



Viral disease of tomato crops (*Solanum lycopersicum* L.): an overview

Sheue Ni Ong¹ · Sima Taheri¹ · Rofina Yasmin Othman^{1,2} · Chee How Teo¹

Received: 3 March 2020 / Accepted: 25 April 2020 / Published online: 6 May 2020
© Deutsche Phytomedizinische Gesellschaft 2020

Abstract

Global production of tomato has been hampered by the increased incidences of tomato viral disease. The high genetic heterogeneity of tomato plant viruses, because of their high mutation rates, has led to ineffective control strategies and the fast spread of the viruses. Viruses utilize the resources in host plants for their replication. Therefore, identification and removal of the non-redundant proteins in the tomato plant based on the biological properties of the virus combined with an RNAi strategy may be a future control strategy. In this review, fourteen tomato viral diseases and their causal agents are reviewed and the control strategies for tomato viral diseases are discussed.

Keywords Tomato · Plant virus · Symptoms · Genomes · Insect vector · Plant virus control

Introduction

Tomato, *Solanum lycopersicum* L., is a major cultivated agriculture crop all around the globe, which garnered a worldwide production of over 180 million tonnes in 2017 (FAOSTAT 2019). Based on the data from FAOSTAT (2019), China has the highest tomato production with over 59 million tonnes in 2017 followed by Turkey, USA, Egypt, Italy, Spain, Mexico, Nigeria, Brazil and the Russian federation. Tomato can be consumed fresh or sold as soups, sauces and ketchup (Harvey et al. 2002). Besides being an edible food, several secondary metabolites found in tomato can be used as anti-oxidant and may also have anti-cancer functions (Raiola et al. 2014). However, as a crop, the high susceptibility of tomato to virus disease causes yield decline of between 70 and 95% and could affect supply (Rashid et al. 2016). Plant viruses consist of both DNA and RNA viruses where they can be in the form of a single- or double-stranded DNA or RNA (Wang et al. 2012). The difference

between DNA and RNA viruses is their mode of replication where DNA viruses rely on the DNA replication machinery of the host and RNA viruses do not rely on the cellular DNA machinery of the host (Wang et al. 2012). Control of plant viruses remains an important agriculture issue due to its high mutation rate that promotes divergence of genetic strains (Garcia-Arenal et al. 2001). This leads to the need to study the host–virus interactions and viral gene expression to develop sustainable and efficient viral control strategies. This review targets to collate the current information on the viral genome, transmission methods, viral vectors and host plants as well as disease symptoms of virus diseases infecting tomato to provide a better understanding of each virus. Additionally, current and potential control strategies will be discussed.

Types of tomato plant viruses

Tomato DNA virus

The genomes of tomato plant viruses are either DNA or RNA (Table 1). Among all the major tomato viral diseases, only viruses from the family *Geminiviridae* are DNA viruses. In this family, the genus begomovirus plays a crucial role as a pathogen that causes serious impact on economically important crops globally (Zubair et al. 2017). Geminiviruses are ranked second for the number of viruses in its family that affects both monocot and dicot plants (Rojas 2004).

✉ Rofina Yasmin Othman
yasmin@um.edu.my

✉ Chee How Teo
cheehow.teo@um.edu.my

¹ Centre for Research in Biotechnology for Agriculture (CEBAR), University of Malaya, 50603 Kuala Lumpur, Malaysia

² Faculty of Science, Institute of Biological Sciences, University of Malaya, 50603 Kuala Lumpur, Malaysia

Table 1 Tomato plant viruses and their corresponding GenBank accession number and genome size

