Global Weed-Infecting Geminiviruses

Poonam Roshan, Aditya Kulshreshtha, and Vipin Hallan

Abstract

Weeds are invasive species that grow along with cultivated plants due to their high phenotypic plasticity. They serve as reservoirs of geminiviruses during off-season for main crops and provide the source of virus inoculum during their plantation. Geminiviruses are single-stranded DNA viruses enclosed in icosahedral geminate particles. These viruses can be either monopartite or bipartite, depending upon the number of genomic circles present. The members of genus *Begomovirus* are responsible for huge economic crop losses and are transmitted through insect vector *Bemisia tabaci*. The majority of the weed-infecting monopartite begomoviruses are associated with *Betasatellite* genus of Tolecusatellitidae family and alphasatellites. Geminiviruses are reported to infect a variety of weeds in South-east Asia, Mediterranean region, Western Europe (mainly Spain and France), Africa, Latin America, Central America, Caribbean region, and Australia. Weeds harbor the mixed infection of viruses; therefore, these plants serve as melting pots for recombination and evolution of begomoviruses. This chapter presents the geminivirus infection on weeds, their recombination, and their spread to newer hosts.

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R. V. Kumar (ed.), *Geminiviruses*, https://doi.org/10.1007/978-3-030-18248-9_6

1 Introduction

The plant viruses of *Geminiviridae* family consist of circular single-stranded DNA as genetic material enclosed in icosahedral geminate capsid (Lazarowitz 1992). The family is classified into nine different genera: *Mastrevirus*, *Becurtovirus*, *Begomovirus*, *Capulavirus*, *Curtovirus*, *Eragrovirus*, *Grablovirus*, *Topocuvirus*, and *Turncurtovirus* on the basis of genome organization, insect vector, and host range. The members are transmitted by leafhoppers (*Mastrevirus*, *Becurtovirus*, and *Curtovirus*), treehoppers (*Curtovirus*, *Grablovirus*, and *Topocuvirus*), whitefly (*Begomovirus*), and aphid (*Capulavirus*) (Zerbini et al. 2017). Geminiviruses are able to infect both monocots and dicots; therefore, they are responsible for worldwide crop losses (Moffat 1999). The genome of these viruses can be monopartite or bipartite, based on the number of genomic components (Harrison and Robinson 1999). Monopartite geminiviruses possess single genomic component which encodes the proteins required for replication, encapsulation, movement, transcription, and suppression of gene silencing. Bipartite begomoviruses consist of two genomic components: DNA-A and DNA-B. DNA-A is homologous to DNA-A of monopartite geminiviruses and encodes proteins required for encapsulation, replication, transcription, and suppression of gene silencing. DNA-B encodes only two proteins, essential for intra- and intercellular movement (Hanley-Bowdoin et al. 2000). The viral genome replicates via rolling circle replication (RCR) mechanism that is initiated at stem-loop structure containing nonanucleotide sequence (TAATATT/AC). The *Begomovirus* is the largest genus of *Geminiviridae* family that infects dicots and is transmitted by whitefly (*Bemisia tabaci*) vector (Brown et al. 2015). Begomoviruses are distributed into two groups on the globe: old world (OW) and new world (NW) (Paximadis et al. 1999). The majority of monopartite begomoviruses are associated with members of *Betasatellite* genus and alphasatellite molecules which form disease complex in plants (Kulshreshtha et al. 2017; Sharma et al. 2019a; Zhou 2013).

Weeds are unwanted plants which grow along with cultivated crops and decrease their yield. They are responsible for 43% loss in crop yield and destroy the native habitats (Oerke 2006). Due to high environmental plasticity, weeds are widely distributed and are able to adapt in different ecological habitats (Holm et al. 1979). Weeds serve as reservoir host for the viruses and play important role in their persistence and spread (Hallan et al. 1998). During off-season of crops, they become main host for the virus population. The earliest record of geminivirus symptoms on a weed was described in a Japanese poem written 1265 years ago (Saunders et al. 2003). In this chapter, we described various geminiviruses-infecting weeds, their symptoms, and emergence.

2 Global Status of Weed-Infecting Geminiviruses

Begomovirus infection causes devastating disease and huge crop losses worldwide (Varma and Malathi 2003). The monopartite begomoviruses and some bipartite begomoviruses are present in OW. The majority of bipartite begomoviruses are present in the NW, which suggested their origin from OW begomoviruses (Rybicki 1994). The only exception is tomato leaf deformation virus (ToLDeV), a monopartite begomovirus present in NW (Melgarejo et al. 2013). The agricultural practices, trafficking of infected plant material by humans, and invasive polyphagous vectors are responsible for the global spread and diversification of geminiviruses. The best example is the spread of tomato yellow leaf curl virus (TYLCV) through infected seedlings from Israel to tomato-growing regions of NW during the early 1990s (Duffy and Holmes 2007). Similarly, the introduction of NW cotton to the Indian subcontinent resulted in incidence of leaf curl disease of cotton in Pakistan (Briddon and Markham 2000). The invasive polyphagous whitefly vector also (*Bemisia tabaci*) resulted in the transmission of native begomovirus to the new hosts and emergence of novel viruses. The yellow leaf curl-like symptoms were observed on tomato in the 1940s due to outbreaks of sweetpotato whitefly population and the infection was due to the presence of a geminivirus TYLCV (Cohen and Antignus 1994). Later on, TYLCV infection was reported on weeds such as *Euphorbia* sp., *Lamium amplexicaule*, *Malva parviflora*, and *Ageratum conyzoides* (Papayiannis et al. 2011; Kil et al. 2014). The weed species belonging to family Euphorbiaceae, Asteraceae, Fabaceae, Malvaceae, Solanaceae, Amaranthaceae, and Lamiaceae harbor virus inoculum in NW as well as OW. The weeds growing in South-east Asia are infected with both monopartite–satellite complex and bipartite begomoviruses. Therefore, South-east Asian region can be regarded as diversification center for weed-infecting begomoviruses (Fig. 1). Most of the weed species display chlorosis, yellow mosaic, vein yellowing symptoms, and stunting upon geminivirus infection (Fig. 2).

