Classification, Taxonomy and Gene Function of Geminiviruses and Their Satellites

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Abstract

The major constraint for the crop productivity throughout the world is due to the diseases caused by viruses. These plant-infecting viruses emerged as an unavoidable limiting factor and are responsible for severe crop losses in all major economically important plants. Among them, the members belonging to the family, *Geminiviridae*, are the most devastating pathogens that are transmitted by insect vectors. These geminiviruses cause diseases such as chlorotic, dwarf, leaf curl, mosaic, yellow mosaic and yellow vein in monocots and dicots across the tropical and sub-tropical countries. In addition, these geminiviruses use weeds as reservoir for the spread of diseases. Moreover, these viruses encode only a fewer proteins and rely majorly on the host factors for their replication, disease development and spread. This chapter introduces the readers to the classification and taxonomy of geminiviruses, genus/species demarcation thresholds and the nature of genomic component and satellites associated with geminiviral disease complexes. It also discusses the genome organization of viruses grouped into different genera, before giving a glimpse of the important functions of gene products it encode.

1 Family: *Geminiviridae*

Geminiviridae comprises of a group of plant-infecting insect-transmitted viruses containing non-enveloped circular ssDNA genome of ~2.8 kb in size. These viruses cause substantial crop losses in a large number of economically important vegetable

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and food crops, ornamental plants and fibre crops worldwide (Navas-Castillo et al. 2011). In 1977, Harrison et al. coined the term '*Geminivirus*' based on their nature of twinned icosahedral particles. The geminate particles are packed in two incomplete icosahedra containing 22 pentameric capsomeres (Hesketh et al. 2018). Within one twinned particle, only one molecule of ssDNA can be encapsidated; thus for a bipartite genome, DNA-A and DNA-B are carried by two twinned particles (Jeske 2009). Virus replication occurs through rolling-circle and recombination-dependent mechanisms, but they do not encode any DNA polymerase (Jeske 2009). Hence they rely entirely on the infected cells for synthesizing their complementary strand in the nucleus by employing various host replication factors. For viral gene expression, the virus transcription occurs bi-directionally, and produces transcripts from both the complementary and virion sense strands leading to the generation of several overlapping viral transcripts (Brown et al. 2012).

1.1 Geminivirus Taxonomy

The usage of new molecular tools, such as rolling-circle amplification and high-throughput sequencing in the last decades have greatly helped the geminivirologists in identifying several novel geminivirus-like genomic components (Roossinck et al. 2015). Because of this near-global occurrence of several distinct geminiviruses, the *International Committee on Taxonomy of Viruses* (ICTV) has devised several guidelines for classifying the geminiviruses at genus level. Based on the insect vector, genome organization, genome-wide pairwise sequence identities and host range, nine genera, such as *Becurtovirus, Begomovirus, Capulavirus, Curtovirus, Eragrovirus, Grablovirus, Mastrevirus, Topocuvirus* and *Turncurtovirus* are included in *Geminiviridae* by geminivirus study group of the ICTV (Zerbini et al. 2017). Aphids, leafhoppers, treehoppers or whiteflies can transmit these geminiviruses.

1.1.1 Genus: *Becurtovirus*

The type species of the genus *Becurtovirus* is *Beet curly top Iran virus* (BCTIV) and two closely related groups, *Spinach curly top Arizona virus* (SCTAV) and *Exomis microphylla latent virus* are also included in this genus. Among these two species, BCTIV comprises four different strains (BCTIV-A, B, C, D). Unlike other geminiviruses, these members possess unique nona-nucleotides (TAAGATTCC) with a spliced replication-initiator protein (Rep) in the complementary sense strand (Fig. 1). The species and strain demarcation threshold value for this genus is fixed as 80% and 94%, respectively (Varsani et al. 2014a). The isolates belonging to BCTIV (A–D) has so far found infecting various dicot hosts, such as *Beta vulgaris*, *Vigna unguiculata*, *Solanum lycopersicum* and *Phaseolus vulgaris* in Iran (Yazdi et al. 2008; Soleimani et al. 2013). Moreover, an isolate of SCTAV was identified from *S. oleracea* plants in the Arizona region of USA (Hernandez-Zepeda et al. 2013). These dicot plants infecting becurtoviruses are reported to be transmitted by leafhoppers (Zerbini et al. 2017).

