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Review Article

Status of geminiviruses in Iran, incredible plant pathogens

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ABSTRACT- The family *Geminiviridae* with fourteen accepted genera and an increasing number of unassigned species is currently identified as the largest family of plant-infecting viruses. Their twinned icosahedral particles contain single-stranded genomic DNAs that are naturally transmitted by Hemiptera insects including whitefly (*Bemisia tabaci*), several species of leafhoppers, treehoppers and one species of aphid in a wide range of host plants. Also, some geminiviruses are transmitted by seeds in certain hosts. In addition to climate changes, industrial cultivations, and the development of global trade, the genetic flexibility of geminiviruses has led to an increase in the rate of their distribution. Diseases caused by geminiviruses constitute a serious constraint to tropical and sub-tropical agroecosystems worldwide. The economic losses caused by geminivirus infections have grown especially in open fields and greenhouses in Iran during the last years. Defining two distinct genera by having unique molecular and biological characteristics, *Becurtovirus* and *Turncurtovirus*, and the presence of different species and strains of other geminiviruses introduces Iran as a putative origin of diversification for old-world monopartite geminiviruses. This review presents the occurrence and diversity of the members of *Geminiviridae* in Iran. Moreover, some applicable control measures have been proposed based on compatibility with the Iran agroecosystem which would also be recommended for other tropical and subtropical regions of the world.

INTRODUCTION

Geminiviruses are a group of small, non-enveloped plant viruses with genomes containing one or two circular single-stranded DNA(s) (ssDNA), 2.5–5.2 kb in size. At present, the family *Geminiviridae* comprises 14 accepted genera including *Becurtovirus*, *Begomovirus*, *Capulavirus*, *Citlodavirus*, *Curtovirus*, *Eragrovirus*, *Grablovirus*, *Maldovirus*, *Mastrevirus*, *Mulcrilevirus*, *Opunvirus*, *Topilevirus*, *Turncurtovirus* and *Topocuvirus*, with an increasing number of unassigned species which has been making it the most enormous plant virus family (Roumagnac et al., 2022). Infections of crops, fruit trees, ornamental and fiber plants by geminiviruses have resulted in considerable losses in production, which had a significant economic impact worldwide (Rojas et al., 2018). Moreover, recently, progressing experimental methods such as rolling circle amplification (RCA) (Jeske, 2018), next-generation sequencing (NGS) and metagenomics analyses (Moitinho-Silva et al., 2017) revealed new symptomatic and symptomless infections by geminiviruses and/or geminivirus like genomic components in a wide range of the host plants and insects (Fontenele et al., 2020). These circular DNA molecules have shown different genome organizations with a high potential for evolution (Roumagnac et al., 2022).

In general, geminiviruses pose a significant threat to universal agriculture, particularly in developing countries. Since a large number of geminiviruses (i. e. beet curly top Iran virus, BCTIV; turnip curly top virus, TCTV and turnip leaf roll virus, TLRV) are indigenous to Asia (Bolok Yazdi, et al, 2008; Briddon et al., 2010; Heydarnejad et al, 2013b; Kamali et al, 2016; Soleimani et al., 2013), agricultural activities are more reliant on the management of geminiviruses in these areas. Here, based on various studies, a review of the geminivirus situation in Iran, as well as some measures to control damage caused by these viruses, has been presented.

General Characteristics of Geminiviruses

Genome organization and biological characteristics of geminiviruses are the most important criteria in their taxonomy. With regard to the genomic criterion, it must be pointed out that the small genome of geminiviruses (2.5 kb to 5.2 kb in size) encodes for 4-8 required proteins (Roumagnac et al., 2022) by using open reading frames (ORFs) on the both of virion- and complementary-sense strands (Fondong, 2013) (Fig. 1). Geminiviruses have been all identified by having one ssDNA genomic fragment except those in the genus *Begomovirus* that have either one (monopartite) or two genomic (bipartite) components (Rojas et al., 2005; Zerbini et al., 2017). Circular ssDNA genomes of geminiviruses replicate through dsDNA intermediates in infected cells Hanley-Bowdoin et al., 2000). These viruses utilize three replication modes: complementary-strand replication, rolling-circle replication and recombination-dependent replication (Jeske et al., 2001).

It is a common feature for all members of the family to have an intergenic region (IR or LIR) having an inverted repeat sequence capable of forming a stem-loop (hairpin) structure. There is a genus-specific conserved nonanucleotide sequence (5′-TAATATTAC-3′ or 5′- TAAGATTCC-3′) within the loop of the hairpin structure region, which is an active site for the genome replication through rolling circle replication (RCR) by replication-associated protein (Rep) (Brown et al., 2012, see below as well). The short intergenic region (SIR), another non-coding sequence between 3'-ends of virion- and complementary sense ORFs, has been only found within the genome of becurtoviruses, capulaviruses, eragroviruses, mastreviruses, and grabluviruses (Varsani et al., 2017 and Fig. 1).

Geminiviruses depend entirely on their small and multifunctional proteins to manipulate the host DNA replication and protein-encoding machinery (Luna and Lzano-Duran, 2020). These proteins are involved in the replication, movement, encapsidation, and pathogenicity of the virus and exert their effect through various interactions with pathways and internal factors of the host cell. Geminiviruses use bidirectional transcription (Rojas et al., 2005) and overlapping genes to efficiently express their proteins (Fig. 1). The bidirectional transcription results in encoding coat protein (CP) and movement protein (MP) on the virion-sense strand of genomes of monopartite geminiviruses (Briddon et al., 1990; Hanley-Bowdoin et al., 2000); while movement proteins are encoded by AV1 and BC1 ORFs on DNA A and DNA B genomic components of bipartite begomoviruses, respectively (Brown et al., 2012). DNA B also encodes the Nuclear Shuttle Protein (NSP), while other essential proteins are encoded by virion- and complementary-sense strand ORFs in monopartite geminiviruses or DNA A in bipartite begomoviruses.

The ORF V1 and AV1 of monopartite and bipartite geminiviruses, respectively, encode the coat protein (CP) which encapsidates the viral DNA of the virus (Brown et al., 2012). CP acts as an NSP and regulates the balance of ssDNA and dsDNA accumulation in mastreviruses (Tijssen, 2005). It has been reported that CP is also involved in virus movement and insect vector transmission in curtoviruses and some monopartite begomoviruses (Stanley, 2008). All monopartite geminiviruses, upstream of the CP gene, encode a small reading frame called V2 (AV2). V2 (AV2) protein is a multifunctional protein that, as a host defense protein, suppresses post-transcriptional gene silencing (PTGS) in most of the geminivirus species tested to date (Amin et al., 2011; Bahari et al., 2022; Li et al., 2021; Luna et al., 2020; Mubin et al., 2010; Sharma & Ikegami, 2010; B. Wang et al., 2014; Yang et al., 2018; Zhai et al., 2022; Zhang et al., 2012; Zrachya et al., 2007). The New World bipartite begomoviruses lack an AV2 ORF. The V3 ORF located downstream of the V2 ORF and upstream of the V1 ORF in curtoviruses (Fig. 1) is suggested to be involved in the regulation of the relative levels of ssDNA and dsDNA. The becurto- and capulaviruses also encoded V3 protein (Fig. 1); however, the function of V3 protein has been not identified yet in these viruses. Replication-associated protein (Rep) encodes by the C1/AC1 ORF and is the only required protein for geminivirus replication. Rep is encoded through a C1/C2 (C2) spliced transcript in *Becurtovirus*, *Capulavirus*, *Mastrevirus* and *Grabluvirus* members (Varsani et al., 2017). Rep initiates viral DNA replication by binding to reiterated motifs (iterons) within the intergenic region (Behjatnia et al., 1998) and introducing a nick into the genus-specific conserved nonanucleotide sequence (5′-TAATATT/AC-3′ or 5′- TAAGATT/CC -3′) binds to the plant homolog of retinoblastoma-like protein to regulate cell-cycle progression, altering the environment of terminally differentiated cells to provide host factors that support viral DNA replication. The transcription activator protein (TrAP) expressed by the C2/AC2 ORF is associated with gene silencing during transfection and also functions in the suppression of PTGS. This protein is also a transcription factor that trans-activates the expression of virion-sense genes from both DNA A and DNA B (CP and NSP, respectively) in bipartite begomoviruses. C2 acts as a pathogenicity factor in some hosts of curtoviruses and begomoviruses (Lozano-Duran et al., 2012; Stanley, 2008; Tu et al., 2017). The replication enhancer protein (REn), expressed by the C3/AC3 ORF is required for effective viral DNA replication. C4 protein is an important symptom determinant implicated in cell-cycle control that may play a role in suppressing PTGS (Brown et al., 2012, Hanley-Bowdoin et al., 2013), and AC4 protein may counter a host response to Rep expression (Ferreira et al., 2021).

Biologically, it has been accepted that geminiviruses are naturally transmitted by a wide range of insect vectors in the order Hemiptera (*Insecta*). However, viruses from each of the different geminivirus genera are transmitted by only one or a few very closely related vector species within the same genus. All begomoviruses are transmitted by a single species in the genus *Bemisia* (i.e. *B. tabaci*) (Cohen and Antignus, 1994; Fiallo-Olive´ et al., 2020; Navas-Castillo et al., 2011). Becurtoviruses, curtoviruses, and turncurtoviruses are transmitted by leafhoppers in the genus *Circulifer* (Fatahi et al., 2012; Heydarnejad et al., 2013; Razavinejad et al., 2013; Taheri et al., 2012). *Tomato pseudo-curly top virus,* the only known species

in the genus *Topocuvirus*, is transmitted by a treehopper species in the genus *Micrutalis* (Tsai, 2004), Grabloviruses are transmitted by treehoppers in the genus *Spissistilus*, and capulaviruses by aphids in the genus *Aphis* (Roumagnac et al., 2015; Varsani et al., 2017). In the case of mastreviruses, different virus species are transmitted by insects belonging to different leafhopper species in a number of insect genera including *Cicadulina*, *Orosius*, *Psammotettix*, and *Nesoclutha* (Muhire, et al., 2013).