Ageratum conyzoides is a member of Asteraceae family and native of Central America. It is an annual invasive weed in tropical subtropical regions of the world and reported as natural host for ageratum yellow vein virus (Tan and Wong 1993; Saunders and Stanley 1999; Saunders et al. 2004), ageratum enation virus (Tahir et al. 2015), ageratum leaf curl virus (Huang and Zhou 2006a), chilli leaf curl virus (Iqbal et al. 2016), cotton leaf curl Rajasthan virus (Mubin et al. 2009), and malvastrum yellow vein virus (Jiang and Zhou 2004) in South-east Asia. *A. conyzoides* also serve as reservoir host for TYLCV in Tanzania and Mediterranean region as this weed grows along with tomato plantations (Papayiannis et al. 2011).

Datura stramonium commonly known as devil's snare and jimson weed is a member of Solanaceae family. It is a native of America and is now distributed to tropical and subtropical regions and parts of Europe. A novel begomovirus datura leaf distortion virus was found to infect this weed in Venezuela (Fiallo-Olive et al. 2013). Leaf curl disease of jimson weed was found to be associated with tomato yellow leaf curl China virus (TYLCChV) and a betasatellite (Ding et al. 2007). In France and Spain, this weed was infected with monopartite TYLCV (Bedford et al. 1998).

Croton bonplandianum is an annual weed found in Asia and is infected with croton yellow vein virus, croton yellow vein mosaic virus, and tomato leaf curl New Delhi virus (Hussain et al. 2011; Pramesh et al. 2013; Chowda-Reddy et al. 2005).

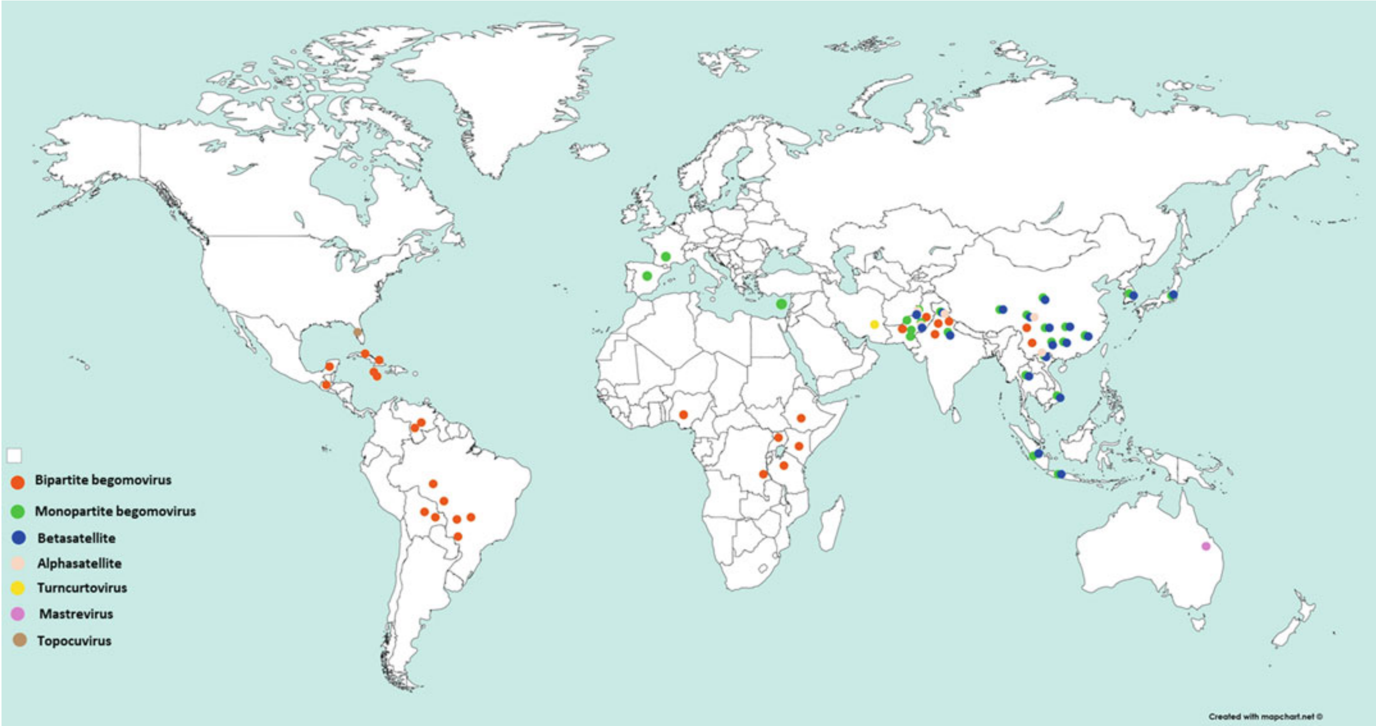

Fig. 1 Global distribution of geminiviruses-infecting weeds in NW and OW. Majority of bipartite begomoviruses are present in NW, whereas monopartite begomoviruses are found along with betasatellites and alphasatellites in South-east Asia