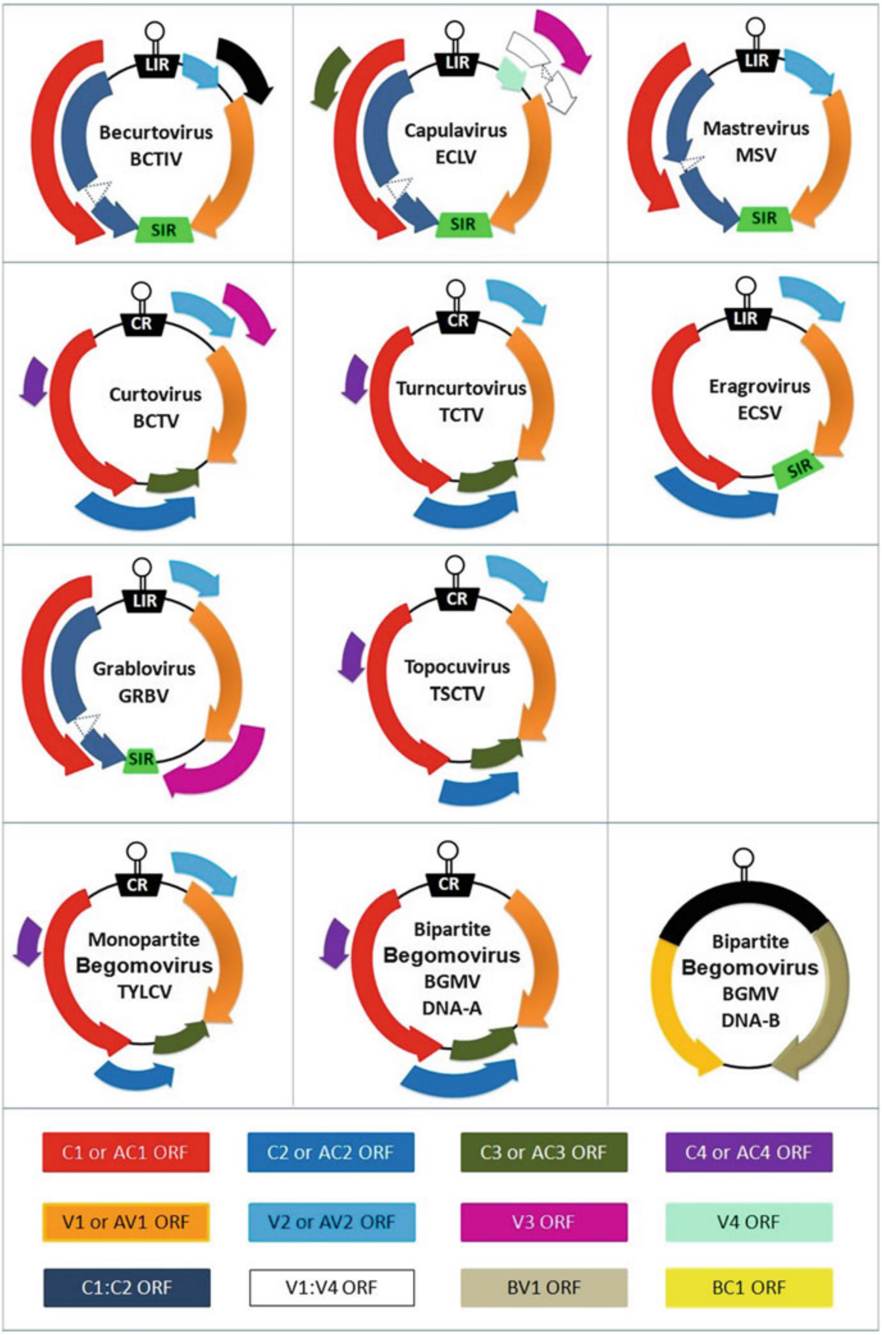

Fig. 1 *Genome organization of the representative geminiviruses belonging to different genera in the Geminiviridae family*. The virus-encoded ORFs are given in different colours and its description is provided at the bottom of the figure. The stem and loop structure indicates location of nonanucleotides in the genome. The CR, SIR and LIR refer to common region, short intergenic region

