in vegetables contributed by begomoviruses varies from 20 to 100%, depending on host, vector, environment, and virus strain (Alvarez and Abud-Antún 1995; Caballero and Rueda 1993).

26.1 Okra (*Abelmoschus esculentus*)

26.1.1 Yellow Vein Mosaic Disease (YVMD)

Yellow symptoms on the leaves of okra were first reported by Kulkarni (1924) from Mumbai. Later, it was reported from other places of India and named as yellow vein

Fig. 26.2 Yellow vein mosaic disease of okra (*Abelmoschus esculentus*)

mosaic of okra (Uppal et al. 1940). The causal organism was found to be a virus and more precisely the serological evidences show it belonged to begomovirus group. Latter the virus was named as Bhendi yellow vein mosaic virus (BYVMV) (Harrison et al. 1991). The disease can infect 100% of okra plant covering from leaves to fruit resulting in yield loss of 40–94% (Fajinmi and Fajinmi 2010). The YVMV causing most of the begomoviruses are found to be monopartite however, association with betasatellite was found regularly. One bipartite *Bhendi yellow vein Delhi virus* was recently reported (Venkataravanappa et al. 2012). Alone the BYVMV DNA of monopartite virus can produce the symptom of yellow vein mosaic, however a typical symptom is produced when associated with betasatellite DNA (Jose and Usha 2003) (Fig. 26.2).

Several studies were carried out to decipher the genetics of YVMV resistance. The genetics were governed by a single dominant gene (Jambhale and Nerkar 1981; Dutta 1984), two dominant genes (Sharma and Dhillon 1983), two recessive genes (Singh et al. 1962), two complimentary genes (Sharma and Sharma 1984; Dhankhar et al. 2005), additive genes (Vashisht et al. 2001), duplicate dominant gene (Sharma and Dhillon 1983; Pullaiah et al. 1998; Seth et al. 2017), and complex inheritance (Vashisht et al. 2001; Dhankhar et al. 2005; Arora et al. 2008).

26.1.2 Okra Enation Leaf Curl Disease (OELCD)

A new disease from Bangalore (Karnataka) was observed as curling and upward cupping of leaves, reduced leaf area along with enation and petiole bending. The resultant plant showed stunting, reduced yield, deformed fruits unsuitable for marketing and in severe condition a yield loss of 80–90% (Singh 1996; Sanwal et al. 2014) (Fig. 26.3). This disease was named as okra enation leaf curl disease (OELCD). Recently, this disease broke resistance in almost all the released varieties across the country (Sanwal et al. 2014) making it as disease of economic importance that is

Fig. 26.3 Enation leaf curl disease of okra (*Abelmoschus esculentus*)

going to be a future menace for the okra cultivation. The virus causing this disease belongs to a monopartite group of begomoviruses with beta- and alphasatellite DNA, along with all genes encoded by virion-sense and complimentary-sense were present. The viral genome has highest sequence similarity of 87.2% with *Mesta yellow vein mosaic virus* (MeYVMV) and 84.5% similarity with *Bhendi yellow vein mosaic virus* (BYVMV) (Venkataravanappa et al. 2015). This distinct virus was named as *Okra enation leaf curl virus* (OELCuV) and is transmitted by whitefly. Till date the genetics of resistance of this disease is unknown. Several research groups are working to identify the source of resistance and deciphering the genetics as well as the mechanism of resistance against this devastating disease. The new recombination and strain evolution is the major cause of the emergence of this disease.

26.2 Cassava (*Manihot esculenta*)

Cassava, an important food crop, is widely grown in tropical countries of the world. The cassava mosaic disease is a major disease, limiting its cultivation. The disease was introduced from America to Africa and Africa to India. In India, it is considered as the major threat for cultivation of Cassava in the early 1940s (Abraham 1956). Cassava mosaic disease (CMD) had been reported in India in 1966 (Alagianagalingam and Ramakrishnan 1966). The primary source of transmission of this begomovirus is whitefly however, the advertent use of infected material was a major cause of the spread of the disease (Malathi et al. 1989). CMD has subsequently become