Although insect transmission is known to be the only way of transmission of geminiviruses, seed transmission of some destructive geminiviruses has recently been reported, which would provide logical reasons for the presence of these viruses in regions without the presence of their vectors (Anabestani et al., 2017; Kim et al., 2015; Kil et al., 2016; Sangeetha et al., 2018). Seed transmission has a significant role in epidemiological studies of geminiviruses to have an accurate understanding of the origin and distribution patterns of these viruses (Anabestani et al., 2017).

Geminiviruses Reported in Iran

Geminiviruses cause diseases in several economically important crops including alfalfa, barley, chickpea, common bean (and other legumes), cotton, pepper, sugar beet, tomato, turnip, watermelon, and wheat reported from Iran, where they can cause substantial economic losses. Geminiviruses exhibit considerable diversity in their genome structure and sequence, host range, tissue tropism and insect vectors. Based on these properties, geminiviruses have been classified into fourteen genera ratified by the International Committee on Taxonomy of Viruses (ICTV, Roumagnac et al., 2022). To our knowledge and on the basis of ICTV criteria, so far one curtovirus, one capulavirus, three turncurtoviruses, one becurtovirus, three mastreviruses and twelve begomoviruses were recorded from Iran (Table 1).

Fig. 1. Genomic organization of geminiviruses reported in Iran. ORFs are denoted as being encoded on the virion-sense (V) or complementary-sense (C) strand, and corresponding protein products are coded by color. The position of the stem-loop containing the conserved sequence located in the long intergenic region (LIR) is shown. For begomoviruses, V2/AV2 is not present in New World viruses. For becurtoviruses, an intron is predicted to occur between ORFs C1 and C2. CR, common region; CP, coat protein; IR, intergenic region; MP, movement protein; NSP, nuclear shuttle protein; REn, replication enhancer protein; Rep, replication-associated protein; SIR, small intergenic region; TrAP, transcriptional activator protein (Adapted from Varsani et al., 2014b).

Table 1. Some characteristics of geminiviruses reported in Iran

Species	Genus	ACC. No.*	Reference
Alfalfa leaf curl virus (ALCV)	*Capulavirus*	MH603829	Davoodi et al. (2018b)
Beet curly top Iran virus (BCTIV)	*Becurtovirus*	EU273818	Bolok-Yazdi et al. (2008)
Beet curly top virus (BCTV)	*Curtovirus*	M24597	Briddon et al. (1998)
Bean golden mosaic virus (BGMV)	*Begomovirus*	●	Ghorbani et al. (2010)
Chickpea chlorotic dwarf virus (CpCDV)	*Mastrevirus*	MK641863, MN699955	Farzadfar et al. (2008); Askari et al. (2021)
Chili leaf curl virus	*Begomovirus*	OM885882-OM885884	Salehzadeh et al. (2022); Salari et al. (unpublished)
Cotton leaf curl Alabad virus (CLCuAlV)	*Begomovirus*	ON982790	Unpublished
Cotton leaf curl Gezira virus (CLCuGV)	*Begomovirus*	MN328258	Bananej et al., (2021)
Cotton leaf curl Multan virus (CLCuMuV)	*Begomovirus*	OP080331	Mosharaf et al., (2020)
Okra enation leaf curl virus (OELCuV)	*Begomovirus*	KJ397533	Bananej et al., (2016)
Parsley yellow leaf curl virus (PYLCV)	*Begomovirus*	MN243534	Hasanvand et al., (2020)
Tomato leaf curl Karnataka virus (ToLCKV)	*Begomovirus*	AY297924	Behjatnia et al., (2004)
Tomato leaf curl New Delhi virus (ToLCNDV)	*Begomovirus*	KP793719	Yazdani-Khameneh et al., (2016)
Tomato leaf curl Palampur virus (ToLCPMV)	*Begomovirus*	JQ825226	Heydarnejad et al., (2009)
Tomato yellow leaf curl virus- Iran (TYLCV)	*Begomovirus*	MH507499.1	Bananej et al., (2004)
Tomato yellow leaf curl virus-Abadeh (TYLCV-[Ab])-One strain of TYLCV-IL	*Begomovirus*	FJ355946	Pakniat-Jahromy et al., (2010) Fazeli et al., (2009)
Tomato yellow leaf curl virus-[Kahnooj] (TYLCV-[Ka]) Another strain of TYLCV-IL		EU635776	
Tomato yellow leaf curl virus-[Iran-2] (TYLCV-Ir2) Another strain of TYLCV-IL		EU085423	Azizi et al., (2011)
Turnip curly top virus (TCTV)	*Turncurtovirus*	GU456685	Briddon et al., (2010)
Turnip leaf roll virus (TRLV)	*Turncurtovirus*	KT388087	Kamali et al. (2016)
Sesame curly top virus (SeCTV)	*Turncurtovirus*	MH595443-54	Hasanvand et al. (2018)
Watermelon chlorotic stunt virus (WmCSV)	*Begomovirus*	AJ245652	Kheyr-Pour et al., 2000
Wheat dwarf virus (WDV)	*Mastrevirus*	FJ620684	Behjatnia et al., (2011)
Oat dwarf virus (ODV)	*Mastrevirus*	KX533458 and KX533459	Kamali et al. (2017)

*ACC. No.: GenBank Accession Number

● Detection by ELISA or unpublished sequence data

Curtovirus and *Becurtovirus* Genera

Iranian beet curly top viruses (IBCTVs); BCTIV and BCTV

History of IBCTVs Classification

The latest classification proposal of curtoviruses established 77% and 94% genome-wide pairwise identity as species demarcation and strain demarcation threshold, respectively (Varsani et al., 2014a). ICTV criteria divided members belonging to the previously accepted genus *Curtovirus* into two distinct genera, *Curtovirus* and *Becurtovirus*, based on genomic differentiation (Bolok-Yazdi et al., 2008; Varsani et al., 2014a). Currently, the genus *Curtovirus* comprises three species causing curly top disease in dicot host plants including *Beet curly top virus* (BCTV), *Horseradish curly top virus* (HrCTV) and *Spinach severe curly top virus* (SpSCTV) (Roumagnac et al., 2022). Until now, HrCTV and SpSCTV have not been reported from Iran.

BCTV and *Beet curly top Iran virus* (BCTIV, *Becurtovirus* genus) are responsible agents causing curly top disease in sugar beet and many other dicot plants in Iran (Anabestani et al., 2016; Gharouni Kardani et al., 2013; Majidi et al., 2017). Previously serological methods using polyclonal antibodies were able to detect these viruses based on the similarity of their coat proteins but cannot differentiate them from each other (Heydarnejad et al., 2007). Until 2008, there were no sequence data to differentiate between two species and their strains. Providing more complete sequences revealed a low full-length genome sequence identity between Iranian beet curly top viruses to classify as the same genus. Subsequently, genomic studies defined a new nonanucleotide motif (TAAGATT/CC) for a group of isolated strains with different ORFs organizations that expressed Rep using a spliced transcript. These findings suggested the occurrence of a distinct curly top virus species in infected hosts in Iran which was then released as BCTIV (Bolok-Yazdi et al., 2008). Finally, with a lower than 77% genome-wide pairwise identity to other curtoviruses, the genus *Becurtovirus* was established as a new genus including BCTIV and other similar members (Varsani et al., 2014a). This genus contains three accepted species including BCTIV, *Spinach curly top Arizona virus* (SpCTAV) and *Exomis microphylla latent virus* (Roumagnac et al., 2022). BCTIV has been reported recently in Turkey (Yildirim et al., 2022).

Biological Properties

Natural and Experimental Hosts

Based on studies have been done to date on the determination of natural hosts of BCTV and BCTIV (Anabestani 2012; Bolok-Yazdi et al. 2008; Ebadzad Sahraei 2008; Gharouni Kardani et al. 2013; Ghodoum Parizipour 2011; Jahanbin et al., 2015; Tahan et al., 2019),

natural infections of crop hosts such as sugar beet, turnip, pepper, tomato, common bean, spinach, petunia, and weeds such as redroot pigweed (*Amaranthus retroflexus*), *Chenopodium album*, field bindweed (*Convolvulus arvensis*), datura, *Physalis* sp. and nightshade (*Solanum nigrum*) were detected separately for each virus. While the natural infections of *Beta vulgaris* var. *esculenta*, radish, eggplant and the weed *Descurainia sophia* have only been detected by BCTV, the natural infections of *Beta vulgaris* subsp. *Maritima*, eggplant and cowpea have only been detected by BCTIV (Table 2). It is worth mentioning that mixed and simultaneous infections of both viruses in sugar beet, petunia and the weed redroot pigweed have been reported (Ebadzad Sahraei 2008). The simultaneous infection of these plants and possibly other hosts with BCTV and BCTIV is not only a sign of the lack of cross-protection between these viruses but also can be a prerequisite for recombination between them and the emergence of new viral species (Garcia-Andres et al., 2007).

For the experimental host range determination of both viruses, Jahanbin et al (2016) grew a number of plants in the greenhouse. Their seedlings were agroinoculated with the infectious clone of each virus. The results showed that BCTV had a wider experimental host range than BCTIV. These results indicated that members of Solanaceae, Brassicaceae, Fabaceae and Amaranthaceae are most frequently infected by BCTV and BCTIV.