1.1.2 Genus: *Begomovirus*

The genus name is derived from the name of its type member, *Bean golden mosaic virus* (BGMV). *Begomovirus* is the largest genus of the *Geminiviridae* family containing ~300 ICTV recognized virus species (Zerbini et al. 2017). The insect vectors, whiteflies (*Bemisia tabaci Genn.*) can transmit these viruses, and infect both monocots and dicots (Navas-Castillo et al. 2011; Brown et al. 2012). These begomoviruses are classified either as monopartite or bipartite (Brown et al. 2012) (Fig. 1). Monopartite begomoviruses that contain only DNA-A-like molecule are phloem limited and are not sap transmissible, whereas sap transmissible bipartite begomoviruses (with similar-sized DNA-A and DNA-B molecules) infect both phloem and non-phloem tissues (Melgarejo et al. 2013). According to the genome organization and phylogenetic segregation, these begomoviruses are divided into two regions: 'Old world (OW)' that includes Africa, Asia, Australia and Europe and 'New World (NW)' that includes America, Brazil and Mexico (Brown et al. 2012). However, the probable centre of its origin is found to be around South-east Asia (Nawaz-ul-Rehman and Fauquet 2009). Several factors such as recombination, pseudo-recombination, synergism, microsatellites, mutation, nucleotide diversity/ substitutions and vector transmission might be influencing the evolution of these begomoviruses and their associated satellites (Chakraborty et al. 2008; Melgarejo et al. 2013; Lima et al. 2017; Kumar et al. 2015b, 2017; Kumar and Chakraborty 2018). The strain demarcation threshold for this genus has been fixed as 94%, however the pairwise sequence identities of 91% have been proposed for demarcation of new species (Brown et al. 2015).

The DNA-A component have a conserved arrangement of six open reading frames (ORFs): two ORFs in the virion strand (AV1, AV2 in bipartite and V1, V2 in monopartite) and four in the complementary strand (AC1–AC4 in bipartite and C1–C4 in monopartite) (Fig. 1). The DNA-B component of bipartite viruses encode a movement protein (BC1) and a nuclear shuttle protein (BV1) to help in intra- and inter-cellular viral movements (Brown et al. 2012; Hanley-Bowdoin et al. 2013). A highly conserved non-coding region called common region (CR) separates the bidirectional transcription units of DNA-A and DNA-B (Lazarowitz and Shepherd 1992; Brown et al. 2012). The CR contains stem loop-structured nona-nucleotide (TAATATTAC) which acts as a cleavage site for Rep to initiate viral replication (Hanley-Bowdoin et al. 2013). Monopartite begomoviruses are often found along with satellite molecules namely, alphasatellites, betasatellites and deltasatellites (Nawaz-ul-Rehman and Fauquet 2009; Fiallo-Olive et al. 2012; Kumar et al. 2015a, 2017; Lozano et al. 2016).

Fig. 1 (continued) and long intergenic region, respectively. The full name of the virus isolates abbreviated here is *BCTIV Beet curly top Iran virus*, *ECLV Euphorbia caput-medusae latent virus*, *MSV Maize streak virus*, *BCTV Beet curly top virus*, *TCTV Turnip curly top virus*, *ECSV Eragrostis curvula streak virus*, *GRBV Grapevine red blotch virus*, *TSCTV Tomato pseudo curly top virus*, *TYLCV Tomato yellow leaf curl virus* and *BGMV Bean golden mosaic virus*

1.1.3 Genus: *Capulavirus*

The type species for the genus *Capulavirus* is *Euphorbia caput-medusae latent virus* (EcmLV). These EcmLV isolates were reported to infect *Euphorbia caput-medusae* plants in the South Africa. Roumagnac et al. (2015) observed the geminate particles by transmission electron microscopy from the purified preparations of EcmLV. Some of the virus species, such as *Alfalfa leaf curl virus* (ALCV), *French bean severe leaf curl virus* (FbSLCV) and *Plantago lanceolata latent virus* (PlLV) are also included in this genus. ALCV isolates were transmitted by aphids and are reported to infect *Medicago sativa* plants in France (Roumagnac et al. 2015). Similarly, in India, FbSLCV causes severe leaf curl disease in *Phaseolus vulgaris* and PlLV was identified in *Plantago lanceolata* from Finland (Roumagnac et al. 2015; Susi et al. 2017; Varsani et al. 2017).