prevalent in southern India (Calvert and Thresh 2002), resulting in yield losses of between 10 and 15%. Eleven different bipartite begomoviruses strains are associated with this disease across the globe, (Berrie et al. 1998; Hong et al. 1993; Rybicki and Pietersen 1999; Saunders et al. 2002; Fondong 2017). While, the two strains *Sri Lankan cassava mosaic virus* (SLCMV) and *Indian cassava mosaic virus* (ICMV) are associated viruses causing CMD in India. Analysis of virus infected samples collected from India showed that the SLCMV is more widespread than the ICMV, high recombination was also reported among the two viruses (Patil et al. 2005; Rothenstein et al. 2006). In a whitefly transmission study conducted in meristem culture developed material of cassava, it was found that the symptom starts appearing 25 days after inoculation with a transmission efficiency of 85% (Duraisamy et al. 2012). Pseudo-recombination between SLCMV and ICMV was reported from the samples collected from Kerala, India. The trans-replication of ICMV DNA B by SLCMV DNA A was also reported (Karthikeyan et al. 2016). Virus-induced PTGS results in recovery from the disease symptoms and this phenomenon is related to the accumulation of siRNA (Chellappan et al. 2004a, b). Also, an interesting phenomenon of the emergence of a latent strain of ICMV was reported in the absence of non-persistent SLCV isolate in the vegetative collection of symptomless plant which was earlier harboring the SLCV strain. For such phenomenon to occur the siRNA plays an important role and it was conclusively proved that in the plants infected with SLCV, the symptom recovered plant carry a high level of viral siRNA however, the ICMV only appear after the complete loss of viral siRNA. This shows that SLCMV suppresses ICMV, which result in prevalence of SLCMV over ICMV in the cassava of the Indian subcontinent (Karthikeyan et al. 2016).

26.3 Cucurbitaceous Vegetables

Cucurbits are extensively cultivated in India, consumed as salad (*Cucumis sativus*), vegetable (*Citrullus vulgaris*, *Coccinia indica, Cucurbita maxima, Cucurbita pepo, Lagenaria siceraria, Luffa acutangula, Luffa cylindrica, Momordica charantia, Trichosanthes anguina, and Trichosanthes dioica*), or either as fruits (*Benincasa hispida*, *Cucumis melo, and Citrullus lanatus*). Several begomoviruses are associated with cucurbitaceous vegetables viz., *Tomato leaf curl New Delhi virus* (Sohrab et al. 2010; Nagendran et al. 2014), *Squash leaf curl China virus* (Singh et al. 2007; Tiwari et al. 2012b), *Pepper leaf curl Bangladesh virus* (Raj et al. 2010), *Mesta yellow vein virus* (Khan et al. 2002), *Bitter gourd yellow mosaic virus* (Rajinimala et al. 2005), *Indian cassava mosaic virus* (Rajinimala and Rabindran 2007), *Tomato leaf curl Palampur virus* (Namrata et al. 2010), *Ageratum enation virus* (Raj et al. 2011), *Coccinia mosaic virus*, and *Pumpkin yellow mosaic virus* (Muniyappa et al. 2003).

26.3.1 Bitter Gourd (*Momordica charantia*)

Bitter gourd is utilized not only as a vegetable, but also, as traditional medicine. The fruit juice and leaf extract has been widely used as an antidiabetic, against wound,

infection and as a blood purifier. Cultivation of bitter gourd is severely affected by begomovirus causing yellow mosaic disease (Uppal 1933), which reduces yield up to 100% (Giri and Mishra 1986; Matthew et al. 1991), simultaneously hampering the nutrient and antioxidant properties of the fruits (Raj et al. 2005b). The disease is transmitted by the whitefly (Mathew and Alice 2002) and molecular analysis of the infected plants with begomovirus specific primers and southern hybridization gave conclusive proof about the existence of begomovirus as the causal agent of this disease. The virus was named as *Bitter gourd yellow mosaic virus* (BGYMV; Raj et al. 2005b). Later, by immunological and PCR analysis, Indian cassava mosaic virus (ICMV) was also found to be present in bitter gourd (Rajinimala and Rabindran 2007). Complete sequencing of DNA A component of the virus was performed and highest similarity of 86.9% was found with *Tomato leaf curl New Delhi virus* (ToLCNDV), while the DNA B component of the genome showed 97.2% similarity with an Indian strain of *Squash leaf curl China virus* (Tiwari et al. 2010a). BGYMV is likely to be emerged as the recombinant virus between the ToLCNDV and *Tomato leaf curl Bangladesh virus* (Tahir et al. 2010).