Genus	Species	Genome size (bp)	GenBank accession no	References
DNA virus				
<i>Curtovirus</i>	<i>Beet curly top virus</i> (BCTV)	2930	KU892789	Rondon et al. (2016)
<i>Begomovirus</i>	<i>Ageratum yellow vein virus</i> (AYVV)	2750	KM051527	Mahmoudieh et al. (2016)
		1342	KM051528	
RNA virus				
<i>Potexvirus</i>	<i>Pepino mosaic virus</i> (PepMV)	6450	AF484251	Aguilar et al. (2002)
<i>Tobamovirus</i>	<i>Tomato mottle mosaic virus</i> (ToMMV)	6398	KF477193	Li et al. (2014)
<i>Potyvirus</i>	<i>Tobacco etch virus</i> (TEV)	9539	DQ986288	Martinez et al. (2016)
<i>Tombusvirus</i>	<i>Tomato bushy stunt virus</i> (TBSV)	4776	NC_001554	Hearne et al. (1990)
<i>Crinivirus</i>	<i>Tomato chlorosis virus</i> (ToCV)	8595	AY903447.1	Lee et al. (2018)
		8249	KJ815045.1	
<i>Torradovirus</i>	<i>Tomato torrado virus</i> (ToTV)	7808	NC_009013.1	Verbeek et al. (2007)
		5403	NC_009032.1	
<i>Alfamovirus</i>	<i>Alfalfa mosaic virus</i> (AMV)	3644	NC_001495	Cornelissen et al. (1983a)
		2593	NC_002024	Cornelissen et al. (1983b)
		2037	NC_002025	Barker et al. (1983)
<i>Cucumovirus</i>	<i>Cucumber mosaic virus</i> (CMV)	3382	MG182148	Moyle et al. (2018)
		3050	MG182149	
		2218	MG182150	
<i>Anulavirus</i>	<i>Pelargonium zonate spot virus</i> (PZSV)	3383	JQ350736	Giolitti et al. (2014)
		2433	JQ350739	
		2655	JQ350737	
<i>Illavirus</i>	<i>Tobacco streak virus</i> (TSV)	3523	FJ561302	Usha Rani et al. (2009)
		2903	FJ561303	
		2213	FJ561301	
<i>Orthospovirus</i>	Tomato spotted wilt virus (TSWV)	8897	NC_002052	De Haan et al. (1991)
		4821	NC_002050	Kormelink et al. (1992)
		1404	NC_002051	De Haan et al. (1990)

However, according to Cantu-Iris et al. (2019), begomoviruses infect dicot plants solely. According to Zhou (2013), begomovirus affects a wide range of dicot host species including *Carica papaya*, *Capsicum annuum* and another 40 hosts that are listed in his review. Begomoviruses which replicate in the nucleus of the host have a twinned capsid morphology, with either a monopartite or bipartite circular single-stranded DNA (ssDNA) (Hosseini et al. 2010). Satellite DNAs such as alpha satellites and beta satellites (Fig. 1) can be associated with the monopartite begomoviruses (Zhou 2013). There are also delta satellites which are non-coding satellites associated with the begomovirus (Hassan et al. 2016). According to Rojas et al. (2005), these viruses replicate through double-stranded DNA (dsDNA) by a rolling circle replication (RCR) mechanism. First, a dsDNA intermediate will be formed from the ssDNA genome and the viral ssDNA begins to amplify through the starting position of RCR which is found within the conserved sequence TAATATTAC. Finally, the newly formed ssDNA will be

encapsidated and then moved to the adjacent cells (Gutierrez 2002). Among begomoviruses, the *Tomato yellow leaf curl* (TYLC) has the most significant impact over tomato production by causing disease in subtropical and tropical regions worldwide (Moriones et al. 2011). A review of the “top 10 plant virus list” by Scholthof et al. (2011) showed that TYLC ranked third based on its scientific and economic importance while Suresh et al. (2017) listed a total of 96 other species of begomovirus across the world that are infecting tomato.

There are six proteins (two ORFs in the virion sense and four ORFs in the complementary sense in DNA A; Fig. 1) encoded by monopartite begomoviruses, which are the genes that encode for the coat protein (V1), pre-coat protein (V2), replication-associated protein (C1), transcriptional activator protein (C2), the replication enhancer protein (C3) and the protein involved in movement and symptom development (C4, Ammara et al. 2015). V1 and V2 are in virion sense strand, whereas C1, C2, C3 and C4 in complementary sense strand