The origin of replication sequence of this group of closely related viruses is found to be TAATATTAC. In common with the viruses belonging to the genus, *Becurtovirus* and *Mastrevirus*, the members of this genus also possess a long intergenic region (LIR) and a short intergenic region (SIR) along with a Rep protein which is expressed as a spliced complementary strand transcript (Varsani et al. 2017). The presence of a possible movement protein encoding ORF located in the 5′ direction from the coat protein differentiates them from the members of the other established genera of the *Geminiviridae* family (Fig. 1).

1.1.4 Genus: *Curtovirus*

The name *Curtovirus* was derived from the name of the type species of this genus: *Beet curly top virus* (BCTV) which is of the size of nearly 3 kb (Zerbini et al. 2017). Additionally, the *Spinach severe curly top virus* (SpSCTV) and *Horseradish curly top virus* (HrCTV) infecting *Spinacia oleracea* and *Armoracia rusticana* plants, respectively, are also grouped to this genus. They are transmitted by beet leafhopper (*Circulifer tenellus*) and infect several dicotyledonous plants, such as *Beta vulgaris*, *Capsicum annum*, *Phaseolus vulgaris* cv. Aluvori, *Solanum lycopersicum* and *Spinacia oleracea* (Stenger et al. 1990; Soto and Gilbertson 2003; Hernandez-Zepeda et al. 2013). Its geographical range was found around the Mediterranean region, the Middle East, the Indian subcontinent and North and Central America (Varsani et al. 2014b). Like other genera, they are monopartite in nature sharing less sequence homology with them. Its genome encodes for three ORFs in the virion strand and four ORFs in the complementary strand along with a SIR (Fig. 1). Virion sense strand encodes a coat protein, a regulator protein and a putative movement protein, whereas complementary sense strand encodes a Rep, replication enhancer (REn) protein, a silencing suppressor protein and a pathogenicity associated protein (Hormuzdi and Bisaro 1995).

1.1.5 Genus: *Eragrovirus*

Currently, *Eragrostis curvula streak virus* (ECSV) is the only species included in this genus. This virus codes for four ORFs (two ORFs each in the virion sense and the complementary sense strand) and the isolates of ECSV have nona-nucleotide motif as TAAGATTCC, at their presumed origin of viral DNA replication (Varsani et al. 2014a). The coat protein of ECSV resembles to the members of *Mastrevirus*, but the replication protein is quite similar to the viruses belonging to the genus, *Begomovirus*. The two strains of ECSV (A and B) were reported to be infecting a monocot species (*E. curvula*) in the South Africa (Varsani et al. 2009). The genome-wide per cent pairwise comparisons of 75% (for species) and 94% (for strain) are proposed as the demarcation threshold for the members of *Eragrovirus* (Varsani et al. 2014a).

1.1.6 Genus: *Grablovirus*

The type species of *Grablovirus* genus is *Grapevine red blotch virus* (GRBV) and *Prunus latent virus* and *Wild Vitis latent virus* are the other two virus species assigned to this genus. The isolates of GRBV are transmitted by the alfalfa treehoppers (Krenz et al. 2012; Bahder et al. 2016). The GRBV isolates infecting *Vitis vinifera* have been reported mainly from USA, followed by Canada and South Korea (Cieniewicz et al. 2018). These viruses possess TAATATTAC as the nona-nucleotide sequence for the initiation of virion sense strand synthesis (Varsani et al. 2017). The genome arrangement of its complementary sense strand appears similar to the members of *Capulavirus*, whereas it encodes three ORFs (V1, V2 and V3) in its virion sense strand (Fig. 1).