26.3.2 Pumpkin (*Cucurbita moschata*)

The disease is characterized as leaf curl, chlorotic patches, and stunting of plants. Pumpkin yellow vein mosaic disease was reported from north (Vasudeva and Lal 1943), central, and western part of the country and is transmitted by the whitefly (Varma 1955). Initial characterization of *Pumpkin yellow vein mosaic virus* (PYVMV) coat protein showed similarity with ToLCNDV (Muniyappa et al. 2003). Latter Phaneendra et al. (2012) carried out extensive characterization of PYVMV. The DNA-A shared maximum similarity of 98.1% with ToLCNDV. Association of betasatellite was not reported in the present condition which is required for severe symptom development in tomato leaf curl caused by the same virus. Reports are also available where *Squash leaf curl China virus* is found to be associated with the yellow vein mosaic disease of pumpkin in India (Singh et al. 2007; Hamsa et al. 2016). *Tomato leaf curl Palampur virus* is also reported to be associated with the disease (Jaiswal et al. 2011). Several biochemical changes in infected plants, like reduction of protein, vitamin C, and antioxidants content in leaf and fruits, however increase in superoxide dismutases (SOD), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), and catalase (CAT) was observed.

26.3.3 Sponge Gourd (*Luffa cylindrica*)

Yellow mosaic, curling and distortion of leaves was observed on the newly emerged leaves of sponge gourd. Under severe infection 100% plants get infected. The causal organism was found to be whitefly transmitted begomovirus (Sohrab et al. 2003). The molecular analysis of DNA-A component showed highest similarity of 95.1% with ToLCNDV (Sohrab et al. 2003; Tiwari et al. 2012a). Similar type of symptoms

as were reported from ridge gourd (*Luffa acutangula*) were also observed in sponge gourd. The causal organism was also found to be ToLCNDV (Tiwari et al. 2012a).

26.3.4 Ivy Gourd (*Coccinia grandis*)

Recently, a new species of begomovirus was found to be associated with mosaic disease of Ivy gourd. The causal virus was characterized as bipartite begomovirus and not associated with betasatellite. Sequence analysis of DNA-A component showed 78% similarity with coat protein of *Tomato leaf curl New Delhi virus*. However, complete sequence analysis of DNA-A of this virus showed highest similarity of 78% with *Loofa yellow mosaic virus* (LYMV-[VN]-AF509739). The complete sequencing of DNA-B component showed highest similarity of 76% with ToLCNDV. This new virus was named as the *Coccinia mosaic virus* (CoMoV-Ivy gourd [TN TDV Coc1]) (Nagendran et al. 2016). However, Venkataravanappa et al. (2018) reported association of ToLCNDV with the samples collected from Northern part of the country. The virus has emerged through recombination of virus previously affecting chilli and cucurbits (Venkataravanappa et al. 2018).

26.4 Legumes

Legumes are the richest source of vegetable protein to poor people of Asia and Africa. Different types of vegetable legumes like, cowpea (*Vigna unguiculata*), dolichos bean (*Dolichos lablab*), common bean (*Phaseolus vulgaris*), and soybean etc. are occupying a major area in the country and constitute the major dietary constituent. These crops suffer losses due to one or more viral disease. The begomoviruses are of prominent economic importance causing mosaic diseases.

26.4.1 Cowpea (*Vigna unguiculata*)

Cowpea is the major legume vegetable grown in the central, northern, and northeastern part of the country. This crop often faces yield loss of 60–70% due to viral infestation (Kumar et al. 2017). The infected plants show stunting, reduced growth, sterility, leaf curling, and mosaic. In a survey conducted in the central and eastern part of the Indian subcontinent showed association of begomovirus. Initial molecular characterization showed the presence of bipartite virus. Sequence characterization showed highest similarity (97%) with *Mungbean Yellow Mosaic India virus (MYMIV)* and also association of *cowpea golden mosaic virus* (CGMV) and *Frenchbean severe leaf curl virus (*FbSLCV) (Kumar et al. 2017). Agroinfiltration of the MYMIV of cowpea was also carried out in its natural host mungbean and infectivity was proved.

26.4.2 French Bean (*Phaseolus vulgaris*)

Leaf curl of French bean was observed in the Kanpur region of the country during 2010–2012. The molecular characterization of the samples collected from the symptomatic plants confirms presence of begomovirus. The genome size of this virus id 2741 nucleotide with two ORFs in virion-sense and five ORFs in complimentary sense strands separated by intergenic regions. The identified virus showed highest similarity of 80% with the *Cotton leaf curl Bangalore virus.* Thus this was named as new virus as *French bean leaf curl virus* as new virus causing this disease. This virus is associated with betasatellite with single ORF (Kamaal et al. 2013). The same research group also reported presence of *Tomato leaf curl Gujarat virus* as the causal organism of the leaf curl disease of the French bean (Kamaal et al. 2015).

MYMIV also infects Dolichos bean, *Dolichos lablab* (Singh et al. 2006) and Soybean, *Glycine max* (Varma et al. 1992). Pseudorecombinant of MYMIV was found to be associated with cowpea mosaic (John et al. 2008).