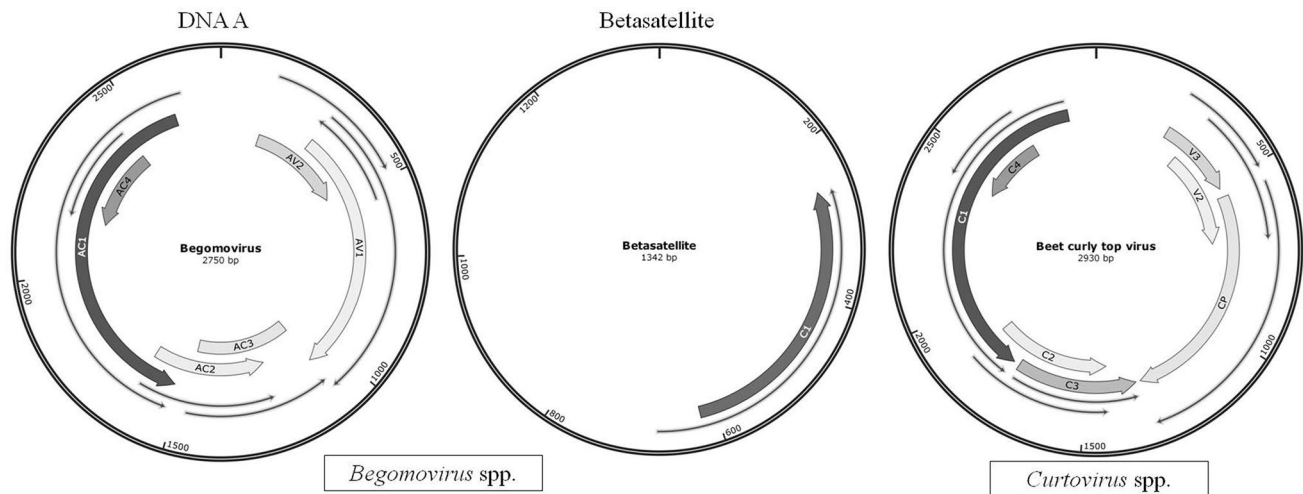


Fig. 1 Genome structure of circular single-stranded DNA viruses from genus *Begomovirus* and *Curtovirus*. Betasatellite is associated with some begomoviruses. There are six ORFs shown in DNA A of *Ageratum yellow vein virus* and seven ORFs shown in *Beet curly*

top virus. Both have coding regions in both the virion and complementary sense strands. Sequence extracted from GenBank accession number of KM051527 and KM051528 for *Begomovirus* spp. and KU892789 for *Curtovirus* spp.

(Srivastava et al. 2015). Each protein holds a different function; for instance, the coat and pre-coat protein is responsible for virus movement in the plant, but the coat protein is also responsible for the movement between plants through insect vectors (Diaz-Pendon et al. 2019). While C1 and C3 ORFs are involved in replication, C2 is involved in transactivation expression of the virion sense genes and C4 determines (or is related to) pathogenicity (Zerbini et al. 2017).

Beet curly top virus (BCTV; Table 1; Fig. 1) is the causal agent of the curtovirus disease from the family *Geminiviridae* that is classified in the genus *curtovirus* (Jeger et al. 2017). This species was first discovered infecting sugar beet in 1967 in Iran (Gibson 1967). The susceptible hosts comprise of cucurbit, bean, pepper, beet, tomato, potato and weed species (Lam et al. 2009). These viruses have circular ssDNA genome and encapsidated within twinned icosahedral particles (Lam et al. 2009). The genome of this genus possesses one intergenic region (IR), three virion sense and four complementary sense ORFs (Varma and Malathis 2003; Fig. 1). The complementary sense gene products are replication and transcription regulator proteins such as C2, C4, replication protein (Rep) and replication enhancer proteins (REn/C3) (Bolok Yazdi et al. 2008). Three other proteins are coded by the virion sense strand, including a V2 protein, movement protein (MP) and coat protein (CP) (Gutierrez 2002; Hosseini et al. 2010).