Transmission of BCTV and BCTIV

Natural transmission of BCTV and BCTIV occurs by cicadellid leafhoppers in a persistent (circulative non-propagative) manner. *Circulifer haematoceps*, the dominant leafhopper species found in sugar beet fields in Iran (Ebadzad Sahraei, 2008), is the vector of both BCTV and BCTIV in this country (Fatahi et al., 2012; Taheri et al., 2012). *C. tenellus*, which occurs in a low population in sugar beet fields in Iran (Ebadzad Sahraei 2008), is also the vector of BCTV, whereas it is the only known vector of beet curly top virus in the USA (Bennett, 1971).

Whereas the transmission of BCTV and BCTIV by insect vectors has already been reported to be the only natural transmission, the seed transmission of these viruses (Anabestani et al., 2017) was demonstrated in the natural infection of a local cultivar of petunia in Iran. The seed transmission rate of BCTV and BCTIV in petunia at the 6-8 leaf stage of the tested plant was estimated to be 45.5 and 35.5 %, respectively. At the same time, *Dianthus barbatus* was reported as the new seed-borne host of BCTIV. The seed transmission rate of BCTIV in *D. barbatus* was estimated to be 40 % at the four-leaf stage of the plant and 100 % five weeks later (Ahooei, 2017). The results of another survey (Torab Jahromi et al., 2018a) indicated that the infection rates of BCTV and BCTIV in infected plants collected from Shiraz Street green sites (23 plants) were determined to be 52.85% and 32.85%, respectively. The infection rate of the first generation-seedlings (45 seedlings) developed from seeds of the infected plants were 47 and 40% for BCTV and BCTIV, respectively, and in the second generation (45 seedlings), 40 and 33% for BCTV and BCTIV, respectively. The results of this survey indicated that BCTV infects petunia plants and their developed seeds in Shiraz street green sides at a higher rate than that BCTIV. In another study on the impact of BCTV and BCTIV infection on the flowers and seed production of petunia, Torab Jahromi et al. (2018b) reported that the average number of flowers and capsules and finally the seeds of infected petunia plants (either virus singly or mixed infected plants) differed significantly ($P \leq 0.01$) with those of healthy petunia (control) plants. However, there was no significant difference in the average number of flowers, capsules and seeds between BCTIV- and BCTV-infected plants. There was also no significant difference in the data between plants infected by a single virus or both viruses.

A low rate of mechanical transmission of BCTV by needle injection has also been reported (Bennett, 1971). On the other hand, cloned genomic DNAs of geminiviruses have been widely used as infectious constructs in *Agrobacterium*-mediated experimental transmission (agroinoculation) of these viruses (Briddon, et al., 1998; Boulton, 1995; Ebadzad Sahraei et al., 2008; Heydarnejad et al., 2013; Soleimani et al., 2013).

Incidence and Diversity of IBCTVs in Iran

A study of the incidence and diversity of IBCTVs showed that the incidence of BCTIV in sugar beet was higher than that of BCTV, while BCTV was more frequent in other plants such as tomato, pepper and bean (Anabestani et al., 2016). It has also been shown that BCTIV has a high distribution in commercial sugar beet fields in different provinces in Iran including Fars, Khorasan-e-Razavi, Boushehr and Kermanshah (Fig. 2, Anabestani, et al., 2016). It has been shown that the distribution patterns of BCTIV and BCTV are according to the leafhopper vector activation pattern. Also, phylogenetic analyses pointed out the geographical divergence of BCTIV isolates and the deposit of BCTV isolates without significant genomic divergence based on the geographical distribution (Anabestani et al., 2016). These results suggest a more extended evolutionary history of BCTIV or its more rapid evolutionary rate in Iran (Anabestani et al., 2016).

Looking at the IBCTVs Interference Phenomenon

In experimental agro-inoculation of different hosts and surveys of natural infections by BCTV and BCTIV, it has been shown that BCTV has a wider host range and expresses more severe symptoms than those of BCTIV (Anabestani et al., 2016; Jahanbin et al., 2015). Furthermore, the coincidence of both viruses in a single host plant results in an interference phenomenon with more severe symptoms than a single infection and higher BCTIV genomic DNA accumulation than that of BCTV (Majidi et al., 2017). These results suggest more fitness value for BCTIV in competition with BCTV. Possible mechanisms can be either using of suppressors gene silencing of both viruses in the mixed infection to increase BCTIV genome replication (Majidi et al., 2017), or a high affinity of Rep to bind on BCTIV nonanucleotide and beginning replication with a high rate in comparison to BCTV and recruitment of BCTV encoded Rep to increase BCITV genome replication during mixed infections (Majidi et al., 2017, Tabein et al., 2022).

Table 2. Natural hosts of BCTV and BCTIV reported from Iran

Plant scientific name (common name)	BCTV	BCTIV	Reference
Amaranthus retroflexus (redroot pigweed)	+	+	(Anabestani, 2012; Ebadzad Sahraei, 2008)
Beta vulgaris (sugar beet)	+	+	(Anabestani, 2012; Ebadzad Sahraei, 2008; Gharouni Kardani et al., 2013; Ghodoum Parizipour, 2011; Jahanbin et al., 2015)
Beta vulgaris var. *esculenta*	+	NF	(Ghodoum Parizipour, 2011)
Beta vulgaris subsp. *maritima*	NF	+	(Gharouni Kardani et al., 2013)
Brassica campestris (turnip)	+	+	(Anabestani, 2012; Ghodoum Parizipour, 2011; Jahanbin et al., 2015)
Capsicum frutescens (bird chili)	+	+	(Anabestani, 2012; Ebadzad Sahraei, 2008; Ghodoum Parizipour, 2011; Jahanbin et al., 2015)
Chenopodium album	+	+	(Anabestani, 2012; Ghodoum Parizipour, 2011)
Convolvulus arvensis (field bindweed)	+	+	(Anabestani ,2012)
Datura spp.	+	+	(Ebadzad Sahraei, 2008; Ghodoum Parizipour, 2011)
Descurainia sophia (flixweed)	+	NF	(Anabestani, 2012)
Petunia spp.	+	+	(Anabestani, 2012; Ebadzad Sahraei, 2008; Ghodoum Parizipour, 2011; Jahanbin et al., 2015)
Phaseolus vulgaris (red bean)	+	+	(Anabestani, 2012; Gharouni Kardani et al., 2013; Ghodoum Parizipour, 2011)
Physalis spp.	+	+	(Anabestani, 2012; Ebadzad Sahraei, 2008)
Raphanus sativus (radish)	+	NF	(Anabestani, 2012; Jahanbin et al., 2015)
Spinacia oleracea (spinach)	+	+	(Ghodoum Parizipour, 2011; Jahanbin et al., 2015)
Solanum lycopersicum (tomato)	+	+	(Anabestani, 2012; Gharouni Kardani et al., 2013; Ghodoum Parizipour, 2011)
Solanum melongena (eggplant)	+	NF	(Anabestani, 2012; Jahanbin et al., 2015)
Solanum nigrum (nightshade)	+	+	(Anabestani, 2012)
Vigna unguiculata (cowpea)	NF	+	(Gharouni Kardani et al., 2013)

+: Found; NF: Not found

To investigate the possible contribution of the interaction between Rep and the nonanucleotide motifs in the interference between BCTIV and BCTV in mixed infections, the validity of the second hypothesis was assessed using an *in silico* approach. Results showed that the energy structure and binding affinity of both Rep molecules of BCTIV and BCTV toward BCTIV nonanucleotide were significantly higher than the nonanucleotide of BCTV (Tabein et al., 2022). Further functional genomics and chimeric studies seem to be necessary to determine the exact mechanism of this interference phenomenon.

Genomic Properties (Genome Organization)

Despite its similar biological properties including transmission by the leafhopper *C. haematoceps* (*Cicadellidae*), (Heydarnejad et al., 2013; Soleimani et al., 2013), transmission through some host plants seeds (Anabestani et al., 2017), symptoms and similar host range in dicot plants in Iran, BCTIV is a genetically divergent species when its genome organization is compared to members of the genus *Cutrovirus*. Curtoviruses show three and four ORFs on the virion- and complementary-sense strands, respectively (Fig. 1). While the BCTIV genome has five ORFs including three ORFs on the virion-sense strand (Fig. 1) which are related to the corresponding genes of curtoviruses (Fig. 1), and two ORFs on the complementary-sense strand (Fig.1) which have been distantly related to those of mastreviruses (Bolok-Yazdi et al., 2008 and Fig. 1). Furthermore, in contrast to all known curtoviruses which possess TAATATT/AC nonanucleotide sequence motif within a putative stem-loop structure in the IR of their genome, becurtoviruses possess a different nonanucleotide sequence which is TAAGATT/CC (Bolok-Yazdi et al., 2008).

Sub-genomic DNAs Associated with IBCTVs Infection

There are commonly defective DNA molecules (defective DNAs) in curly top viruses' infection without any responsibility for the viral replication and infection which are produced via incomplete RCR cycles (Frischmuth and Stanley, 1992; Stenger et al., 1992). However, Frischmuth and Stanley (1994) showed that *Nicotiana benthamiana* plants transformed with a partial repeat of a sub-genomic DNA derived from BCTV produced ameliorated symptoms when agroinoculated with BCTV. On the basis of these observations, the BCTV sub-genomics DNAs have been recognized as defective-interfering DNAs. Variability of BCTV defective DNAs by size in different hosts has suggested that their production maybe is influenced by the host species (Stenger et al., 1992).

Newly described minicircle forms of hybrid virus/host DNA molecules are detected in infected sugar beet (*B. vulgaris*) by BCTIV (Catoni et al., 2018). These hybrid minicircles replicate, encapsidate and spread systemically throughout infected plants in parallel with the viral infection. Based on the ability of these newly defined hybrid minicircles to replicate and transcript in other sensitive host plants, it can be used as a new path for virus-mediated horizontal transfer of chromosomal DNA between plant species (Catoni et al., 2018).