Soybean is also infected by MYMIV causing mosaic disease and high divergence was observed for the strains collected from central and southern India (Girish and Usha 2005). Similarity among the two stain for DNA-A and DNA-B was 82% and 71%, respectively (Usharani et al. 2004a).

26.5 Solaneceous Vegetables

These are the largest group of vegetables grown across the world. They serve as main vegetables for dishes and condiments. Vegetables like tomato, potato, brinjal, and chillies are major of these vegetables. The two crops, i.e., chili and tomato suffers great loss due to infection of begomoviruses. The insecticide used to control the virus vector possesses a great threat for export industry where several consignments were rejected every year due to the presence of high quantity of pesticides.

26.5.1 Potato (*Solanum tuberosum*)

The leaf curl, crinkle, and mosaic followed by stunting of the potato plant was observed during 1999 (Garg et al. 2001). The early sown crop is severely affected by apical leaf curl (Lakra 2003). A bipartite begomovirus was identified as the causal organism of the disease. The sequence comparison of DNA-A component of this virus showed 93–95% similarity with ToLCNDV (Usharani et al. 2004b). The causal virus had been named as *Potato apical leaf curl virus* (Venkatasalam et al. 2005). Infection of 40–75% was observed in the cultivars grown in the North India (Venkatasalam et al. 2011). PCR amplification of most common 22 cultivars showed that varieties like *Kufri Anand*, *Kufri Chandramukhi*, *Kufri Chipsona 1, Kufri Chipsona 2, Kufri Chipsona 4, Kufri Gaurav, Kufri Himalini, Kufri Khyati, Kufri Pukhraj,* and *Kufri Satlej* acquired the virus at a faster rate during early October. However, all the 22 cultivars acquired ToLCNDV at some time (Bhatnagar et al.

2017). The possible reason for the evolution of this disease is the early crop cultivated during October which earlier was absent due to cultivation during winter season and low population of whitefly.

26.5.2 Brinjal (*Solanum melongena*)

Brinjal also known as eggplant, was supposed to be immune to begomoviruses however, recently, from fields of Maharashtra and central part of India 50–60% plants showing yellowing and mottling symptoms were observed. Initial identification of whitefly on the plants indicated toward the association of begomovirus with the mosaic disease. The initial report about the presence of begomovirus with eggplant was available from Thailand, where same mosaic and mottling symptom was observed (Green et al. 2003). The associated begomovirus is bipartite and was distinctly novel from others. The sequence analysis showed the similarity of DNA-A and DNA-B component with ToLCNDV. Hence, this showed that the ToLCNDV has started invading a new host, eggplant (Pratap et al. 2011).

26.5.3 Tomato (*Solanum lycopersicum*)

Tomato leaf curl is the most explored begomovirus disease across the world. This disease commonly occurs in all the tomato growing part covering north (Vasudeva and Sam Raj 1948), central (Varma 1959), and south (Govindu 1964; Sastry and Singh 1973) of the country. The infected plants show leaf curling, vein clearing, and ultimately sterility (Saikia and Muniyappa 1989) (Fig. 26.4). The causal organism was named as *Tomato leaf curl virus* (ToLCV) and subsequently isolates were characterized (Padidam et al. 1995). Five isolates viz., ToLCNDV-Severe and ToLCNDV-Mild from Delhi (Padidam et al. 1995), one from Lucknow (Srivastava et al. 1995), and three from Bengaluru (Chatchawankanphanich et al. 1993; Hong and Harrison 1995). It was also interesting to note that the isolates from North India are bipartite and south India are monopartite (Muniyappa et al. 2000). Latter other isolates like ToLCV-Ban-2, ToLCV-Ban-4, ToLCBV-Ban-5, and ToLCV-Kolar were reported in the tomato growing part of Karnataka (Kirthi et al. 2002) and *Tomato leaf curl Gujarat virus* (ToLCGV) from Varanasi, Uttar Pradesh (Chakraborty et al. 2003). The leaf curl virus is highly diverse in India extending from monopartite to bipartite and also pseudorecombinant as observed from Palampur (Kumar et al. 2008). Recombination was also reported in ToLCNDV (Pandey et al. 2010). The synergistic effect of recombination was also found between ToLCNDV-Severe and ToLCGV where DNA-A of one virus enhances replication of DNA-B of another virus (Chakraborty et al. 2008). ToLCV across India is associated with betasatellite DNA. The betasatellite from North India is distinct from that of south and central India (Sivalingam et al. 2010). These betasatellites have ability to move across the species and enhances the spectrum of symptom when associated (Tiwari et al. 2010b).