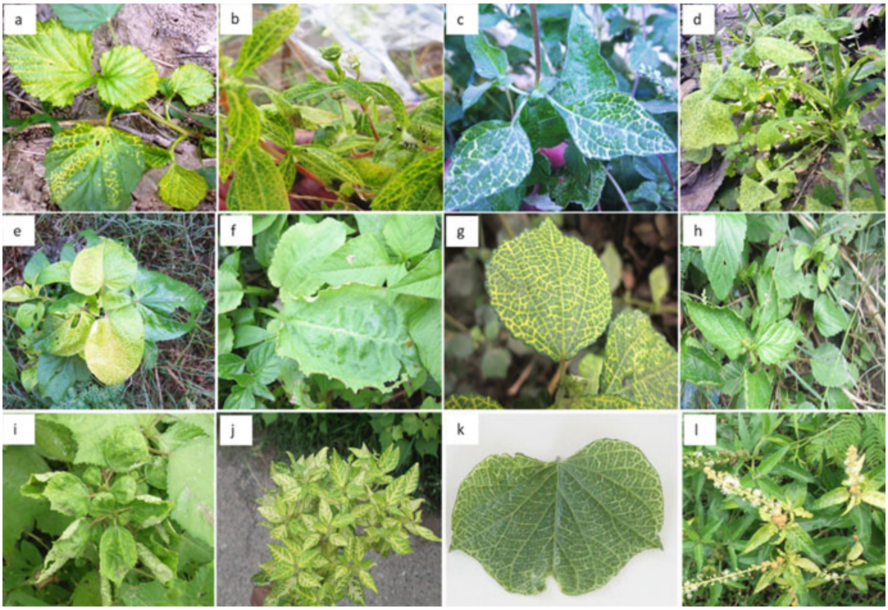

Fig. 2 Typical symptoms of vein yellowing, leaf curling, enation and chlorosis on weeds. (**a–l**) *Malvastrum coromandelianum*, *Eclipta* sp., *Synedrella* sp., *Sonchus asper*, *Ageratum conyzoides*, *Rumex* sp., *Urena lobata*, *Malvastrum* sp., *Urena lobata*, *Croton* sp., *Ipomea* sp. and *Croton* sp.

Malvastrum coromandelianum is an annual weed native to North America and now distributed in Africa, Asia, and South America. It acts as alternative host for monopartite begomoviruses such as malvastrum yellow mosaic virus, malvastrum leaf curl virus, malvastrum leaf curl Guangdong virus, and TYLCChV (Guo et al. 2007; Wu et al. 2007; Liu et al. 2011). In NW, it is reservoir host for sida golden yellow vein virus, sida golden mosaic Florida virus, and malvastrum yellow mosaic Jamaica virus (Fiallo-Olive et al. 2010, 2012; Graham et al. 2010).

Sida sp. is an invasive perennial weed found in tropical and subtropical areas of the world. *S. acuta* has been reported as natural host of sida golden mosaic virus and sida yellow mosaic China virus (Wong et al. 1993; Xiong et al. 2005). *S. micrantha* has been reported as reservoir host of abutilon mosaic virus, abutilon mosaic Bolivia virus, sida mosaic Bolivia virus 1, and sida golden mosaic buckup virus (Wyant et al. 2011; Stewart et al. 2014). In Brazil, *Sida* sp. served as reservoir host for sida micrantha virus and tomato mild mosaic virus which were found to infect tomatoes and beans (Castillo-Urquiza et al. 2010). The detailed information of geminivirus members infecting various weeds is given in Table 1.

Table 1 Geminivirus members and associated betasatellites infecting weeds

Name of the virus and genus	Geographical distribution	Weed host	Associated betasatellite	Associated satellite molecule/s	Symptom produced	References
Abutilon mosaic virus Bipartite begomovirus	Bolivia India	*Sida micrantha*, *Abutilon pictum*	–	–	Mosaic, bright yellow mosaic	Wyant et al. (2011) and Jyothsna et al. (2013)
Abutilon mosaic Bolivia virus Bipartite begomovirus	Bolivia	*S. micrantha*, *Abutilon* sp.	–	–	Yellow mosaic	Wyant et al. (2011)
African cassava mosaic virus Bipartite begomovirus	Nigeria	*Combretum confertum*	–	–	Chlorotic mosaic	Alabi et al. (2008)
Ageratum enation virus Monopartite begomovirus	India Pakistan	*Ageratum conyzoides*, *Cleome gynandra*, *Crassocephalum crepidioides*, *Sonchus oleraceus*	Ageratum yellow leaf curl betasatellite	Nanovirus-like DNA1	Vein enation, yellowing, stunting	Raj et al. (2010), Kumar et al. (2011) and Tahir et al. (2015)
Ageratum yellow vein virus Monopartite begomovirus	China Singapore	*A. conyzoides*	Ageratum yellow leaf curl betasatellite	Nanovirus-like DNA1	Vein yellowing, stunting	Tan and Wong (1993), Saunders and Stanley (1999) and Saunders et al. (2004)
Alternanthera yellow vein virus Monopartite begomovirus	China	*Alternanthera philoxeroides*, *Eclipta prostrata*	–	–	Yellow vein	Guo and Zhou (2005) and He et al. (2008)
Blainvillea yellow spot virus Bipartite begomovirus	Brazil	*Blainvillea rhomboidea*	–	–	Mosaic, yellowing and stunting	Castillo-Urquiza et al. (2008)

Blechum yellow vein virus Monopartite begomovirus	Philippines	*Blechum pyramidatum*	–	–	Yellow/ chlorotic leaf veins	Tsai et al. (2014)
Chilli leaf curl virus Monopartite begomovirus	Pakistan	*Urtica dioica*	Ageratum yellow leaf curl betasatellite	Ageratum yellow vein Pakistan alphasatellite, Bhendi yellow vein alphasatellite	Leaf curling, vein-yellowing	Iqbal et al. (2016)
Cotton leaf curl Rajasthan virus Monopartite begomovirus	Pakistan	*Digera arvensis*	Ageratum yellow leaf curl betasatellite, Tobacco leaf curl betasatellite	–	Yellow vein disease	Mubin et al. (2009)
Cotton leaf curl Burewala virus Monopartite begomovirus	Pakistan	*Xanthium strumarium*	Tomato yellow leaf curl Thailand betasatellite	Potato leaf curl alphasatellite	Leaf curling, vein thickening	Mubin et al. (2012)
Crassocephalum yellow vein virus Monopartite begomovirus	China	*C. crepidioides*	–	–	Vein yellowing	Dong et al. (2008)
Croton yellow vein mosaic virus Bipartite begomovirus	India	*A. conyzoides*, *Croton bonplandianum*, *Euphorbia geniculate*, *S. brachyotis*	–	–	Bright yellow vein, leaf curl	Pramesh et al. (2013)
Dalechampia chlorotic mosaic virus Bipartite begomovirus	Venezuela	*Boerhavia diffusa*, *Dalechampia* sp.	–	–	Vein yellowing	Fiallo-Olive et al. (2013)

(continued)

Table 1 (continued)