Begomovirus

The genus *Begomovirus* with more than 400 assigned species, today is the largest genus of viral taxonomy (ICTV, https://ictv.global/taxonomy). In the past,

begomoviruses were commonly divided into two sub-groups, New World (NW) and Old World (OW), based on genome arrangement and phylogenetic studies (Nawaz-ul-Rehman et al., 2009). Most of the bipartite begomoviruses are distributed in NW, while OW begomoviruses are mostly monopartite and associated with different sub-viral fragments (alphasatellites, betasatellites and deltasatellites) (Lozano et al., 2016). However, it has been reported that deltasatellites are associated with NW begomoviruses as well (Fiallo-Olivé et al., 2012; Fiallo-Olivé et al., 2016)

Alphasatellites are small circular ssDNA molecules (~ 1000-1400 nt) associated with the major genome of nanoviruses and certain geminiviruses belonging to the *Begomovirus* and *Mastrevirus* genera which encode a replication-associated protein (Rep) (Briddon et al., 2018). These Rep-encoding satellite molecules have been assigned to the family *Alphasatellitidae* to which two subfamilies, *Geminialphasatellitinae* and *Nanoalphasatellitinae*, have been established to respectively accommodate the geminivirus- and nanovirus-associated alphasatellites (Briddon et al., 2018).

Betasatellites are small circular ssDNAs (~1350 nt) that have been isolated from plants infected with certain monopartite begomoviruses such as *Ageratum* yellow vein virus, cotton leaf curl virus, tomato yellow leaf curl China virus and bhendi yellow vein mosaic virus. The induction of disease symptoms in some host plants of these viruses has been shown to depend on the presence of betasatellite molecules (Briddon et al., 2001; Jose and Usham 2003; Saunders et al., 2000; Zhou et al., 2003). Betasatellites, except for a conserved hairpin structure and a TAATATTAC loop sequence, have little sequence similarity to the DNA molecules of the respective helper viruses (Briddon et al., 2003; Mansoor et al., 2003; Mansoor et al., 2006; Stanley, 2004). Analysis of betasatellite sequences has revealed a conserved organization consisting of a single complementary-sense ORF (βC1), an adenine-rich region, and a satellite-conserved region (SCR) that contains sequences similar to tomato leaf curl virus-Australia [ToLCV-Au) satellite-DNA, Dry et al., 1993)]. ToLCV-Au satellite-DNA (ToLCV-sat), now, is classified as a deltasatellite (see below). The βC1 ORF of all betasatellite molecules is also conserved in position and size Zhou et al., 2003) and is responsible for betasatellite-induced disease symptoms (Saeed et al., 2005).

Deltasatellites are also small circular, ssDNA molecules of between 700 and 1,350 nts. Like betasatellites, deltasatellites contain a predicted stem-loop structure containing the nonanucleotide TAATATTAC, an adenine rich region, and an SCR. However, the deltasatellites also contain a second predicted stem-loop. The deltasatellites include the two groups of satellites, the satellites associated with sweepoviruses infecting *Ipomoea* sp. in Spain and *Merremia* in Venezuela (Lozano et al., 2016), ToLCV-sat (Dry et al., 1993), the small molecules identified in *Croton* from India and *Malvastrum* from the Philippines, and two deltasatellites found in the NW and identified by Fiallo-Olivé et al. (2016) that isolated from *Malvastrum* and *Sidastrum*, as well as a group of small molecules identified in *B. tabaci* whiteflies originating from the United States of America (Ng et al., 2011). Deltasatellites do not encode proteins and may constitute defective betasatellites (Lozano et al., 2016). NW deltasatellites did not affect the symptoms induced by the helper viruses but in some cases reduced their accumulation. Moreover, one NW deltasatellite (e. i. a deltasatellite from *Malvastrum coromandelianum* was shown to be transmitted by the whitefly *B. tabaci*, the vector of its helper begomoviruses. These results confirm that these molecules are true satellites (Fiallo-Olivé et al., 2016).

All aforementioned satellites require a helper virus for replication, encapsidation, insect transmission and movement in plants (Dry et al., 1993.

Emerging Begomovirus/Satellite Complexes in Iran

To date, different studies revealed the incidence of 12 begomovirus species with different strains in tomato and some other dicotyledonous plants in Iran (Table 1). Previously, Benanj et al., (2009), in a study that investigated the begomoviruses associated with tomato yellow leaf curl disease (TYLCD) in Iran suggested that the differences of these viruses are in a range that different strains or species from *Tomato yellow leaf curl virus* (TYLCV) and *Tomato leaf curl virus* (ToLCV) are associated with TYLCD in Iran. In another study (Shirazi et al., 2014) two geographically separated clades of TYLCV were detected based on phylogenetic analyses of the partial nucleotide sequences of the coat and movement protein-coding regions of the viral genome with a total size of approximately 608 base pairs. Isolates collected from Hormozgan, Khuzestan and Kerman provinces were grouped together with other Iranian isolates including TYLCV-Ir2, TYLCV-Kahnooj, and an isolate from Oman. It was also revealed that isolates collected from Boushehr, Fars, Tehran, and Isfahan were close to the Iranian isolate TYLCV-Abadeh (Pakniat et al., 2010) and isolates reported from Israel and Egypt. No correlation was found between the genetic variation and the host species, but selected Iranian isolates were grouped on the basis of their geographical origins. The results of this study also indicated a high genetic diversity among Iranian TYLCV isolates (Shirazi et al., 2014).

The tomato-infecting begomoviruses in Iran have monopartite genomes, except for ToLCPMV (Heydarnejad et al., 2009) and ToLCNDV (Yazdani-Khameneh et al., 2016). It has been reported that ToLCPMV has a widespread distribution in southern regions of the country causing economic losses in tomato and cucurbit fields which have been estimated to be complete infections in some cases (Sabouri and Heydarnejad, 2013). ToLCNDV is the newly emergent bipartite begomovirus in Iran with incidence on cucurbit plants. ToLCNDV has been reported only in Khuzestan province where there is a low incidence rate, suggesting it is not widely distributed (Yazdani-Khameneh et al., 2016). However, it seems that it has already been detected in Sistan and Baloochestan Province as the sequences of the two segments of the complete genome of ToLCNDV were deposited in the GenBank under

Accession Numbers KP641673 and KP641674 by Abkhoo in 2015.

TYLCV is another destructive and widespread species, in southern Iran. TYLCV is the causative agent of TYLCD in tropical and subtropical regions of the world, resulting in crop losses of up to 100% (Makkouk et al., 1979). It has been shown that naturally infected tomato plants show symptoms like upward leaf curling, severely reduced leaf size, yellowing of the leaf margins and veins, flower abscission and stunting (Pakniat Jahromy et al., 2010). The presence of at least five strains of TYLCV in Iran, (Hosseinzadeh et al., 2014) suggested Iran is a potential center for genomic diversification for populations of this species.

Many techniques, such as ELISA, PCR, Dot and Sothern blotting, have been used to detect TYLCD-causing viruses و including TYLCV strains و which according to Razmi et al. (2019), require multistep procedures and rely on sophisticated equipment. Razmi et al. (2019) introduced an easy, fast, sensitive and promising way to detect TYLCV-infected plants. In this regard, they used gold nanoparticles (AuNPs) as colorimetric probes for the detection of TYLCV and they claimed that by using the localized surface plasmon resonance of AuNPs a rapid detection of unamplified genomic DNA of TYLCV in infected plant samples has been provided.

In a study on the incidence and severity of TYLCD and population dynamics of *Bemisia tabaci*, the vector of TYLCV, in three tomato cultivars namely Yellow Round Multiple Truss (YRMT), PANDA F1, Black Russian ST 175 (BRST) in commercial greenhouse cultivation in Shiraz, Fars Province, Iran, Baghernejad et al. (2018) found that significant differences in disease incidence (DI), disease severity and vector population dynamics between three aforementioned tomato cultivars. The DI was estimated to be 6.6% to 86.6% at 40 and 100 days after planting, respectively. The incidence and severity of disease and insect vector populations in YRMT and PANDA-F1 cultivars showed a higher trend and rose more sharply than in those of the BRST cultivar. BRST was comparatively more resistant than the two other cultivars (YRMT and PANDA) which were susceptible to TYLCV (Baghernejad et al., 2018).

Two cotton-infecting begomoviruses, cotton leaf curl Gezira virus (CLCuGV) and cotton leaf curl Multan virus (ClCuMuV), are newly reported species from Iran (Bananej et al., 2021; Mosharaf et al., 2020; Salari et al., 2020). CLCuGV was detected to be associated with tomato leaf curl betasatellite (ToLCB) or cotton leaf curl betasatellite in the infection of papaya, sunflower, okra or marshmallow plants in southeastern Iran (Bananej et al., 2021; Salari et al., 2020). Previously, the full-length DNA genome of cotton leaf curl Multan betasatellite (CLCuMuB) was amplified from cotton samples collected from the Khir region, Fars province in southern Iran using the universal primer pair β01/β02 (Behjatnia and Karimi, 2015) and sequence data. However, different analyses could not identify a co-infected helper begomovirus with the CLCuMuB cotton infection. This suggested the need for further studies based on using of new amplification and sequencing methods to determine the infection of cotton plants in Khir region. This is especially important since ClCuMuV was detected in Khuzestan Province on hibiscus chines (*Hibiscus rosa-sinensis* L.) plants (Mosharaf et al., 2020), adjacent to Fars Province. Recently, two alphasatellite molecules including *Cotton leaf curl Gezira alphasatellite* and *Gossypium darwinii symptomless alphasatellite* were found to be associated with CLCuGV in sunflower, okra or marshmallow plants in southeastern and southern Iran (Salari et al., 2023).