Fig. 26.4 Leaf curl disease of tomato

26.5.4 Chilli (*Capsicum* spp.)

Chilli is an indispensable ingredient of Indian cuisines. Leaf curl of chilli is characterized by shortening of leaves and stem, vein thickening, vein clearing, and curling of leaves. The infected plants reduce yield and produces few flowers and fruits only (Fig. 26.5). Chilli leaf curl disease was first observed in India by Vasudeva (1954) and its etiology was proved during 1960s (Mishra et al. 1963; Dhanraj and Seth 1968). The virus associated with this disease was called *Chilli leaf curl virus* (ChiLCV) and is reported to be a monopartite virus associated with betasatellite DNA (Khan et al. 2006; Senanayake et al. 2006, 2007). At least six strains of ChiLCV are associated with the production of the disease symptoms in different part of the world. The four strains, i.e., ChiLCV, TOLCNDV, *Chilli leaf curl Palampur virus* and *Tomato leaf curl Joydebpur virus* was reported from India (Shih et al. 2007; Khan et al. 2006; Senanayake et al. 2012) For efficient infection and complete symptom development betasatellite is required (Kumar et al. 2011). Several reports of recombination and the emergence of new virus strain causing ChiLCD is available; even the emergence of new virus through interspecific recombination is also reported for ChiLCV (Kumar et al. 2011). Besides, its infectivity was demonstrated in the natural host (Chattopadhyay et al. 2008). The infectivity analysis showed that a single whitefly can cause 66.6% infection in plants while,

Fig. 26.5 Leaf curl disease of chilli

eight whiteflies can successfully develop 100% infection. The virus can be transmitted to four different plant species of solanacea family viz. *Capsicum annuum, Solanum lycopersicum, Nicotiana tabacum, and Nicotiana benthamiana* (Senanayake et al. 2012). Mix infection of two or three viruses associated with chilli leaf curl was also reported from Pakistan (Yasmin et al. 2017). In genetic study carried out by Jindal et al. (2019) it was found that the resistance against this disease is by a single dominant gene, however earlier reports suggested contrary results (Kumar et al. 2009; Rai et al. 2010; Anandhi and Khader 2011; Rai et al. 2014).

26.6 Management of Begomoviruses

26.6.1 Cultural Practices

Most of the plant diseases, including the viral can be effectively managed by dealing one of the components of the disease triangle constituting of pathogen (virus), host, and environment. This management option primarily emphasizes on riding. Primary inoculum can be reduced by proper weeding (weed such as croton, Acalpha, Malvatrum, platinum, Sida, etc. are the potential inoculum reservoir for the begomoviruses) alternate host, alternate cropping with non-host crop, use of shiny metallic-coated construction paper or reflective plastic mulches (silver or white) can

repel whiteflies, especially away from small plants (Brown and Bird 1992). Begomovirus infects weeds and wild plants in the surrounding of sowing host crops. Beside crops, many weed species have been reported as hosts of begomoviruses in several countries (Morales and Anderson 2001; Barbosa et al. 2009). The viruses have wide weed hosts viz. Croton, Acalpha, Malvatrum, Parthenium, Sida, *Ageratum conyzoides*, *Acalypha indica*, *Croton bonplandianum*, *Eclipta prostrata*, *Physalis minima*, *Nicandra physalodes*, *Solanum nigrum*, *Datura stramonium*, *Datura Metel,* and other weeds which act as potential reservoirs of begomovirus. Murant and Taylor (1965) established relationship between the infectious nature of virus transmitting nematodes and weed seed. Cooper and Harrison (1973), identified two weeds, *Stellaria media* and *Viola arvensis* as key overwintering hosts of TRV where the virus was found to be retained by the vector *Trichodorus pachydermis* for long periods. Hence eradication of perennial weeds from around greenhouses, gardens, and fields to eliminate possible sources of virus therefore, may prove helpful (Agrios 1978). Eradication of weed host was found effective in the management of *Cucumber mosaic virus* (CMV) in cucumber and celery (Rist and Lorbeer 1989). Weeds act as inoculum reservoir during non-cropping period for *Tomato yellow leaf curl virus* (TYLCV) (Salati et al. 2002). Therefore, these weeds must be removed from and around the agricultural crop fields to minimize the source of reservoirs of many begomoviruses which also provide the shelter to whitefly, the known vector for transmission of a variety of begomoviruses. Shiny metallic-coated construction paper or reflective plastic mulches can repel whiteflies, especially away from small plants, and the other methods include the use of yellow sticky traps, early sowing, and proper plant spacing. In addition to repelling whiteflies, aphids, and leafhoppers, the mulch will enhance crop growth and control weeds. Reflective mulches have been shown to deter pests that transmit viruses in commercial vegetable crops, perhaps helping to reduce disease incidence and crop loss. When summertime temperatures get high, remove mulches to prevent overheating plants.