Tomato RNA virus

Tomato Monopartite RNA virus

The RNA viruses that affect tomato are all single-stranded viruses, but the genomes are either monopartite, bipartite or tripartite. *Potexvirus* (family: *Alphaflexiviridae*; King et al. 2012), *Tobamovirus* (family: *Virgaviridae*; King et al. 2012), *Potyvirus* (family: *Potyviridae*; Gibbs and Ohshima 2010) and *Tombusvirus* (family: *Tombusviridae*; Nasir et al. 2016) are made up of monopartite positive single-stranded RNA (ssRNA) genome (Table 1; Chung et al. 2008; Jeger et al. 2017; Luria et al. 2017; Verchot-Lubicz et al. 2007). *Pepino mosaic virus* (PepMV; Fig. 2) from genus *Potexvirus* is a flexuous, rod-shaped particle (Hanssen et al. 2010). The *Potexvirus* spp. consists of a ssRNA of positive polarity and contains five ORFs (Verchot-Lubicz et al. 2007; Fig. 2). The ORFs include replicase gene, triple gene block (TGB) encoding TGB1, TGB2 and TB3 for viral movement and suppress silencing and lastly coat protein (Agirrezabala et al. 2015). According to Moreno-Perez et al. (2014), molecular and biological characteristics of PepMV categorize it into six strains, including the North American strain (US1/CH1), the

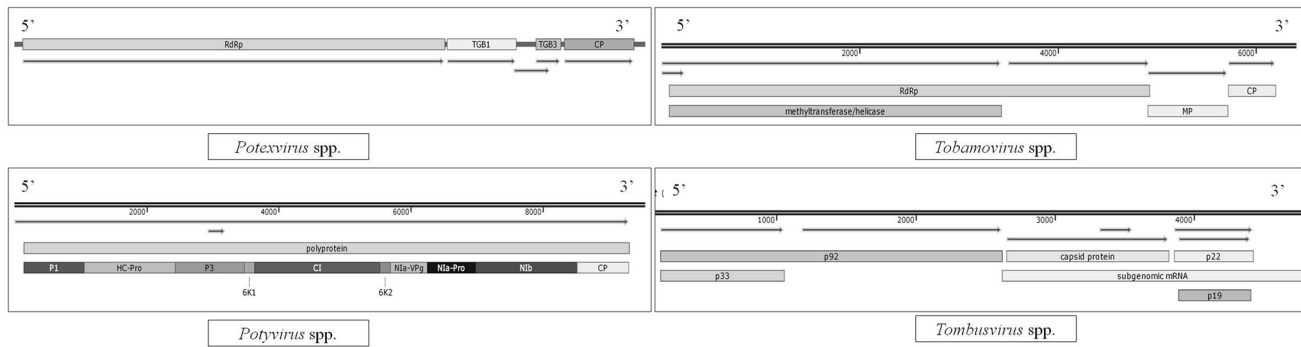


Fig. 2 Genome structure of positive-strand monopartite RNA viruses from genus *Potexvirus*, *Tobamovirus*, *Potyvirus* and *Tombusvirus*. Sequences extracted from GenBank accession number AF484251, KF477193, DQ986288 and NC_001554, respectively

recombinant strain (US2), European strain (EU), Chilean strain (CH2), the original Peruvian strain (LP) and the new Peruvian strain (PES). PepMV was found to infect solanaceous crops as well as test plants such as *S. tuberosum*, *S. melongena*, *Physalis florida*, *Nicotiana benthamiana* and *Datura stramonium*, with most of the host species in the *Solanaceae* family (Blystad et al. 2015).

For the tobamoviruses genus, viruses that have been found in tomato are *Tobacco mosaic virus* (TMV), *Tomato mottle mosaic virus* (ToMMV; Table 1; Fig. 2), *Tomato mosaic virus* (ToMV), *Tobacco mild green mosaic virus* (TMGMV) and *Tomato brown rugose fruit virus* (ToBRFV) (Dombrovsky and Smith 2017). TMV, TMGMV and ToMV affect tomato production worldwide (Suresh et al. 2017). Tobamoviruses have rod-shaped particles (Luria et al. 2017). The susceptible crops of the tobamovirus include the *Cucurbitaceae* and *Solanaceae* families (Dombrovsky and Smith 2017). Their genome possesses four ORFs (Li et al. 2017). The first two ORFs encode the replication protein while ORF-3 and ORF-4 encode MP and CP, respectively (Ishibashi and Ishikawa 2016; Fig. 2).