Name of the virus and genus	Geographical distribution	Weed host	Associated betasatellite	Associated satellite molecule/s	Symptom produced	References
Datura leaf distortion virus Bipartite begomovirus	Venezuela	*Datura stramonium*	–	–	Vein yellowing	Fiallo-Olive et al. (2013)
Deinbollia mosaic virus Bipartite begomovirus	East Africa	*Deinbollia borbonica*	–	–	Yellow mosaic	Kyallo et al. (2017)
Dicliptera yellow mottle virus Bipartite begomovirus	Cuba	*Dicliptera vahliana*	–	–	Yellow mottling	Echemendía et al. (2003)
East African cassava mosaic Cameroon virus Bipartite begomovirus	Nigeria	*C. confertum*		–	Chlorotic mosaic	Alabi et al. (2008)
Emilia yellow vein virus Bipartite begomovirus	China	*C. crepidioides*	–	–	Yellow vein	Yang et al. (2012)
Erectites yellow mosaic virus Monopartite begomovirus	Vietnam	*Erectites valerianifolia*	Erectites yellow mosaic betasatellite	–	Vein yellowing, leaf curling, chlorosis	Ha et al. (2008)

Euphorbia mosaic virus Bipartite begomovirus	Yucatan Peninsula	*Euphorbia heterophylla*	–	–	Golden mosaic	Hernandez-Zepeda et al. (2007)
Euphorbia yellow mosaic virus Bipartite begomovirus	Brazil	*E. heterophylla*	–	–	Bright yellow mosaic	Fernandes et al. (2011)
Honeysuckle yellow vein virus	Japan	*Lonicera japonica*			Vein yellowing	Ogawa et al. (2008)
Lindernia anagallis yellow vein virus Monopartite begomovirus	Vietnam	*Lindernia procumbens*	Lindernia anagallis yellow vein betasatellite	–	Vein yellowing and leaf curling	Ha et al. (2008)
Ludwigia yellow vein virus Monopartite begomovirus	China	*Ludwigia hyssopifolia*	Ludwigia yellow vein betasatellite	–	Vein yellowing	Huang et al. (2006)
Macroptilium yellow spot virus Bipartite begomovirus	Brazil	*Macroptilium lathyroides*	–	–	Mosaic, yellowing and stunting	Da Silva et al. (2011)
Malvastrum leaf curl virus Monopartite begomovirus	China	*Malvastrum coromandelianum*	Sida yellow vein China betasatellite	–	Leaf curling, vein thickening	Huang and Zhou (2006a, b)
Malvastrum yellow vein virus Monopartite begomovirus	China	*A. conyzoides*	Malvastrum yellow vein betasatellite	–	Yellow vein	Jiang and Zhou (2004)

(continued)

Table 1 (continued)

Name of the virus and genus	Geographical distribution	Weed host	Associated betasatellite	Associated satellite molecule/s	Symptom produced	References
Merremia mosaic virus Bipartite begomovirus	Belize	*E. heterophylla*, hot pepper, sweet pepper	–	–	Leaf curling, yellowing, mottling, mosaic	McLaughlin et al. (2008)
Papaya leaf curl China virus Monopartite begomovirus	China	*Corchoropsis timentosa*	–	–	Leaf curling	Huang and Zhou (2006a, b)
Rhynchosia yellow mosaic virus Bipartite begomovirus	Pakistan	*Rhynchosia minima*	–	–	Yellow mosaic	Ilyas et al. (2009)
Rhynchosia yellow mosaic India virus Bipartite begomovirus	India	*R. minima*	–	–	Yellow mosaic	Jyothsna et al. (2011)
Sida golden mosaic Buckup virus Bipartite begomovirus	Jamaica	*Sida* sp.	–	–	Yellow mosaic	Stewart et al. (2014)
Sida leaf curl virus Monopartite begomovirus	China	*S. cordifolia*	Ageratum leaf curl betasatellite	Sida leaf curl virus DNA1	Mild upward leaf curling	Guo and Zhou (2006)

Sida yellow mosaic China virus Monopartite begomovirus	China	*S. acuta*	Ageratum yellow vein betasatellite	–	Yellow mosaic	Xiong et al. (2005)
Sida mosaic Bolivia virus 1 Bipartite begomovirus	Bolivia	*S. micrantha*	–	–	Bright yellow mosaic	Wyant et al. (2011)
Tobacco leaf curl Cuba virus Bipartite begomovirus	Jamaica	*Malachra alceifolia*	–	–	Yellow mosaic	Hall et al. (2008)
Tomato leaf curl virus Monopartite begomovirus	India	*Parthenium hysterophorus*	Papaya leaf curl betasatellite	Ageratum yellow vein alphasatellite	Leaf curl, stunting	Kumar et al. (2016)
Tomato leaf curl New Delhi virus Bipartite begomovirus	Pakistan	*Eclipta prostrata*, *Calotropis procera*	–	–	Yellow vein, yellow mosaic	Haider et al. (2005) and Zaidi et al. (2017)
Tomato yellow leaf curl virus Monopartite begomovirus	Spain, France, Cyprus, Korea	*Euphorbia* sp., *Solanum nigrum*, *Datura stramonium*, *Malva* sp., *Lamium amplexicaule*	–	–	Leaf yellowing and curling	Bedford et al. (1998), Dalmon and Marchoux (2000), Papayiannis et al. (2011) and Kil et al. (2014)
Tobacco yellow dwarf virus Mastrevirus	Australia	*Rapistrum rugosum*	–	–	Necrosis and dwarfing	Schwinghamer et al. (2010)
Tomato pseudo curly top virus Topocuvirus	Florida	*Solanum nigrum*, *Datura stromonium*, *Stellaria media*	–	–	Leaf cupping and chlorosis	Tsai and Brown (1991)

(continued)

Table 1 (continued)

Name of the virus and genus	Geographical distribution	Weed host	Associated betasatellite	Associated satellite molecule/s	Symptom produced	References
Turnip curly top virus Turncurtovirus	Iran	*Solanum nigrum*, *Anchusa arvensis*	–	–	Inward rolling of the leaf margins	Razavinejad et al. (2013)
Wissadula golden mosaic virus Bipartite begomovirus	Jamaica	*Wissadula amplissima*	–	–	Leaf curling. Yellow mosaic	Collins and Roye (2006)