In vegetable gardens, yellow sticky traps can be placed around the garden to trap adults that are most useful for monitoring and detecting whiteflies rather than controlling them. Commercial traps or sticky cards are available in stores and online. They can be home made by using 1/4-inch plywood or masonite board, painted bright yellow, and mounted on pointed wooden stakes. Drive stakes into the soil close to the plants that are to be protected. Although commercially available sticky materials such as Tanglefoot are commonly used as coatings for the traps, you might want to try to make your own adhesive from one-part petroleum jelly or mineral oil and one-part household detergent. This material can be easily cleaned off boards with soap and water, whereas a commercial solvent must be used to remove the other adhesives. Periodic cleaning is essential to remove insects and debris from the boards and maintain the sticky surface. Barissicae family plants are highly susceptible to whitefly and it is being used as trap crops in tomato fields to localize vector population spreading the TYLCV in Israel (Cohen et al. 1988). Intercropping of cucumber or pumpkin with tomato may delay PYMV-TT infection in tomato. Intercropping lead to change in the feeding behavior of the whitefly vector which leads at shorter feeding time intervals which further reduces the transmission ability

of the vector (Bernays 1999). Application of heat therapy (35–54 °C), use of meristem tip cultures, cold treatment, and chemotherapy to produce healthy plant material can avoid the primary inoculum in the cropping areas. Use of virus free planting material may help in delaying virus spread and further the build of infected vector population (Raychaudhuri and Verma 1977).

26.6.2 Vector Management

Discriminate, frequent, and nonjudicial use of insecticides for management of vector insects leads to the development of resistance to insect beside their detrimental effect on environmental and human health. Reducing the vector population by means of chemicals has some challenges. Vector eggs and nymphs generally colonize the lower canopies where assess by contact insecticides is limited and systemic insecticides have their own limitations. However a sensible approach, including resistant crop varieties, use of natural enemies and insecticides can provide a sustainable management option. Most of less-toxic products such as insecticidal soaps, neem oil, or petroleum-based oil control only those whiteflies that are directly sprayed. Therefore, plants must be thoroughly covered with the spray solution and repeat applications may be necessary. Be sure to cover undersides of all infested leaves; usually these are the lowest leaves and the most difficult to reach. Systemic insecticide like imidacloprid can control whitefly nymphs, but can have negative impacts on natural enemies, honey bees, and other pollinators in the garden, especially when applied as a foliar spray (Flint 1998; Bellows et al. 2006). Spray solution concentration of 0.2% of Malathion (50% E.C.) at 21 day intervals was found effective on chilli in field conditions in effectively reducing the whitefly population, which minimizes the leaf curl disease incidence (Khan et al. 2006). General predators of whiteflies include lacewings, bigeyed bugs, several small lady beetles, including *Clitostethus arcuatus* (on ash whitefly), scale predators Scymnus or *Chilocorus* species, Asian multicolored lady beetle, *Harmonia axyridis* etc. Green lacewings feed on whitefly eggs or nymphs so if released at the beginning of the season can significantly bring down the primer vector population. Similarly, *Amblyseius swirskii* are predatory mites effective in warm, humid areas. *Encarsia* spp. and *Eretmocerus* spp. have been identified as parasitoids against *Bemisia tabaci* in Africa widely observed for management (Kamau et al. 2005). Parasitic fungus *Beauveria bassiana* (BotaniGard, BioCeres, Mycotrol) are effective in control of whiteflies by slow feeding/reproduction and killing the infected pests. Another fungus *Metarhizium anisopliae* is effective against sucking pests. In Holland, "Vertalec" a commercial available formulation of *Verticillum Lecanii* can effectively bring down whiteflies populations in glass-house vegetables. Similarly, the US company 'Thermo Trilogy' is marketing the *Paecilomyces fumosoroseus* based product PFR-97TM for the management of whiteflies/thrips in Glasshouse crops (Ramanujam et al. 2014).