Species of *Potyvirus* genus include *Potato virus Y* (PVY) and *Tobacco etch virus* (TEV) (Table 1; Fig. 2). The genome of potyviruses consists of a short ORF placed in the long ORF (Chung et al. 2008). Potyviruses have a positive-sense RNA genome with flexuous filament particles (Kenyon et al. 2014). This RNA can perform as a messenger RNA (mRNA) where the 5' non-coding part can be used as a promoter for translation (Sharma et al. 2014). The long ORF in the genome will be translated into a polyprotein and further cut into 10 useful proteins by virus-encoded proteinase (Trigiano et al. 2003; Fig. 2) including the CP, nuclear inclusion b protein (Nib), nuclear inclusion a protein (NIa-Pro), nuclear inclusion a linked VPg protein (NIa-VPg), 6K2 protein, C1 protein, 6K1 protein, P3 protein, helper component protein (HC-Pro) and P1 protein (Trigiano et al. 2003). The most distinctive characteristics of the potyviruses are the formation of the inclusion bodies in the affected cells (Edwardson

1974). Based on the supplementary data of Gibbs and Ohshima (2010), host plants of PVY are not only tomato but *Capsicum* and *Solanaceae* species as well. Tsdaley (2015) has also compiled the natural and experimental host range of PVY in his review which includes *Capsicum* and *Solanaceae* species as well as ornamental plants and weeds.

Similar to *Potyvirus*, *Tomato bushy stunt virus* (TBSV; Table 1; Fig. 2) which is a part of *Tombusvirus* genus has a tiny unenclosed virus with isometric particles of diameter approximately 30 nm (Nawazet al. 2014). This monopartite positive-sense ssRNA virus possesses five ORFs in its genome (Nawazet al. 2014; Fig. 2). Proteins coded by the first and second ORF are needed for replication of the virus (Scholthof et al. 1995). ORF-3 coded for coat protein, while the viral movement protein codes for cell-to-cell movement of the virus and in some plants for symptom determination is encoded by ORF-4 (Scholthof et al. 1993). ORF-5 plays a part in causing the necrotic symptoms as well as virus long-distance transmission (Hafez et al. 2010). TBSV affected areas are Tunisia, USA, Portugal, Morocco, Germany, Canada, France, Italy, Great Britain, Spain and Argentina (Suresh et al. 2017). The hosts of this virus are lettuce, spinach, apple, pear, tobacco, tomato, eggplant, tulip and pepper (Artelli et al. 2001).

Tomato bipartite RNA virus

The genus *Crinivirus* belongs to the family of *Closteroviridae* and consists of positive-sense bipartite ssRNA genome (Wintermantel 2004). The member of this family all consists long and flexuous rod-shaped virions (Kiss et al. 2013). The first RNA encodes four ORFs for replication-associated proteins (ORF1a, ORF1b, ORF2 and P5; Fig. 3). RNA-2 on the other hand codes for putative MP, CP, CPm (minor coat protein) and HSP70 homolog (Wintermantel et al. 2005). According to Wisler et al. (1998), this tomato virus was first assigned to the genus *Closterovirus*, but later it was attributed to the genus *Crinivirus* (Fauquet and Mayo 1999).

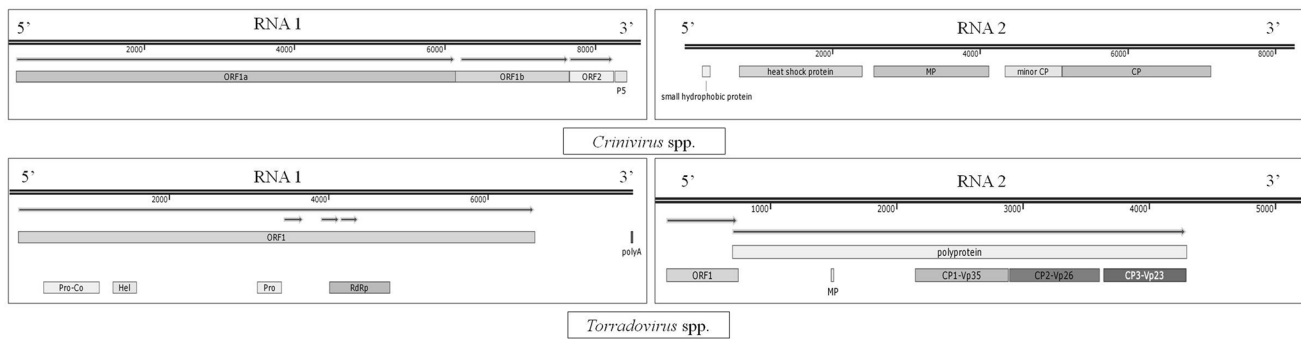


Fig. 3 Genome structure of positive-strand bipartite RNA viruses from genus *Crinivirus* and *Torradovirus*. Sequences extracted from GenBank accession number AY903447.1 (RNA-1), KJ815045.1 (RNA-2) and NC_009013.1 (RNA-1), NC_009032.1 (RNA-2), respectively