3 Weeds as Mixing Vessels for Recombination and Assortment of Viruses

Recombination, mutation, and pseudo-recombination between variants, species, and genera of the virus significantly contribute to genetic diversity, local adaptation, and emergence of new viruses (Pita et al. 2001; Martin et al. 2005; Graham et al. 2010). It has been demonstrated that recombination in geminiviruses is dependent on parental virus strain, host plant, and inoculum (Padidam et al. 1999). Weeds harbor mixed infections of geminiviruses which result in the evolution and emergence of new virus species or strains. The mixed infections result in the association of betasatellites with helper begomoviruses which led to emergence of more virulent strains or species. These satellite molecules are known to enhance the symptom severity and disease epidemics in new environments (Sharma et al. 2019b; Saunders et al. 2001; Briddon et al. 2004). The evolution of sida micrantha mosaic-associated viruses and alternanthera yellow vein virus is a result of recombination in the weed hosts (Jovel et al. 2007; Mubin et al. 2010). The recombinants of begomoviruses associated with cassava mosaic disease in Africa showed increased virulence in comparison to parental strains (Zhou et al. 1997). In Brazil, multiple recombination events among cleome leaf crumple virus isolates were reported in a single weed *Cleome affinis* (Da Silva et al. 2011). Furthermore, sida mottle virus and sida micrantha mosaic virus were originally characterized from weed species that were transmitted to crops by insect vector (Castillo-Urquiza et al. 2007, 2010). Weeds belonging to Euphorbiaceae and Fabaceae family are reported as reservoir host for cassava-infecting begomoviruses in Africa (Alabi et al. 2008). Therefore, weeds are designated as “mixing vessels” for genetic recombination between begomoviruses. Ageratum enation virus is a monopartite begomovirus associated with betasatellite and alphasatellite, is widely distributed in South-east Asia, and infects non-cultivated plants such as *Sonchus oleraceus* and *A. conyzoides* (Tahir et al. 2015). Two weeds *Chrozophora hierosolymitana* and *Herniaria* sp. were reported to harbor the TYLCV inoculums in Iran (Fazeli et al. 2009).

4 Relationship Between Weed, Virus Disease Complex, and Insect Vector

Weeds act as alternate host for both virus and insect vector during off-season of the main crops. As a result, these plants prevent the extinction of virus populations in the absence of annual crops (Seal et al. 2006). In such conditions, a dramatic increase in the whitefly-transmitted geminiviruses (WTG) population has been reported. The virus-infected plants have a greater tendency to attract the insect vector in comparison to healthy plants. Furthermore, virus infection alters the morphology and defense system which increases the infestation and fitness of the insect vector (Awmack and Leather 2002; Chen et al. 2013). The invasive polyphagous B-biotype *B. tabaci* is found to be responsible for the TYLCV disease epidemic in the Mediterranean region. The invasive whitefly species is reported to transmit about 200 species of the begomoviruses in both cultivated and non-cultivated plants (Delatte et al. 2005; Hogenhout et al. 2008). The mobile and polyphagous nature of this insect allows the dissemination of viral diversity into new crops (Lefeuvre et al. 2007). The association of betasatellites and alphasatellite with helper begomovirus offers a selective advantage for helper begomovirus to produce symptoms on the weed. The yellow vein disease of *A. conyzoides* was due to infection of ageratum yellow vein virus and a betasatellite. In the absence of betasatellite, the weed failed to develop the typical symptoms (Saunders et al. 2001). Similarly, the yellow vein disease of *C. bonplandianum* was associated with infection of a monopartite begomovirus and a betasatellite (Hussain et al. 2011). In case of tomato leaf curl virus infection on *Parthenium hysterophorus*, the betasatellite and alphasatellite complex developed typical leaf curling symptoms (Kumar et al. 2016). The begomovirus disease complex including multiple and recombinant betasatellites was reported from a common weed, *Digera arvensis*, in Pakistan (Mubin et al. 2009). The widespread distribution of weeds and polyphagous invasive whitefly vector in the warmer regions provides favorable platform for virus proliferation. The whitefly population prefers high temperature for reproduction, but is adversely affected by prolonged winters. Under such circumstances, weed species serve as reservoir inoculums for viral diversity and global warming in temperate areas offers great advantage for the virus spread.

5 Conclusion

The increasing incidence of geminivirus infection on economic important crops has become a major concern, and it has been found that weeds or non-cultivated hosts serve as source of virus infection. The presence of mixed infection renders the weeds as melting pots for begomovirus recombination and led to emergence of more fit variants of the virus. Additionally, the increasing population insect vector contributed to the spread of begomoviruses in new hosts. Therefore, reservoir host, insect vector, and virus constitute a cycle which seems to be the main reason for the outbreak and emergence of begomovirus disease complex in newer hosts. However, it is unclear whether weeds act as indigenous host of viruses or they get infected from the infected crop host? To address this question, further studies are required to demonstrate the role of weeds in primary source of virus inoculum and evolution of novel viruses. The outcome of such studies will reveal a potential way to combat the geminivirus infection in cultivated crops.

Acknowledgements Authors acknowledge Director CSIR-IHBT for providing the research facilities. PR is thankful to Council of Scientific and Innovative Research for providing Junior and Senior Research Fellowship. AK thanks the University Grants Commission (UGC) for providing Junior and Senior Research Fellowship. PR and AK duly acknowledge Academy of Scientific and Innovative Research (AcSIR), New Delhi, India.