In addition to cotton leaf curl Gezira viruses, it has been reported that the watermelon chlorotic stunt virus (WmCSV) is another widespread begomovirus in south Iran, especially during dry and warm seasons (Kheyr-Pour et al., 2000). Okra enation leaf curl virus (OELCuV) has been the first report of a begomovirus infecting papaya plants in Iran (Bananej et al., 2016). There is also one record of the bean golden mosaic virus (BGMV) from Iran (Ghorbani et al., 2010).

Recently, a novel geminivirus, has been known as parsley yellow leaf curl virus (PYLCV), was identified in a diseased parsley sample showing symptoms such as upward marginal leaf curling, marginal leaf yellowing, dwarfing and reduced leaf size in south-eastern Iran (Hasanvant et al., 2020). Some of the features of this new geminivirus have been reported to be: Its full-length genome share <66 % identity with that of the known geminiviruses. Its genome is chimeric and has at least six ORFs. The encoded CP is phylogenetically clustered with those of becurto- and curtoviruses. The complementary sense-encoded proteins are most similar to those of begomoviruses. Based on the similarity of the CP encoded by PYLCV to those of becurtoviruses and curtoviruses, it is likely that leafhoppers may be the vector of the virus (Hasanvand et al., 2020).

Biological Properties

Natural and Experimental Hosts

The natural host range of TYLCV-[Ab] (Table 1) seemed to be very narrow as this virus has been isolated only from tomato fields in Iran (Pakniat Jahromy et al., 2010; Jahanbin et al., 2015). However, under greenhouse conditions, some plants including bean, nasturtium, petunia, redroot pigweed, datura, nightshade and ground cherry were infected by this virus (Jahanbin et al., 2015).

ToLCPMV was the first bipartite begomovirus detected in tomato in 2006 in Hormozgan Province (southern Iran) (Heydarnejad et al., 2009; Heydarnejad et al., 2012). Following this, the ToLCPMV incidence has progressively increased amongst several cultivated plants and to new geographical regions within Iran. ToLCPMV was detected in six crop species including tomato, cucumber, three different local cultivars of melon, squash, watermelon and bean in commercial greenhouses, plastic tunnels and/or open farms. Squash, watermelon, bean and two weed species, *Chenopodium* sp. and *Heliotropium europaeum*, represent new natural hosts of ToLCPMV globally. The ToLCPMV epidemic has particularly devastated on cucumber, melon, and squash crops. Infections rates of between 50 and 100 % were identified amongst greenhouse-grown cucumbers

and melons farms. However, the rate of infection in watermelon and bean were negligible. Heydarnejad et al., (2013a) suggested that the movement of ToLCPMV from south-eastern Iran to south, northeast and central regions with warm climatic conditions threatens the cultivation of cucurbits and tomatoes in these regions, which are the major production areas for these crops.

The Iranian isolate of tomato leaf curl Karnataka virus (ToLCKV-Ir; Table 1) has been reported to cause tomato leaf curl disease in Iranshahr (Sistan and Baloochestan province, Iran) (Behjatnia et al., 2009). In a study conducted by Behjatnia et al., (2009) a range of potential hosts including tomato, tobacco, Datura, *Nicotiana benthamiana* and some other indicator plants were agroinoculated with a bacterial culture of an infectious construct of ToLCKV-Ir (Behjatnia et al., 2009). Mild curling and yellowing symptoms were observed on newly developed leaves of tomato plants within 30 to 45 days post-inoculation (dpi). However, the next phase of symptom development on tomato occurred 2-3 months after inoculation and produced elongated spindly shoots, smaller leaves and severe leaf cupping on the newly developed leaves. *N. benthamiana* plants agroinoculated by ToLCKV-Ir also showed severe symptoms including leaf curling and leaf cupping within 21 to 30 dpi. No symptoms were observed on other agroinoculated plants but dot blot and PCR analysis using ToLCKV-Ir-specific probes and primers, respectively, confirmed the presence of the viral DNA in *D. stramonium* and *N. tabacum* plants, indicating that these plants are symptomless hosts of the ToLCKV-Ir. On the basis of host range, symptom severity, the timing of symptom appearance and the level of replication of the virus in host plants in comparison with a severe isolate of TLCV, i.e., the Australian isolate of TLCV, ToLCKV-Ir was considered as a mild strain of tomato-infecting begomoviruses in Iran (Behjatnia et al., 2009).

Impact of Leaf Curl Viruses on Tomato

The yield losses caused by TYLCV-[Ab] and ToLCKV-IR were estimated in two tomato cultivars including Rio Grande (RG) and Grosse Lisse (GL). For this, tomato seedlings of each cultivar were separately agroinoculated with either virus and disease development was monitored over four-time intervals (Hamzehzarghani et al., 2020). Initial disease severity (DS), evaluated visually using an ordinal rating scale, in plants infected by ToLCKV-IR was less than those infected by TYLCV-[Ab]. The studied pathosystems were arranged as ToLCKV-IR-infected GL>TYLCV-Ab-infected GL> TYLCV-[Ab]- infected GL> ToLCKV-IR-infected RG based on descending order of rates of disease increase for the aforementioned pathosystems. DS was reduced in both cultivars inoculated with either of the two viruses with delaying inoculation. The highest crop loss disease threshold, estimated by measuring vegetative indices including wet and dry weight and height of the aerial and underground parts of the plants, was observed for GL cultivar irrespective of the inoculated virus. Curvilinear tolerance or slope did not show any significant difference between the infected-GL plants to either virus and TOLCKV-IR-RG, while TYLCV-[Ab]-RG showed the highest curvilinear tolerance. It has been suggested that the findings of this study can be applied in screening tolerant tomato plants (Hamzehzarghani et al., 2020).

In another survey, Baghernejad (2017) studied the effects of the mixed infection of TYLCV and cucumber mosaic virus (CMV) on tomato under greenhouse conditions. Standard PCR tests of this study indicated that CMV was detectable sooner than TYLCV on infected tomatoes. CMV also produced more severe symptoms in tomato than those produced by TYLCV on tomato at the same time after simultaneous inoculation of both viruses on different seedlings. Analysis of the real-time PCR data revealed that in simultaneous infection, the concentration of both viruses decreased compared to a single infection of each virus, indicating an antagonistic interaction between two studied viruses (Baghernejad 2017).

Interaction of TYLCV-[Ab] with Other Viruses Infected Tomato

The interaction of BCTV and BCTIV with TYLCV-[Ab] has been studied in tomato (Jahanbin et al., 2015). Analysis of the real-time PCR data showed the antagonistic interaction in the simultaneous infection of BCTV or BCTIV with TYLCV-[Ab] as evidenced by a decrease in accumulation of each virus involved in the mixed infection compared to single infections. TYLCV-[Ab] was generally dominant and seemed more adaptive to tomato compared to BCTV and BCTIV in mixed infections (Jahanbin 2013).

Transmission of Begomoviruses

Begomoviruses are naturally transmitted by the whitefly, *Bemisia tabaci*, as a complex species. Recently, seed transmission of some destructive begomovirus species including tomato yellow leaf curl virus (TYLCV) (Kil et al., 2016) and tomato leaf curl New Delhi virus (ToLCNDV) (Sangeetha et al., 2018) has been demonstrated in their natural infections. However, it has been shown that there is no evidence of seed transmission in the Sardinian tomato yellow leaf curl virus (Tabein 2021).

Turncurtovirus

Turnip curly top virus (TCTV) is the first defined species within the established genus *Turncurtovirus* in the family *Geminiviridae*, which originated from Iran. The primary isolates have all been recovered from either *Brassica rapa* or *Raphanus sativus* (Briddon et al., 2010; Razavinejad et al., 2013). Then, different isolates were detected in *Descurainia sophia*, *Anchusa* sp., *Solanum americanum* and *Hibiscus trionum* using PCR (Razavinejad et al., 2013). Transmission of TCTV has been recorded by the leafhopper *C. haematoceps* under greenhouse conditions (Razavinejad et al., 2013).

Based on the pairwise identity between different TCTV isolates, a tentative turncurtovirus strain demarcation threshold of 95% was proposed by Varsani et al. (2014b). Subsequent studies identified a new turncurtovirus species, *Turnip leaf roll virus* (TLRV), having lower than 80% genome-wide pairwise identity

with TCTV (Kamali et al., 2016). Moreover, the latest species in this genus was detected in sesame (*Sesame indicum*) in Iran and Pakistan (Hasanvand et al., 2018). Symptomatic sesame plants in sesame fields in Jiroft, Kerman Province, showed yellowing, boat-shaped leaf curling and vein swelling on the lower leaf surfaces (Hasanvand et al., 2018). The newly defined turncurtovirus in Iran, *Sesame curly top virus* (SeCTV), has ~87% wide pairwise identity with another SeCTV strain from Pakistan as sesame yellow mosaic virus (SeYMV). It has been reported that the full-length genome of SeCTV and SeYMV sequences share < 70% genome-wide pairwise identity with TCTV and TLRV, which suggests they are new species in the genus *Turncurtovirus* (Hasanvand et al., 2018).

Mastrevirus

The genus *Mastrevirus* with 45 classified species is the second-largest genus within the family *Geminiviridae* (Fiallo-Olivé et al., 2021). Mastreviruses are known to be infectious to either monocot or dicot plants in association with ssDNA satellite molecules (Kumar et al., 2014; Hamza et al., 2018). Mastreviruses have monopartite genomes with ~2.5 to 2.7 kb in size that are transmitted by different leafhopper species (family *Cicadellidae*) (Ghodoum Parizipour et al., 2016). A typical mastrevirus genome encodes four proteins including MP (V1), CP (V2), Rep A (C1) and Rep (C1:C2). The C2 ORF always lacks an AUG start codon and is only expressed following the splicing of an intron, resulting in a single in-frame coding region including C1 and C2 ORFs which encodes the main viral replication-associated protein (Rep). The mastrevirus genome also contains two non-coding regions including LIR and SIR (Fig. 1). The LIR contains important sequences required for the viral replication by the rolling circle replication (RCR) mechanism (Heyraud et al., 1993). SIR contains important sequences required for the regulation of gene expression by harboring polyadenylation signals. Furthermore, SIR has a region on which a short complementary primer binds and starts the second strand synthesis (Kammann et al., 1991).