26.6.3 Breeding for Disease Resistance

Breeding for disease resistance is the most effective, economical and environmentally safe way of management. However, identification of such genes requires screening of large numbers of germplasm, genetics of resistance and mode of action of the resistance genes. Finding some durable resistance genes is really a tedious job and transfer of such genes in good agronomic background has several complications. Incorporation of these genes can be achieved with backcross breeding, however it takes several generations to achieve the characteristics of good cultivars. But with the advent of molecular breeding these seemingly daunting task can be done easily. The narrow genetic base of the crops makes it difficult to identify resistance sources in the cultivated background. Harping the search programs into wild relatives has more chances of finding resistance genes. Several key genes in tomato against the ToLCV were identified. Till date, six genes governing resistance against this disease were identified viz., *Ty-1, Ty-2, Ty-3, Ty-4, Ty-5,* and *Ty-6* (Scott et al. 2015). Likewise, in cassava two dominant genes governing resistance against *CMD1* and *CMD2* were identified. The resistance source was identified to be wild African cassava (Fondong 2017). The first cassava mosaic resistant variety Sree Padmanabha is released for cultivation in the Indian subcontinent (http://www.isrc.in 2008). In most of the vegetable crops, the resistance breeding had been limited to genetics of resistance and non-targeted incorporation through phenotypic selection. Another method is to achieve the disease escape in which the crop is grown in the environment when there is less likely to develop disease. The breeder should select the cropping cycle early or late in the cropping season (Wood and Lass 2001).

26.7 Molecular Approaches

26.7.1 Molecular Breeding

With the advancement of marker technology and cost effective genotyping facility the tune of resistance development has shifted to molecular techniques. The genetic engineering technique was found to be most promising among all the begomovirus management strategies. For early detection of begomovirus in the plant, markers specific for the genome of the virus specially targeting the coat protein gene was developed (Rojas et al. 1993; Deng et al. 1994). These markers can be utilized for early identification of viruses and the uprooting of the infected plants to prevent the spread of the primary inoculum. The identified resistance genes were transferred into the cultivated background of different varieties, especially in the case of tomato and cassava. In case of tomato, the *Ty* genes associated with transcriptional gene silencing had been successfully transferred to the cultivated background. Pyramiding of these genes was preferred over single gene incorporation. Across the globe, these genes (*Ty-1, Ty-2, Ty-3, Ty-4, Ty-5,* and *Ty-6*) were utilized in the cultivated background (Ji et al. 2007). Prasanna et al. (2015) pyramided *Ty-3* and *Ty-2* in the background of Indian tomato cultivars. It was established that in the lines carrying *Ty-3*

the virus titer to as low as 10% of the susceptible cultivars. The *Ty-2* gene alone provided moderate resistance to monopartite virus while it showed susceptibility to bipartite viruses, however *Ty-3* was providing complete resistance against both monopartite and bipartite viruses (Prasanna et al. 2015). Similarly, the *Ty-2* was also incorporated into the background of CV. Pbc (Kumar et al. 2014). Also, *Ty-2*, *Ty-3,* and *Ty-5* was incorporated into the background of Indian tomato cultivars (Sadashiva et al. 2017).

In case of cassava, two dominant genes *CMD1* and *CMD2* were identified and pyramided in the background of African cultivars (Fondong 2017), however, no pyramiding work was carried out in Indian cassava cultivars.

26.7.2 Transgenic Approaches Using Pathogen-Derived Genes

The first coat protein derived resistance against *tobacco mosaic virus* opened the horizon for transgenic approaches, especially viral genes derived resistance (Powell-Abel et al. 1986). This pathogen-derived resistance was quite successful in the management of RNA viruses (Snehi et al. 2015). The viral genes like coat protein, movement protein, replicase gene, antisense RNA, satellite RNA, defective interfering genes, etc. derived from pathogen genes were used. However, the coat protein followed by movement protein and replicase gene is most commonly used to derive transgene-based resistance. The initial focus was mainly targeted toward the RNA viruses, the first begomovirus resistance was achieved for ToLCV expressing capsid protein genes (Kunik et al. 1994). Small interfering RNA (siRNA) was produced against *African cassava mosaic virus* using the bidirectional promoter of DNA-A in cassava (Vanderschuren et al. 2007). The *AC1* viral gene was silenced by incorporation of RNAi construct in common bean (Bonfim et al. 2007). Apart from capsid gene, replicase gene was also used to derive pathogen-mediated resistance in the host. Virus resistance against ACMV was achieved using replication associated (*AC1*) transgene (Hong and Stanley 1996) and using similar truncated gene (*AC1*) resistance to ToLCV was achieved in tomato (Noris et al. 1996). Resistance against *Tomato golden mosaic virus* (TGMV) was developed by the antisence RNA to the rep protein gene (Day et al. 1991). Similarly, Bendahmane and Gronenborn (1997) developed TYLCV resistance by using antisense RNAs to Rep protein gene. Agrobacterium-mediated transformation of tomato using the ToLCV coat protein gene was successfully done to produce tomato lines, resistance against ToLCV infection (Raj et al. 2005a). Recovery from initial ToLCD symptom was also observed in the case of antisense construct carrying lines associated with virus Rep genes (Praveen et al. 2005a, b). Hairpin RNA-mediated strategy for silencing ToLCV in tomato was developed using *AC-1* and *AC-4* genes to achieve effective resistance (Ramesh et al. 2007). In case of soybean, the resistance is suggested to be due to RNAi-mediated resistance mechanism. Yadav et al. (2009) studied four genotypes of soybean cultivar observed that less viral transcript was accumulated in resistant cultivars as compared to susceptible cultivars and also less production of siRNA in susceptible cultivars. For the group of MYMIV Mishra et al. (2014)