1.1.7 Genus: *Mastrevirus*

The type species for this genus is *Maize streak virus* (MSV), a monopartite virus that is transmitted by leafhoppers (Monjane et al. 2011; Zerbini et al. 2017). Mastreviruses are 2.7–2.8 kb in size and 37 distinct members are considered to be recognized species within this genus (Table 1). Eleven strains of *Maize streak virus* (MSV-A–K) and nine strains of *Panicum streak virus* (PanSV-A–I) are predominantly reported from the African countries (Muhire et al. 2013). The presence of the isolates of *Chickpea chlorosis virus*, *Chloris striate mosaic virus*, *Digitaria ciliaris striate mosaic virus*, *Digitaria didactyla striate mosaic virus*, *Paspalum striate mosaic virus* and *Sporobolus striate mosaic virus-1* and *2* are documented mainly from Australia (Kraberger et al. 2012, 2014). In general, these viruses are mostly found confined to the African countries and Australia, infecting both monocot and dicot plants, such as *Brachiaria* sp., *Cicer arietinum*, *Digitaria* sp., *Panicum maximum*, *Setaria* sp., *Urochloa* sp. and *Zea mays* (Kraberger et al. 2014). Moreover, mastreviruses are also identified from Germany, India, Japan and Pakistan (Muhire et al. 2013; Kraberger et al. 2014). Importantly, *Wheat dwarf virus* isolates infecting *Avena sativa*, *Hordeum vulgare* and *Triticum aestivum* plants are reported from China, Iran and several European countries (Kvarnheden et al. 2002; Ramsell et al. 2009).

The genome of the members of mastreviruses has nona-nucleotides (TAATATTAC) similar to other geminiviruses. Its genome encodes for two ORFs from the virion strand (capsid protein and movement protein) and the complementary strand encoded Rep protein expresses as a splicing product of C1 and C2 ORFs (Fig. 1). The virion sense strand encoded proteins are necessary for viral movement and encapsidation; whereas replication-associated proteins are encoded in the

Table 1 Type species, insect vector and species demarcation threshold of the genera in *Geminiviridae* family

Genera	Type species (abbreviated name)	ICTV recognized virus species	Insect vectors (common name)	Nona-nucleotides	Demarcation threshold at	
					Species level (%)	Strain level (%)
Becurtovirus	*Beet curly top Iran virus* (BCTIV)	3	*Circulifer haematoceps* (Leafhoppers)	TAAGATTCC	80	94
Begomovirus	*Bean golden mosaic virus* (BGMV)	388	*Bemisia tabaci* (Whiteflies)	TAATATTAC	91	94
Capulavirus	*Euphorbia caput-medusae latent virus* (EcmLV)	4	*Aphis craccivora* (Aphids)	TAATATTAC	78	–
Curtovirus	*Beet curly top virus* (BCTV)	3	*Circulifer tenellus* (Leafhoppers)	TAATATTAC	77	94
Mastrevirus	*Maize streak virus* (MSV)	37	*Cicadulina* sp., *Nesoclutha* sp., *Psammotettix alienus, Orosius* sp. (Leafhoppers)	TAATATTAC	78	94
Eragrovirus	*Eragrostis curvula streak virus* (ECSV)	1	Not identified	TAAGATTCC	75	94
Grablovirus	*Grapevein red blotch virus* (GRBV)	3	*Spissistilus festinus* (Treehoppers)	TAATATTAC	80	–
Topocuvirus	*Tomato severe curly top virus* (TSCTV)	1	*Micrutalis malleifera* (Treehoppers)	TTATATTAC	–	–
Turncurtovirus	*Turnip curly top virus* (TCTV)	2	*Circulifer haematoceps* (Leafhoppers)	TAATATTAC	75	95

complementary strand. Further, these ORFs are separated by LIR and SIR containing the origin of replication for the synthesis of virion and complementary strands, respectively (Kammann et al. 1991). They possess a unique characteristic of regulating their own gene expression through a post-transcriptional splicing event (Rojas et al. 2005).

1.1.8 Genus: *Topocuvirus*

A monopartite geminivirus, *Tomato pseudo curly top virus* of ~3 kb in size is the type member of this genus. This virus encodes two ORFs in the virion sense strand and four ORFs in the complementary sense strand. It is transmitted by treehoppers (*Micrutalis malleifera*) to dicot plants in the NW. Based on the genome organization, this virus species appears to be a recombinant between the genera, *Mastrevirus* and *Begomovirus* (Briddon et al. 1996).