Wheat dwarf virus (WDV) is economically one of the most important monocot-infecting mastreviruses. WDV infections were reported in several countries in Europe (Bendahmane et al., 1995; Kundu et al., 2009), Asia (Behjatnia et al., 2011; Ekzayez et al., 2011; Xie et al., 2007), and Africa (Najar et al., 2000; Kapooria and Ndunguru, 2005). It has been reported that wheat and barley cultivations in Iran are also affected by this virus (Behjatnia et al., 2011). The infected plants show variable levels of yellowing, dwarfing, yellow leaf streak, marginal necrosis of leaves, and increased tillering, depending on the time of infection (Lotfipour et al., 2013). There are two strains of WDV; the wheat strain (WDV-Wheat) and the barley strain (WDV-Barley), whose full-length genomes showed a high (78-86%) nucleotide (nt) identity level (Schubert et al., 2007; Lotfipour et al., 2013).

Iran is a part of the Fertile Crescent where the cultivation of cereals started (Harlan, 1971). Considering the co-evolution of hosts and viruses for a long time, high variability within WDV populations is expected in Fertile Crescent (Ghodoum Parizipour et al., 2016). Therefore, the nt sequence analysis of different WDV isolates from Iran revealed a new geographical cluster for WDV-Wheat (Ghodoum Parizipour et al., 2016), and also, older history and lower diversity of WDV-Barley in comparison to WDV-Wheat (Ghodoum Parizipour et al., 2016). These results could verify the co-evolution of cereal mastreviruses with their cultivated and weeds hosts during civilization in Fertile Crescent.

Oat dwarf virus (ODW), another monocot-infecting mastrevirus has also been reported from Iran (Kamali et al., 2017; Pouramini et al., 2019). For the first from Iran the genome sequence of ODW, along with those of three more geminiviruses including BCTIR, TCTV, and WDV, was identified from leafhoppers feeding on beet and turnip plants by Kamali et al. (2017). However, the results of Pouramini et al., (2019) study indicated that, in contrast to WDV, ODV has a low incidence and a narrow host range in gramineous plants.

In addition to monocot-infecting mastreviruses in cereal and sugarcane (Boukari et al., 2017), dicot-infecting mastreviruses, such as *Chickpea chlorotic dwarf virus* (CpCDV), have high economic aspects in Africa, Asia, Australia, and the Middle East (Rojas et al., 2018). CpCDV has caused extensive losses in plants of *Fabaceae*, *Asteraceae*, *Amaranthaceae*, *Brassicaceae*, *Cucurbitaceae*, *Caricaceae*, *Chenopodiaceae*, *Leguminosae*, *Malvaceae*, *Pedaliaceae*, and *Solanaceae* families (Kanakala and Kuria, 2019). For the first time, CpCDV was detected and sequenced in sugar beet plants showing mild chlorosis and stunting, in Iran (Farzadfar et al., 2008). Afterward, natural hosts and genome characterization of an isolate of this dicot-infecting mastrevirus in eastern and southern Iran were identified (Askari, et al., 2018; Askari, et al., 2021). Results of these studies showed that leguminous plants including pulses, vegetables, foliage and wild species crops are infected with the CpCDV in eastern and southern Iran. Furthermore, crops such as fenugreek, common sainfoin, alfalfa and sophora were reported as the new hosts of the virus in Iran indicating that CpCDV has a wide natural host range in the family Fabaceae in Iran (Askari, et al., 2021). However, there is no more information about the incidence, genetic diversification, and severity of other dicot-infecting mastreviruses in Iran which reveals the requirement for more surveys in this country.

Capulavirus

Unlike other geminiviruses, capulavirus genomes have a complex arrangement of possible MP-encoding ORFs upstream of the CP ORF (Fig. 1. *Capulavirus*). Two or more of these ORFs may constitute an intron-containing MP (Fig. 1. *Capulavirus*). The genome of capulaviruses contains a large complementary-sense ORF (C3) that is completely embedded within the Rep (Fig. 1) like begomoviruses and curtoviruses (Varsani et al., 2017). Capulaviruses genomes like the genome of mastreviruses and becurtoviruses have two intergenic regions. Similarly, Rep in capulaviruses is expressed by a spliced complementary strand transcript (Roumagnac et al., 2015).

The genus Capulavirus contains four species including *Alfalfa leaf curl virus (ALCV)*, *Euphorbia*

caput-medusae latent virus, French bean severe leaf curl virus and Plantago lanceolata latent virus (Varsani et al., 2017), among them ALCV has been reported from Iran (Davoodi et al., 2018a). ALCV, as the first aphid-transmitted geminivirus, causes severe disease symptoms in alfalfa (*Medicago sativa*) (Roumagnac et al., 2015). In addition to Iran (Davoodi et al., 2018a), ALCV has been found throughout the Mediterranean basin (Roumagnac et al., 2015) and Argentina (Bejerman et al., 2018). Complete genome analysis of recovered isolates from different countries revealed a high recombination rate in ALCV populations (Davoodi et al., 2018b). Data analysis supported the hypothesis that ALCV emerged and diversified in the Middle East, specifically in Iran, before spreading to the western Mediterranean basin and Argentina (Davoodi et al., 2018b). ALCV worldwide distribution seems to be tightly dependent on the widespread activity of the vector aphid, Aphis craccivora (Davoodi et al., 2018b).

Proposed Control Approaches for Geminiviruses IPM Program in Iran

Iran has been revealed as a noteworthy potential origin of emergence and diversity for some geminiviruses including members of the genera *Becurtovirus*, *Capulavirus and Turncurtovirus*, in an overview based on the presence of members of at least six genera with high distributions (Fig. 2) and genetic variations. Despite their economic and agricultural importance, there is no organized management program to decrease geminivirus losses in Iran. Some compatible approaches have been proposed to progress an Integrated Pest Management (IPM) program about geminivirus infections in Iran.

Approaches Based on the Hosts

Resistant/Tolerant Cultivars; Screening or Breeding

Classical breeding techniques for the selection of crop lines resistant to plant pathogens are more socially accepted and environmentally safe. In this scenario, screening plant commercial genotypes with high yield performances for geminiviruses resistance is needed to increase the number of resistance sources useful for breeding (Tabein et al., 2017).

As mentioned before, tomato (yellow) leaf curl disease (T(Y)LCD) caused by different species of T(Y)LCV, is one of the most destructive and limiting factors in tomato crops worldwide. Since the first TYLCD report in the Jordan Valley in the early 1960s (Czosnek 2008), up to now, six resistance/tolerance genes, i.e. Ty 1-6 genes, have been mapped in wild tomato species and exploited for resistance breeding against T(Y)LCVs. These genes have different abilities to confer resistance against different infecting tomato begomoviruses (Lapidot et al., 2015).

Some commercial tomato genotypes harboring resistance Ty genes exhibit different levels of resistance to T(Y)LCD which will require further investigation. A phenotypic survey was undertaken to evaluate the resistance level to the main TYLCD-inducing viruses, including TYLCV and TYLCSV, in nine Iranian commercial tomato cultivars in south Iran (Tabein et al., 2017). Seven weeks post-agroinoculation (wpi), two cultivars including SJ12 and RFT112, resulted in high resistant phenotypes to both begomoviruses and four cultivars including Super Urbana, Early Urbana-Y, CalJ-N3 and Sunseed 6189 showed tolerance to at least one of the tested viruses. Molecular marker analysis revealed that resistant tomato genotypes (SJ12 and RFT112) harbor *Ty-1/Ty-3* and *Ty-2* (Tabein et al., 2017). Given their high resistance, they can be considered good candidates for cultivation and breeding in Iran's south where the incidence of TYLCD is significantly elevated.