References

Alabi OJ, Ogbe FO, Bandyopadhyay R, Kumar PL et al (2008) Alternate hosts of African cassava mosaic virus and East African cassava mosaic Cameroon virus in Nigeria. Arch Virol 153:1743

Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. Annu Rev Entomol 47:817–844

Bedford I, Kelly A, Banks G, Briddon RW et al (1998) Solanum nigrum: an indigenous weed reservoir for a tomato yellow leaf curl geminivirus in southern Spain. Eur J Plant Pathol 104:221

Briddon RW, Markham PG (2000) Cotton leaf curl virus disease. Virus Res 71:151–159

Briddon RW, Bull SE, Amin I, Mansoor S et al (2004) Diversity of DNA 1: a satellite-like molecule associated with monopartite begomovirus-DNA b complexes. Virology 324:462–474

Brown JK, Zerbini FM, Navas-Castillo J, Moriones E et al (2015) Revision of begomovirus taxonomy based on pairwise sequence comparisons. Arch Virol 160:1593

Castillo-Urquiza GP, Beserra Junior JEA, Alfenas-Zerbini P et al (2007) Genetic diversity of begomoviruses infecting tomato in Paty do Alferes, Rio de Janeiro state, Brazil. Virus Rev Res 12:233

Castillo-Urquiza GP, Beserra JE, Bruckner FP, Lima GSA et al (2008) Six novel begomoviruses infecting tomato and associated weeds in Southeastern Brazil. Arch Virol 153(10):1985–1989

Castillo-Urquiza GP et al (2010) Genetic structure of tomato-infecting begomovirus populations in two tomato growing regions of Southeastern Brazil. In: International geminivirus symposium, 6.; international ssDNA comparative virology workshop, 4., 2010, Guanajuato, Mexico. Program and Abstracts in CD-ROM. Guanajuato, Mexico

Chen G, Pan H, Xie W, Wang S et al (2013) Virus infection of a weed increases vector attraction to and vector fitness on the weed. Sci Rep 3:2253

Chowda-Reddy R, Colvin J, Muniyappa V, Seal S (2005) Diversity and distribution of begomoviruses infecting tomato in India. Arch Virol 150:845

Cohen S, Antignus Y (1994) Tomato yellow leaf curl virus (TYLCV), a whitefly-borne geminivirus of tomatoes. Adv Dis Vector Res 10:259–288. New York: Springer-Verlag

Collins AM, Roye ME (2006) Two new bipartite begomoviruses infecting Wissadula amplissima in Jamaica. New Dis Rep 13:31

Da Silva SJC, Castillo-Urquiza GP, Hora Júnior BT, Assunçao IP et al (2011) High genetic variability and recombination in a begomovirus population infecting the ubiquitous weed Cleome affinis in northeastern Brazil. Arch Virol 156:2205

Dalmon A, Marchoux G (2000) Quelles plantes hotes pour le tomato yellow leaf curl virus? Phytoma 527:14–17

Delatte H, Martin DP, Naze F, Golbach RW et al (2005) South West Indian Ocean islands tomato begomovirus populations represent a new major monopartite begomovirus group. J Gen Virol 86:1533–1542

Ding M, Luo YQ, Dong JH et al (2007) First report of tomato yellow leaf curl China virus with DNA β infecting Datura stramonium in China. Aust Plant Dis Notes 2:63

Dong JH, Zhang ZK, Ding M, Fang Q et al (2008) Molecular characterization of a distinct begomovirus infecting Crassocephalum crepidioides in China. J Phytopathol 156:193–195

Duffy S, Holmes EC (2007) Multiple introductions of the Old World begomovirus tomato yellow leaf curl virus into the New World. Appl Environ Microbiol 73:7114–7117

Echemendía AL, Ramos PL, Peral R, Fuentes A et al (2003) First report of Dicliptera yellow mottle virus (DiYMoV) infecting Dicliptera vahliana in Cuba. Plant Pathol 52:787

Fazeli R, Heydarnejad J, Massumi H, Shaabanian M et al (2009) Genetic diversity and distribution of tomato-infecting begomoviruses in Iran. Virus Genes 38:311–319

Fernandes FR, Albuquerque LC, de Oliveira CL, Cruz AR et al (2011) Molecular and biological characterization of a new Brazilian begomovirus, euphorbia yellow mosaic virus (EuYMV), infecting Euphorbia heterophylla plants. Arch Virol 156(11):2063–2069

Fiallo-Olive E, Martinez-Zubiaur Y, Moriones E, Navas-Castillo J (2010) Complete nucleotide sequence of Sida golden mosaic Florida virus and phylogenetic relationships with other begomoviruses infecting malvaceous weeds in the Caribbean. Arch Virol 155(9):1535–1537

Fiallo-Olive E, Navas-Castillo J, Moriones E, Martínez-Zubiaur Y (2012) Begomoviruses infecting weeds in Cuba: increased host range and a novel virus infecting Sida rhombifolia. Arch Virol 157(1):141–146

Fiallo-Olive E, Chirinos DT, Geraud-Pouey F, Moriones E et al (2013) Complete genome sequences of two begomoviruses infecting weeds in Venezuela. Arch Virol 158:277

Graham AP, Martin DP, Roye ME (2010) Molecular characterization and phylogeny of two begomoviruses infecting Malvastrum americanum in Jamaica: evidence of the contribution of inter-species recombination to the evolution of malvaceous weed-associated begomoviruses from the northern Caribbean. Virus Genes 40(2):256–266

Guo X, Zhou X (2005) Molecular characterization of alternanthera yellow vein virus: a new begomovirus species infecting Alternanthera philoxeroides. J Phytopathol 153:694–696

Guo X, Zhou X (2006) Molecular characterization of a new begomovirus infecting Sida cordifolia and its associated satellite DNA molecules. Virus Genes 33(3):279–285

Guo X, Shi M, Zhou X (2007) Complete nucleotide sequences of Malvastrum yellow mosaic virus and its associated DNAβ molecule. Arch Virol 152(3):641–643

Ha C, Coombs S, Revill P, Harding R et al (2008) Molecular characterization of begomoviruses and DNA satellites from Vietnam: additional evidence that the New World geminiviruses were present in the Old World prior to continental separation. J Gen Virol 89:312–326

Haider MS, Tahir M, Latif S, Briddon RW (2005) First report of tomato leaf curl New Delhi virus infecting Eclipta prostrata in Pakistan. New Dis Rep 11:39

Hall GC, Graham AP, Roye ME (2008) Tobacco leaf curl Cuba virus infects the weed Malachra alceifolia in Jamaica. Plant Pathol 57:398

Hallan V, Saxena S, Singh B (1998) Ageratum, Croton and Malvastrum harbour geminiviruses: evidence through PCR amplification. World J Microbiol Biotechnol 14:931

Hanley-Bowdoin L, Settlage SB, Orozco BM, Nagar S, Robertson D (2000) Geminiviruses: models for plant DNA replication, transcription, and cell cycle regulation. Crit Rev Biochem Mol Biol 35:105–140