1.1.9 Genus: *Turncurtovirus*

Only member in this genus includes *Turnip curly top virus* which is identified from *Brassica rapa* or *Raphanus sativus* plants (Briddon et al. 2010). Recently, *Turnip leaf roll virus* is also included in this genus. These phylogenetically distinct members are most closely resembled to the members of genus, *Curtovirus*. Its genome encodes six rather than seven proteins. It contains nona-nucleotides (TAATATTAC) similar to *Mastrevirus*, *Begomovirus*, *Curtovirus* and *Topocuvirus* (Table 1). A tentative strain demarcation threshold of 95% has been assigned and based on this criterion, four strains of *Turnip curly top virus* (TCTV-A–D) were proposed (Varsani et al. 2014a). These viruses are also identified from *Anchusa* sp., *Descurainia sophia*, *Hibiscus trionum* and *Solanum americanum* plants (Razavinejad and Heydarnejad 2013; Razavinejad et al. 2013).

1.2 Biological Functions of Geminivirus Components

1.2.1 DNA-A Component

The proteins encoded by DNA-A component are involved in the replication, gene expression, virus movement and encapsidation, and suppression of plant immunity.

The C1/AC1 protein is also called as replication-initiator protein (Rep) that is very much essential for the virus replication (Settlage et al. 1996; Hanley-Bowdoin et al. 2013). Though Rep proteins do not possess any similarity with known polymerases, it does share some similarity with the bacterial plasmid-encoded replication initiator proteins which undergo replication through rolling-circle mechanism (Ilyina and Koonin 1992). Also Rep proteins of begomovirus and a mastrevirus have been shown to be RNAi suppressors (Rodriguez-Negrete et al. 2013; Wang et al. 2014).

The transcription activator protein (TrAP) encoded by the C2/AC2 ORF is a multi-functional protein involved in virus replication, transactivation of late viral genes (which are needed for virus encapsidation) and several other host genes (Sunter and Bisaro 1992; Trinks et al. 2005; Caracuel et al. 2012). Several TrAPs also possess transcriptional gene silencing (TGS) and/or post-transcriptional gene silencing (PTGS) suppression activity (Dong et al. 2003; Buchmann et al. 2009; Hanley-Bowdoin et al. 2013; Kumar et al. 2015b).

REn protein encoded by C3/AC3 ORF can form homo-oligomers and it also heterodimerizes with Rep proteins (Pasumarthy et al. 2010). In addition, REn protein is also known to assist Rep protein in virus replication by interacting with various cell cycle regulators, such as pRBR and PCNA (Settlage et al. 1996; Castillo et al. 2003).

Like other viral proteins, C4/AC4-encoded proteins are shown to suppress host's gene silencing machinery, and these proteins also regulate host's brassinosteroid signalling, CLAVATA pathway and cell cycle regulation (Ismayil et al. 2018; Lai et al. 2009; Li et al. 2018; Mei et al. 2018).

The virion sense strand encoded coat protein (V1/AV1) and pre-coat protein (V2/AV2) are mainly involved in intra- and inter-cellular movements, virus encapsidation and insect transmission (Fondong 2013; Rojas et al. 2001; Ward and Lazarowitz 1999). In addition, pre-coat proteins of *Tomato yellow leaf curl virus* and BCTV possess suppression of TGS and PTGS activity, respectively (Wang et al. 2018; Luna et al. 2017). Also the interplay between host's RDR1 and pre-coat protein of tomato-infecting begomoviruses in symptom remission is demonstrated (Basu et al. 2018).

1.2.2 DNA-B Component

The DNA-A and DNA-B sequences are known to be divergent except a 100–200 nucleotide common region (Brown et al. 2012). This region is an important determinant for the replication of the viral genome by Rep proteins (Hanley-Bowdoin et al. 2013). In 1993, Evans and Jeske demonstrated that DNA-B component of *Abutilon mosaic virus* facilitates the spread of DNA-A component, but DNA-B is not found to be essential.

The DNA-B component encodes two ORFs, one each in virion and complementary strands which assist in virus movement (Hehnle et al. 2004; Lewis and Lazarowitz 2010). The BV1 is a movement protein (MP), which localizes in the plasma membrane, and helps in the intra- and inter-cellular movement of the viral molecules. The BC1, a nuclear shuttle protein (NSP) assists in the nucleo-cytoplasmic transport of viral components (Lazarowitz and Shepherd 1992). Hehnle et al. (2004) studied the interaction of NSP with plasmodesmata to increase the size exclusion limit of plasma membrane for the efficient transport of viral components between the host cells. The MPs are pathogenicity determinants and with NSP, they also play an important role in determining the host range (Pascal et al. 1993; Noueiry et al. 1994). In addition to their role in virus transportation, they also modulate host-mediated antiviral properties either by interfering mRNA decapping activity (by MP) or through translational suppression by NSP-interacting kinase 1 (by NSP) (Ye et al. 2015; Zorzatto et al. 2015).