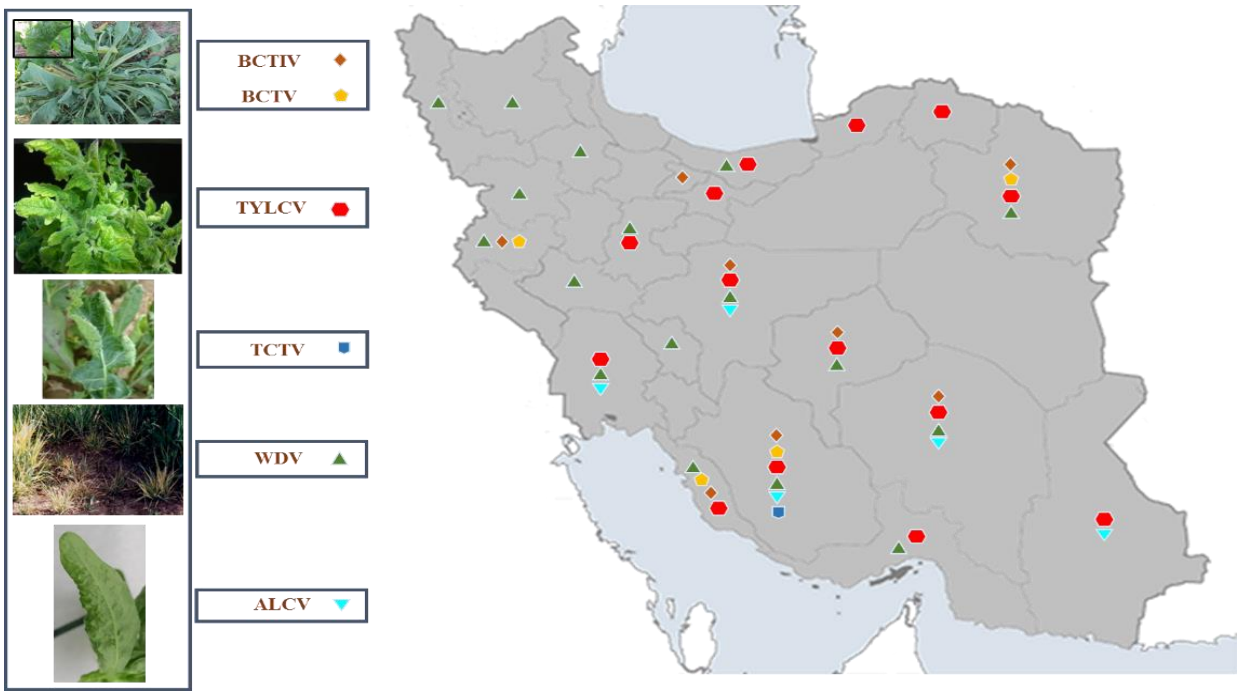

Fig. 2. The geographical map of the areas in Iran (right) where different geminivirus species have been reported. Typical symptoms of BCTV (and BCTIV), TYLCV, TCTV, WDV and ALCV have been shown from top to bottom (left).

In another study (Azizi et al., 2008), 134 accessions of *Solanum lycopersicum* and six accessions of *Solanum peruvianum* were assessed for resistance to an Iranian isolate of TYLCV (TYLCV-Ir2, accession No. EU085423 in NCBI GenBank) using viruliferous whitefly (*Bemisia tabaci*) inoculation method and grafting inoculation methods. All whitefly-inoculated accessions of *S. lycopersicum* demonstrated various degrees of TYLCD disease symptoms. On the other hand, all six whitefly-inoculated accessions of *S. peruvianum* were resistant and remained symptomless. However, the high level of resistance noted in whitefly-inoculated accessions of *S. peruvianum* was not observed in graft-inoculated plants of these accessions. The results suggested that accessions of *S. peruvianum* may be merely resistant to vector inoculation of TYLCV (Azizi et al., 2008). The same TYLCv isolate (TYLCV-Ir2, accession No. EU085423 in NCBI GenBank) was used by Montazeri Hedesh et al. (2011) to evaluate the reaction of 34 common bean lines for their reaction to TYLCV by whitefly inoculation method under greenhouse conditions. Results revealed that five and two lines were identified as resistant and tolerant to TYLCV-Ir2, respectively. The TYLCV-Ir2 vector (*B. tabaci*) feeding preference for common bean lines was also assessed in the aforementioned study. Results indicated a significant difference in adult whitefly numbers among bean lines, but there was no relationship between the number of whiteflies and disease symptom severity. Finally, the authors of this study suggested that the resistance to TYLCY-Ir2 expressed in common bean lines may be useful as a source of resistance for the development of resistant commercial common bean cultivars (Montazeri Hedesh, 2011).

Considering the other geminivirus infectious diseases, it is worth mentioning that curly top disease (CTD), caused by curly top viruses (i. e. BCTV and BCTIV), is one of the most destructive viral diseases of sugar beet and other dicotyledonous plants. Many studies have been performed to evaluate resistance against curly top viruses in Iran. Most of these studies indicated that using resistance sources could be a promising strategy to control CTD, as discussed above for TYLCD. In this regard and in the first effort, screening of sugar beet cultivars to evaluate resistance against an Iranian isolate of BCTV has revealed three distinct susceptibility groups based on the disease severity index (Fatahi et al., 2012). The tolerant group included 7233, H5505, BR1, HM1990 and FIMMA cultivars while Rasoul, Afshari, Balk Shiraz hybrid, Zarghan, P.P.8, P.P.22, Dorothea, Rhizofouret, IC, Flores, Hilma and Polyrow cultivars formed the susceptible group and the Brigita cultivar formed the third group that was super-susceptible (Fatahi et al., 2012). Furthermore, to find a natural resistance source to curly top viruses in Iran (i.e. BCTV and BCTIV), the reaction of 50 sugar beet lines to these viruses was evaluated by Montazeri Hedesh et al. (2016) using agroinfection of sugar beet lines with the infectious clones of the BCTV and BCTIV under greenhouse condition. Five out of 50 lines were found to be resistant to both viruses. These lines could be suggested for cultivation in Iran. In addition, some lines displayed completely different reactions to the viruses indicating different effects of the viruses on sugar beet lines (Montazeri Hedesh, 2016). In another study, thirty-eight genotypes of sugar beet procured from Sugar Beet Seed Institute (SBSI), Karaj, Iran, were screened in terms of their resistance to two species of beet curly top virus, BCTV and BCTIV (Saadati et al., 2021). Results showed six genotypes including S1 91019, S1 91022, S1 91023, S1 91028, S1 91029 and S1-91041 were resistant to both viruses. More screening is necessary to introduce yielding and less susceptible genotypes for beet curly top disease management.

In another series of studies, reactions of some host plants of CTVs to co-infection of these viruses with cucumber mosaic virus (CMV) were studied. Rezaei et al., (2020) evaluated the efficiency of four gene silencing constructs including OUT –h, IN –hp, sense and antisense constructs against CTVs in Arabidopsis thaliana transgenic plants. They indicated that the transformed lines with each of the four constructs were significantly different in the severity of CTD symptoms, plant height and the number of flowering stems compared to their respective controls when the tested plants were infected with BCTV and BCTIV. Although the transgenic plants showed resistance to BCTV and BCTIV, in their challenge inoculation experiments it was shown that these resistances were suppressed by CMV infection (Rezaei et al., 2020). In another study, Astaraki et al., (2021) indicated that co-infection of BCTV and BCTIV with CMV leads to the breakdown of resistance of sugar beet, pepper and bean resistant cultivars to BCTV and BCTIV and induction of severe symptoms in inoculated plants. They concluded that the host plant does not affect the interaction of these viruses (Astaraki et al., 2021).

During the past few years, the development and utilization of tolerant and resistant cultivars of some commercial crops, particularly in south Iran, has caused a decrease in crop losses caused by geminiviruses. As a successful case, in Khuzestan, Fars, and Boushehr provinces, wide plantings of tomato Sunseed 6189 and other resistant cultivars resulted in the reduction of TYLCD symptoms in many regions with low disease pressure (Saeid Tabein, unpublished data). However, the high rate of diversification in geminiviruses is the main challenge in the use of tolerant and resistant cultivars because resistance-breaking strains emerge frequently. Another challenge is maintaining betasatellites by different geminiviruses (Nawaz-ul-Rehman et al., 2009) through interactions with host/virus factors which should be considered.

Approaches Based on the Control of Vectors Populations

Insecticides Application

Using insecticides is the most popular method to control diseases caused by geminiviruses through insect vector management (Rojas et al., 2018). In an IPM protocol, insecticides should only be applied when vector

populations reach a predetermined economic threshold (ET), which should be determined according to each region. Establishing an ET requires a thorough understanding of the pest's population dynamics in the specific crop. Pest and crop phenology, pest population growth and injury rates, and the practical aspects of management tactics must be considered when establishing ETs (Pedigo and Higley., 1992).

The time of insecticide application can be distinguished using yellow cards, which trap vectors and determine their population in protected cultures and open fields (Rojas et al., 2018). The common using methods of systemic insecticides such as neonicotinoids (e.g., acetamiprid, dinotefuran, imidacloprid, and thiamethoxam) are spraying and drip irrigation during semi-mature or mature stages in plants in Iran. While as a preventative measure for the hypersusceptibility of seedlings to geminiviruses, seeds or transplants should be treated with these systemic insecticides in greenhouses or seedbeds (Rojas et al., 2018). Ongoing use of systemic insecticides such as neonicotinoids is suggested along with the application of contact insecticides (e.g., bifenthrin, fenpropathrin, and lambda-cyhalothrin) or insect growth regulators (e.g., buprofezin, pyriproxyfen, and spiromesifen).

Due to the emergence of insecticide-resistant populations, it has become increasingly challenging to control vector populations chemically (Nauen and Delhom, 2005). This problem occurred for B. tabaci in Iran (Basij et al., 2017). Repeated application of similar active ingredients has led to the selection of individuals with resistance to many of the most frequently used insecticides (Horowitz et al., 2004). New emerging populations with resistance to insecticides could be a serious threat when replace with the native populations (Gilbertson et al., 2015). Therefore, it has been suggested to rotate insecticides with different modes of action and apply only the recommended number of applications during a growing season (Rojas et al., 2018). Rotation application of Azadirachtin, Oberon (Spiromesifen), Movento (Spirotetramat), Proteus (Deltametrin+Tiaclopride), Starkle (Dinotefuran), Sivanto (Flupyradofurone), and Applaud (Buprofezin) has been suggested to control sucking insect vectors of geminiviruses including B. tabaci in Iran (Mosallanejad 2020). However, it has been suggested that the ongoing introduction of new compounds, unless carefully regulated and coordinated, seems bound to increase exposure to neonicotinoids and enhance conditions favoring the appearance of resistant phenotypes of insects (Nauen and Denholm, 2005).