Harrison B, Robinson D (1999) Natural genomic and antigenic variation in whitefly-transmitted geminiviruses (begomoviruses). Annu Rev Phytopathol 37:369–398

He ZF, Mao MJ, Yu H, Wang XM et al (2008) First report of a strain of alternanthera yellow vein virus infecting Eclipta prostrate (L.) L. (Compositae) in China. J Phytopathol 156:496–498

Hernandez-Zepeda C, Idris AM, Carnevali G, Brow JK et al (2007) Molecular characterization and experimental host range of Euphorbia mosaic virus-Yucatan Peninsula, a begomovirus species in the Squash leaf curl virus clade. Plant Pathol 56:763–770

Hogenhout SA, Ammar ED, Whitfield AE, Redinbaugh MG (2008) Insect vector interactions with persistently transmitted viruses. Annu Rev Phytopathol 46:327–359

Holm L, Pancho JV, Herberger JP, Plucknett DL (1979) A geographical atlas of world weeds. Wiley, New York, NY

Huang JF, Zhou XP (2006a) Molecular characterization of two distinct begomoviruses from Ageratum conyzoides and Malvastrum coromandelianum in China. J Phytopathol 154:648–653

Huang JF, Zhou XP (2006b) First report of papaya leaf curl China virus infecting Corchoropsis timentosa in China. Plant Pathol 55:291

Huang JF, Jiang T, Zhou XP (2006) Molecular characterization of begomoviruses infecting Ludwigia hyssopifolia. J Phytopathol 88(1):83–88

Hussain K, Hussain M, Mansoor S, Briddon RW (2011) Complete nucleotide sequence of a begomovirus and associated betasatellite infecting croton (Croton bonplandianus) in Pakistan. Arch Virol 156:1101

Ilyas M, Qazi J, Mansoor S, Briddon RW (2009) Molecular characterisation and infectivity of a "Legumovirus" (genus Begomovirus: family Geminiviridae) infecting the leguminous weed Rhynchosia minima in Pakistan. Virus Res 145(2):279–284

Iqbal MJ, Hussain W, Zia-Ur-Rehman M, Hameed U et al (2016) First report of chilli leaf curl virus and associated alpha- and beta-satellite DNAs infecting nettle weed (Urtica dioica) in Pakistan. Plant Dis 100(4):870

Jiang T, Zhou XP (2004) First report of Malvastrum yellow vein virus infecting Ageratum conyzoides. Plant Pathol 53:799

Jovel J, Preiss W, Jeske H (2007) Characterization of DNA intermediates of an arising geminivirus. Virus Res 130:63–70

Jyothsna P, Rawat R, Malathi VG (2011) Molecular characterization of a new begomovirus infecting a leguminous weed Rhynchosia minima in India. Virus Genes 42(3):407–414

Jyothsna P, Haq QMI, Jayaprakash P, Malathi VG (2013) Molecular evidence for the occurrence of abutilon mosaic virus, a New World begomovirus in India. Indian J Virol 24(2):284–288

Kil EJ, Park J, Lee H, Kim J et al (2014) Lamium amplexicaule (Lamiaceae): a weed reservoir for tomato yellow leaf curl virus (TYLCV) in Korea. Arch Virol 159(6):1305–1311

Kulshreshtha A, Roshan P, Sharma D, Hallan V (2017) Molecular characterization of a new begomovirus infecting *Mirabilis jalapa* in northern India. Arch Virol 162(7):2163–2167

Kumar Y, Hallan V, Zaidi AA (2011) First report of ageratum enation virus infecting Crassocephalum crepidioides (Benth.) S. Moore and Ageratum conyzoides L. in India. J Gen Plant Pathol 77:214–216

Kumar S, Srivastava A, Jaidi A, Chauhan PS et al (2016) Molecular characterization of a begomovirus, α-satellite, and β-satellite associated with leaf curl disease of Parthenium hysterophorus in India. Plant Dis 100(11):2299–2305

Kyallo M, Ateka EM, Sseruwagi P, Ascencio-Ibanez JT et al (2017) Infectivity of Deinbollia mosaic virus, a novel weed-infecting begomovirus in East Africa. Arch Virol 162:3439–3445

Lazarowitz SG (1992) Geminiviruses: genome structure and gene function. Crit Rev Plant Sci 11:327–349

Lefeuvre P, Martin DP, Hoareau M, Naze F et al (2007) Begomovirus 'melting pot' in the south-west Indian Ocean islands: molecular diversity and evolution through recombination. J Gen Virol 88:3458–3468

Liu P, Xie Y, Zhou X (2011) Malvastrum coromandelianum is an alternative host of tomato yellow leaf curl China virus. New Dis Rep 17:30

Martin DP, van der Walt E, Posada D, Rybicki EP (2005) The evolutionary value of recombination is constrained by genome modularity. PLoS Genet 1(4):e51

McLaughlin PD, McLaughlin WA, Maxwell DP, Roye ME (2008) Identification of begomoviruses infecting crops and weeds in Belize. Plant Viruses 2(1):58–63

Melgarejo TA, Kon T, Rojas MR, Paz-Carrasco L et al (2013) Characterization of a New World monopartite begomovirus causing leaf curl disease of tomato in Ecuador and Peru reveals a new direction in geminivirus evolution. J Virol 87(10):5397–5413

Moffat AS (1999) Geminiviruses emerge as serious crop threat. Science 286:1835

Mubin M, Briddon RW, Mansoor S (2009) Diverse and recombinant DNA betasatellites are associated with a begomovirus disease complex of Digera arvensis, a weed host. Virus Res 142:208–212

Mubin M, Shahid MS, Tahir MN, Briddon RW et al (2010) Characterization of begomovirus components from a weed suggests that begomoviruses may associate with multiple distinct DNA satellites. Virus Genes 40(3):452–457

Mubin M, Akhtar S, Amin I et al (2012) Xanthium strumarium: a weed host of components of begomovirus–betasatellite complexes affecting crops. Virus Genes 44:112

Oerke EC (2006) Crop losses to pests. J Agric Sci 144(1):31–43

Ogawa T, Sharma P, Ikegami M et al (2008) First report of a strain of tobacco leaf curl Japan virus associated with a satellite DNA in honeysuckle in Japan. Plant Pathol 57:391