1.2.3 Betasatellites

The monopartite begomoviruses are widely evolved by associating themselves with the satellite molecules called as betasatellites (Zhou 2013; Kumar and Chakraborty 2018). These satellite molecules are half the size (1.3 kb) of the helper component and encode a single ORF (βC1) in the complementary strand. These betasatellites require helper begomoviruses for their replication, encapsidation, insect transmission and systemic spread (Briddon and Stanley 2006). The selective replication of betasatellite by helper begomovirus-encoded Rep protein involves a novel DNA motif (Zhang et al. 2015). Furthermore, Ranjan et al. (2014) demonstrate the host specific role in the trans-replication or adaptation of betasatellites by distinct tomato-infecting begomoviruses. Several betasatellites have been reported to be pathogenicity determinant and help in symptom induction (Briddon and Stanley 2006; Gnanasekaran et al. 2019; Sivalingam and Varma 2012; Kumar et al. 2015a).

The betasatellite-encoded βC1 proteins have been found to be localized in the nucleus, cytoplasm and/or chloroplast (Cui et al. 2005; Bhattacharyya et al. 2015). In addition, it has been reported to possess both TGS and PTGS silencing suppression activity (Cui et al. 2005; Yang et al. 2011; Zhou 2013). The βC1 proteins are known to bind DNA, interact with SNF1-related kinase and S-adenosyl homocysteine hydrolase, and subvert host ubiquitination machinery to prevent its degradation (Yang et al. 2011; Shen et al. 2011, 2016; Jia et al. 2016).

1.2.4 Alphasatellites

Alphasatellites are circular ssDNA molecules of ~1.4 kb in size which are generally found with monopartite begomovirus-betasatellite complexes in the ‘OW’ (Zhou 2013; Siddiqui et al. 2016; Kumar et al. 2017). However, a few of them are also reported to be with the ‘NW’ begomoviruses (Paprotka et al. 2010; Romay et al. 2010). These alphasatellites can replicate independently in the infected cells, however, it depends on the helper viruses for insect transmission and systemic spread (Saunders and Stanley 1999; Kumar et al. 2017). A group of alphasatellites have been shown to ameliorate disease in the infected host by decreasing the accumulation of betasatellite molecules (Idris et al. 2011). However, *Chilli leaf curl alphasatellite* is found dispensable for symptom induction in the agro-inoculated *Nicotiana benthamiana* plants (Kumar et al. 2017). The capability of *Euphorbia yellow mosaic alphasatellite* in modulating symptoms, viral accumulation and whitefly transmission of the associated helper virus is recently reported (Mar et al. 2017). Also unusual combination of mastrevirus-satellite complexes have been identified from India and Puerto Rico in wheat and dragonflies, respectively (Rosario et al. 2013; Kumar et al. 2014). But the biological significance of these satellites in spreading the disease is not well studied.

1.2.5 Deltasatellites

Novel classes of helper begomovirus dependent satellite molecules called deltasatellites are identified from both ‘OW’ and ‘NW’. These molecules are one-fourth of the size (600–750 nucleotides) of the helper begomoviruses and possess A-rich region (similar to betasatellites), a primary stem-loop sequence containing the nona-nucleotides, TAATATTAC. In addition, they also have a secondary stem-loop structure located between the SCR-like and A-rich regions. Unlike other geminivirus-associated satellites (alphasatellites and betasatellites), deltasatellites does not encode any ORFs, but it depends entirely on the helper geminiviruses. These molecules were identified from the geminivirus-infected plants, such as *Ipomeas* spp., *Malvastrum coromandelianum*, *Merremia dissecta* and *Sidastrum micranthum* (Fiallo-Olive et al. 2012; Lozano et al. 2016). Furthermore, deltasatellites were identified from *Bemisia tabaci* and are known to reduce the helper virus accumulation (Fiallo-olive et al. 2016). The effect of sweepovirus-associated deltasatellites on their helper viruses and its whitefly transmissibility is also ascertained (Hassan et al. 2016).

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