Biological Control

Biological control can be used to manage insect vectors and subsequently geminiviruses-induced diseases, especially for the whitefly B. tabaci in protected culture (Rojas et al., 2018). It has been reported that different biological control agents are active in the whitefly's egg, nymph and adult stages (Hollis 1991). By releasing common green lacewing (Chrysoperla carnea) insects in the early season, its larvae can feed on whiteflies' eggs and nymphs. *Encarsia formosa and E. eremicus are B. tabaci-specific* parasites effective in many environments while Amblyseius swirskii is a predator mite effective in warm and humid areas (Hollis 1991). Using biological control fungus, Beauveria bassiana, resulted in to decrease in the feeding/reproduction of whiteflies and the killing of infected members (Hollis 1991). As a result, the repeated release of biological control agents before and after planting can decrease whitefly populations and inhibit their ability to reach economic thresholds and transmit geminiviruses.

Agricultural Measures

Plants are most susceptible to geminivirus infections at their early stages, so the highest economic losses will occur when young seedlings are infected in greenhouses or fields (Rojas et al., 2018). In addition to avoiding the highest vector populations and their activity period, using healthy standard tolerant/resistant hybrid seeds and propagative tissues allow young plants to escape the susceptible phase. Moreover, it has been shown that good nutrition stimulates rapid and strong growth in seedlings and induced gene silencing to protect plants against viral infections (Thirumdas et al., 2021). Using microelements and seaweed extracts in Iranian crop fields is necessary for more effective nutrition (Banihashemi, 2016).

Weeds act as reservoir hosts for geminiviruses and/or alternate hosts for feeding insect vectors (Esmaeili and Heydarnejad, 2014; Heydarnejad et al., 2007; Kamali et al., 2018; Pouramini et al., 2019; Shamshiri et al., 2019). Controlling weeds in fields and their borders by tilling and applying herbicides is a common approach to decrease the ability of vectors to spread geminiviruses. Trifluralin, glyphosate, paraquat and metribuzin are some popular herbicides for narrow and broad-leaved weeds in some crops such as cotton, sugar beet, vegetables, tobacco and tomato in Iran. Clodinafop-propargyl, mesosulfuron+idosulfuron+mefenpyr-diethyl are proposed to control narrow-leaved weeds in the cereals while sulfosulfuron is used for broad-leaved weeds and mesosulfuronmethyl+iodosulfuronmethyl-sodium+diflufenican is used for both of weed groups.

RNA Interference (RNAi) as a New Promising Approach against Geminiviruses

RNA interference (gene/RNA silencing) is a defense and gene regulatory pathway in eukaryotic cells that functions as an antiviral system in plants (Bisaro, 2006). Silencing pathways are complex and partially overlapped, but all involve the cleavage of double-stranded RNA (dsRNA) into small interfering RNAs (siRNAs) by Dicer-like (DCLs) proteins (Blevins et al., 2006). In plants, dsRNA or self-complementary hairpin RNA transcribed from engineered inverted repeats were shown to be potent inducers of a gene silencing response when directed against transgenes (Hamilton et al., 1998; Waterhouse et al., 1998; Johansen and Carrington, 2001).

Different genes of geminiviruses are targeted by antisense or hairpin constructs using transformative and non-transformative methods, which decrease viral DNA accumulation and eliminate virus symptoms (reviewed

by Loriato et al., 2020). Nevertheless, some abnormal growth patterns were observed in the first field trial of transgenic tomato plants using hairpin constructs expressing different genes of TYLCV (Fuentes et al., 2016). It revealed that over a long-term time period, the gene expression profile of tomato could be affected by virus-derived siRNAs, highlighting the applicability of limitations of this technique (Fuentes et al., 2016).

As an alternative approach, it has been demonstrated that dsRNAs derived from viral sequences can interfere with plant RNA viruses' infection in a sequence-specific manner by directly delivering dsRNAs into the plant cells (Mitter et al., 2016; Tabein et al., 2020; Tenllado et al., 2004; Petrov et al., 2015) or by spraying bacterially expressed dsRNAs, referred as the external application of dsRNA vaccination (Tenllado et al., 2003; Gan et al., 2010).

Analysis of high-throughput sequencing data in different geminivirus-infected hosts identified hot spots in their genomes that generate the most derived siRNAs (Miozzi et al., 2013; Bai et al., 2016). It has been indicated that this could lead to more interference with virus gene expression if these sequences are targeted (Tabein, 2022). However, *N. benthamiana* plants were not protected from viral infections by targeting the *C1*/*C4* overlapping region and sequence of bidirectional transcription motif as siRNA hot spots in the genome of TYLCV and TYLCSV (Tabein, 2022). The same result was already reported about the external application of dsRNA against tomato leaf curl Gujarat virus (Namgial et al., 2016). However, Melita et al. (2021) recently showed that the topical application of *C4*- and *V2*-derived dsRNAs from a mild strain of TYLCV (TYLCV-Mld) could reduce disease severity and incidence in tomato plants (Melita et al., 2021). Therefore, several factors appear to be involved in the efficiency of exogenously applied dsRNAs against begomoviruses infection.

Exogenously applied dsRNAs is a dose-dependent mechanism (Dubrovina and Kiselev, 2019; Tenllado and Díaz-Ruíz, 2001). External application of dsRNAs introduces a certain amount of dsRNAs that might not be enough to protect plants against a high rate of replication in geminiviruses (Tabein, 2022). In contrast, the hairpin construct provides a higher dsRNA concentration level through the continuous expression of dsRNA (Tabein, 2022). Moreover, the induction of resistance by the external application of dsRNAs largely depends on selecting target sequences (Tabein et al., 2020). It must be considered that using different gene silencing suppressors, including C4 and V2, and nuclear replication in infected host cells (Brown et al., 2012) could protect geminivirus genomes in confronting against RNAi pathway (Hanley-Bowdoin et al., 2013). These results suggest the need for more studies to investigate the efficiency of RNA vaccination by targeting different sequences of geminiviruses and their vectors. Loading of the most suitable candidate dsRNAs on nano-particles/sheets could introduce species-specific biocontrol agents for each geminivirus/vector complex.

CONCLUSIONS

Geminiviruses are remarkable plant pathogens with arising economic losses in Iran. They infect ornamentals, cereals, vegetables and other crops on a large scale, specifically, in south Iran. Climate change has been one of the most important factors in the spread of geminiviruses in the past decade. This phenomenon is linked to an increase in viral vector activity in tropical regions of the country.

BCTIV, TLRV and TCTV, geminiviruses that were only identified in Iran (Bolok Yazdi, et al, 2008; Briddon et al., 2010; Heydarnejad et al, 2013; Kamali et al, 2016; Soleimani et al., 2013) suggest a high potential origin for diversification of members of the family *Geminiviridae* in this country. High genetic variation in WDV, TCTV and ALCV populations in Iran could support this hypothesis. There is a need for more detection studies in order to gain a comprehensive understanding of genetic diversity and phylogenetic analyses of geminiviruses in crops and weeds in Iran. Additionally, by increasing the number of geminiviruses and geminiviruses-like genomes in fruit trees, it is required to screen different fruit tree hosts, including citrus, *Vitis* species and etc, to identify and describe new species for this country.

The application of new insecticides and different agricultural measures in industrial crop fields caused a reduction in viral vector activity during the last years. Moreover, the development of new tolerant and resistant crop cultivars decreased in disease incidence and severity. However, geminiviruses will continue to cause crop losses as long as traditional agriculture is dominant in most regions of Iran. To train control approaches and their application in all regions of the country, a national IPM program is suggested.

However, Geminiviruses will continue to cause crop losses as long as traditional agriculture prevails in most regions of Iran.

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مقاله مروری

وضعیت جمینی‌ویروس‌ها در ایران، بیمارگرهای شگفت‌انگیز گیاهی

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واژه‌های کلیدی:
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چکیده - تیره *Geminiviridae* با چهارده جنس پذیرفته شده و تعداد فزاینده‌ای از گونه‌های نامشخص، در حال حاضر به عنوان بزرگ‌ترین تیره ویروس‌های آلوده‌کننده گیاهان شناخته می‌شود. پیکره‌های بیست‌وجهی دوقلوی آنها حاوی دی‌ان‌ای‌های ژنومی تک‌لا است، که به طور طبیعی توسط حشراتی از راسته نیم‌بالان (Hemiptera) شامل سفیدبالک *Bemisia tabaci* و چند گونه زنجرک و شته در طیف وسیعی از گیاهان میزبان منتقل می‌شوند. همچنین برخی جمینی‌ویروس‌ها در میزبان‌های خاصی توسط بذر انتقال می‌یابند. علاوه بر تغییرات اقلیمی، کشت‌های صنعتی و توسعه تجارت جهانی، انعطاف‌پذیری ژنتیکی جمینی‌ویروس‌ها منجر به افزایش نرخ توزیع آنها شده است. بیماری‌های ناشی از جمینی‌ویروس‌ها یک محدودیت جدی برای اکوسیستم‌های کشاورزی در مناطق گرمسیری و نیمه‌گرمسیری سراسر جهان است. زیان‌های اقتصادی ناشی از آلودگی به جمینی‌ویروس‌ها در سال‌های اخیر به ویژه در مزارع و گلخانه‌های ایران افزایش یافته است. تعریف دو جنس متمایز با داشتن ویژگی‌های مولکولی و زیستی منحصر به فرد شامل جنس‌های *Becurtovirus* و *Turncurtovirus*، و وجود گونه‌ها و سویه‌های مختلف از سایر جمینی‌ویروس‌ها، ایران را به عنوان یکی از منشأهای بالقوه برای تنوع جمینی‌ویروس‌های تک‌بخشی دنیای قدیم معرفی می‌کند. در این بررسی به وقوع و تنوع جمینی‌ویروس‌ها در ایران پرداخته شده است و علاوه بر این، برخی اقدامات کنترلی قابل اجرا بر اساس سازگاری با اکوسیستم کشاورزی ایران پیشنهاد شده است که برای سایر مناطق گرمسیری و نیمه‌گرمسیری جهان نیز قابل توصیه خواهد بود.