Padidam M, Sawyer S, Fauquet CM (1999) Possible emergence of new geminiviruses by frequent recombination. Virology 265:218–225

Papayiannis LC, Katis NI, Idris AM, Brown JK (2011) Identification of weed hosts of tomato yellow leaf curl virus in Cyprus. Plant Dis 95(2):120–125

Paximadis M, Idris AM, Torres-Jerez I, Villarreal A, Rey MEC, Brown JK (1999) Characterization of tobacco geminiviruses in the Old and New World. Arch Virol 144:703–717
Pita JS, Fondong VN, Sangare A, Otim-Nape GW, Ogwal S, Fauquet CM (2001) Recombination, pseudorecombination and synergism of geminiviruses are determinant keys to the epidemic of severe cassava mosaic disease in Uganda. J Gen Virol 82:655–665
Pramesh D, Mandal B, Phaneendra C et al (2013) Host range and genetic diversity of croton yellow vein mosaic virus, a weed-infecting monopartite begomovirus causing leaf curl disease in tomato. Arch Virol 158:531
Raj SK, Snehi SK, Khan MS, Tiwari AK et al (2010) Detection of ageratum enation virus from cat's whiskers (Cleome gynandra L.) with leaf curl symptoms in India. J Gen Plant Pathol 76:292–294
Razavinejad S, Heydarnejad J, Kamali M, Massumi H et al (2013) Genetic diversity and host range studies of turnip curly top virus. Virus Genes 46(2):345–353
Rybicki EP (1994) A phylogenetic and evolutionary justification for 3 genera of Geminiviridae. Arch Virol 139:49–77
Saunders K, Stanley J (1999) A nanovirus-like DNA component associated with yellow vein disease of Ageratum conyzoides: evidence for interfamilial recombination between plant DNA viruses. Virology 264(1):142–152
Saunders K, Bedford ID, Stanley J (2001) Pathogenicity of a natural recombinant associated with ageratum yellow vein disease: implications for geminivirus evolution and disease aetiology. Virology 282:38–47
Saunders K, Bedford ID, Yahara T, Stanley J (2003) Aetiology: the earliest recorded plant virus disease. Nature 422:831
Saunders K, Norman A, Gucciardo S, Stanley J (2004) The DNA β satellite component associated with ageratum yellow vein disease encodes an essential pathogenicity protein (βC1). Virology 324(1):37–47
Schwinghamer MW, Thomas JE, Schilg MA, Parry JN et al (2010) Mastreviruses in chickpea (Cicer arietinum) and other dicotyledonous crops and weeds in Queensland and northern New South Wales, Australia. Australas Plant Pathol 39(6):551–561
Seal SE, Van den Bosch F, Jeger MJ (2006) Factors influencing begomovirus evolution and their increasing global significance: implications for sustainable control. Crit Rev Plant Sci 25:23–46
Sharma D, Kulshreshtha A, Kumar R, Hallan V (2019a) First report of natural infection of alternanthera yellow vein virus and cotton leaf curl Multan betasatellite on a new host *Picrorhiza kurroa*, an important endangered medicinal herb. J Plant Pathol 101(1):149–153
Sharma D, Kulshreshtha A, Roshan P, Hallan V (2019b) Molecular characterization and infectivity analysis of a bipartite begomovirus associated with cotton leaf curl Multan betasatellite naturally infecting Rumex nepalensis in northern India. J Plant Pathol: 1–7
Stewart C, Kon T, Rojas M, Graham A et al (2014) The molecular characterisation of a Sida-infecting begomovirus from Jamaica. Arch Virol 159(2):375–378
Tahir M, Amin I, Haider MS, Mansoor S et al (2015) Ageratum enation virus—a begomovirus of weeds with the potential to infect crops. Viruses 7(2):647–665
Tan HNP, Wong SM (1993) Some properties of Singapore ageratum yellow vein virus (SAYVV). J Phytopathol 139:165–176
Tsai JH, Brown LG (1991) Pseudo-curly top of tomato. Plant Pathol 344:190–191
Tsai WS, Shih SL, Lee LM (2014) First report of a novel begomovirus associated with yellow vein disease of Browne's blechum (Blechum pyramidatum). Plant Dis 98(5):701
Varma A, Malathi VG (2003) Emerging geminivirus problems: a serious threat to crop production. Ann Appl Biol 142(2):145–164
Wong SM, Swanson MM, Harrison BD (1993) A new geminivirus causing vein yellowing of Ageratum conyzoides in Singapore. Plant Pathol 42:137–139
Wu J, Mugiira R, Zhou X (2007) Malvastrum leaf curl Guangdong virus is a distinct monopartite begomovirus. Plant Pathol 56:771–776

Wyant PS, Gotthardt D, Schafer B, Krenz B et al (2011) The genomes of four novel begomoviruses and a new Sida micrantha mosaic virus strain from Bolivian weeds. Arch Virol 156:347

Xiong Q, Guo XJ, Che HY, Zhou XP (2005) Molecular characterization of a distinct begomovirus and its associated Satellite DNA Molecule infecting Sida acuta in China. J Phytopathol 153:264–268

Yang CX, Luo JS, Zheng LM, Wu ZJ et al (2012) First report of the occurrence of Emilia yellow vein virus in Crassocephalum crepidioides in China. J Plant Pathol 94(4):87

Zaidi SS, Shakir S, Malik HJ, Farooq M et al (2017) First report of tomato leaf curl New Delhi virus on Calotropis procera, a weed as potential reservoir begomovirus host in Pakistan. Plant Dis 101 (6):1071

Zerbini FM, Briddon RW, Idris A, Martin DP et al (2017) ICTV virus taxonomy profile: Geminiviridae. J Gen Virol 98:131–133

Zhou X (2013) Advances in understanding begomovirus satellites. Annu Rev Phytopathol 51:387–381

Zhou X, Liu Y, Calvert L, Munoz C et al (1997) Evidence that DNA-A of a geminivirus associated with severe cassava mosaic disease in Uganda has arisen by interspecific recombination. J Gen Virol 78:2101–2111