designed ribozyme targeting Rep-protein encoding RNA. They reported that the catalytic activity was induced by the introduction of either active or inactive ribozyme. Downregulation of target RNA was observed and catalytic activity was found to be true phenomenon. The use of trans-acting siRNA was demonstrated by Singh et al. (2015) for control of TOLCNDV. Targeting multiple gene was possible by use of chimeric vector containing *AC-2* and *AC-4* partial fragments. The infiltrated plant showed less accumulation of target virus and no symptom was produced. Amount of siRNA produced against *AC-2* and *AC-4* was proportional to the resistance level. In case of potato apical leaf curl disease caused by ToLCNDV, resistance in host was achieved through RNAi approach. Replication associated gene (*AC-1*) was used to develop transgenic plants which ultimately lead to development of pathogen-derived resistance. Complete asymptomatic plants were isolated after challenge inoculation (Tomar et al. 2018).

26.7.3 Approaches Utilizing Host-Derived Genes

In nature several plants are not affected by the insect vector like whitefly. It is their innate capacity, which produces certain proteins with insecticidal activity that ultimately affect the life cycle of the whitefly or other sap sucking insects. It is known that fern and mosses are rarely infected by phytophagous insects. In search of such ferns Shukla et al. (2016) identified 38 ferns that were having insecticidal activity and *Tectaria macrodonta* was most potent in the insecticidal activity. They identified that *T. macrodonta* protein (Tma12) has insecticidal activity at 1.49 mg/mL during invitro feeding. The expression of the Tma12 in cotton provided resistance to whitefly and ultimately to *Cotton leaf curl virus,* a member of the genus begomovirus. As the protein Tma12 is isolated from edible plant, therefore this gene has potential to be utilized in vegetable crops for achieving whitefly as well as virus resistance.

26.7.4 CRISPR/Cas9 Genome Editing in Achieving Begomovirus Resistance

Clustered regularly interspaced short palindromic repeats—*CRISPR* associated 9 (*CRISPR*/Cas9) is the most potent genome editing tool available with the molecular biologists for development of resistant cultivar by targeting the host susceptibility factor. This was utilized for improvement of vegetable crop against *Beet severe curly top virus* and *Bean yellow dwarf virus* (Baltes et al. 2015; Ji et al. 2015). The two genes *AC2* and *AC3* were targeted for editing through this system. For achieving TYLCV resistance, the intergenic region (IR) stem loop of the origin of replication was found to be most effective among different sites for editing of Begomoviruses (Ali et al. 2015). The short guide RNA (sgRNA) of TYLCV was transformed through *Tobacco rattle virus* into *Nicotiana benthamiana* over-expressing Cas-9. Infectives clone of TYLCV was then inoculated through agro-infiltration into the

N. benthamiana plants. In the IR mutants very less accumulation of TYLCV genome was observed. In a study conducted to analyze the efficiency of coding and noncoding region as *CRISPR*/Cas9 target of the multiple begomovirus genome. The coding regions mutant were capable of producing movement proteins and capable of replication whereas, the noncoding region mutants are more efficient, providing interference activity and significantly restricts the generation of virus capable of producing systemic infection and replication (Ali et al. 2016). The same group of researchers targeted the coat protein and replicase genes of TYLCV to tackle the begomovirus menace. The target regions severely affect the virus multiplication thus resulted in very low accumulation of TYLCV DNA genome (Tashkandi et al. 2018). In an experiment targeting the resistance against ACMV, Mehta et al. (2018) edited the virus genome to obtain the resistance against ACMV. He reported the success rate of achieving resistance was ranging between 33 and 48% through single nucleotide mutation. He also raised concern regarding evolution of the novel virus that cannot be cleaved again through CRISPR-Cas9. This system has huge potential, however, this technology suffers from off targeting.

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