Members of this genus are *Tomato chlorosis virus* (ToCV; Table 1; Fig. 3) and *Tomato infectious chlorosis virus* (TICV) (Hanssen et al. 2010). ToCV was named after TICV from the differences in RNA sequence, vector specificity and host range. Other than *L. esculentum* (tomato), hosts of ToCV include *Zinnia elegans* (zinnia, Tsai et al. 2004), *C. annuum* (sweet pepper; Lozano et al. 2004) and *S. tuberosum* (potato; Lee et al. 2018). Infected areas of TICV are North America, Europe, Turnisia, Asia and Middle East, whereas ToCV has been found across the globe (Suresh et al. 2017).

Torradovirus genus is a bipartite virus with a positive ssRNA genome encapsidated into nonenveloped icosahedral particles, consisting of three open reading frames (ORF), RNA-1 encodes one ORF and RNA-2 encodes two ORFs (Sanfacon et al. 2009; Verbeek et al. 2013). The ORF in RNA-1 codes for the protease cofactor (Pro-Co), helicase (Hel), protease (Pro) and RNA-dependent RNA polymerase (RdRp) (NC_009013.1). Two ORFs in RNA-2 include ORF1 encoding a polyprotein which includes the movement protein (MP), coat protein Vp35, Vp26 and Vp23 (Fig. 3; NC_009032.1). These viruses were placed in the new family *Secoviridae* that comprises all plant viruses in the order *Picornavirales* and comprises of genus such as *Torradovirus* (Sanfacon et al. 2009). There are three new species belonging to the *Torradovirus* novel genus, which are *Tomato marchitez virus* (ToMarV), *Tomato torrado virus* (ToTV; Table 1; Fig. 3) and *tomato apex necrosis virus* (ToANV; Verbeek et al. 2008). The discovery of these viruses was in 2001 where symptoms such as necrotic or burn-like were seen in tomato crops in the southeast of Spain (Alfaro-Fernandez et al. 2007). The early diagnosis initially showed the presence of PepMV, but after further studies, it showed different symptoms and ToTV was proposed (Verbeek et al. 2007). After 2003, the same disease symptoms were seen in Mexican tomato crops where the tomato spotted wilt virus (TSWV) was first suspected to be the causal agent of this disease (Turina et al. 2007). However, the presence of the isometric viral particles as well as the characterization and

the partial sequencing showed differences; thus, the ToANV was proposed (Turina et al. 2007). Even though it is highly similar to ToTV, the subsequent nucleotide sequence of the three ORFs was distinctive and so the virus ToMarV was suggested (Verbeek et al. 2008). The hosts of the ToTV were experimentally tested by Amari et al. (2008) and showed that this virus systematically infects *S. melongena*, *S. lycopersicum*, *C. annuum*, *Physalis floridana*, *N. tabacum*, *N. rustica*, *N. glutinosa* and *N. benthamiana*.

Tomato Tripartite RNA virus

Among the five genera with tripartite genomes, four out of five are from the family *Bromoviridae*, for instance, *Cucumovirus*, *Alfamovirus*, *Anulavirus* and *Ilarvirus*. Viruses from *Cucumovirus* and *Alfamovirus* have icosahedral capsids (Al-Saleh and Amer 2013; Krenz et al. 2015), whereas *Anulavirus* and *Ilarvirus* have quasi-spherical particles (Bratsch et al. 2019; Lapidot et al. 2010).

Alfalfa mosaic virus (AMV; Table 1; Fig. 4) is a member of the genus *Alfamovirus* and in the family *Bromoviridae* which possesses three plus-sense polarity single-stranded RNA (ssRNA) molecules (Al-Abraham 2014; Fig. 4). The RNA is classified as RNA 1 to RNA 3 in descending order of molecular size, and each is enclosed into B, M and Tb components (Abdalla et al. 2015). AMV also affected some other vegetable crops such as eggplant (*S. melongena* L.), lettuce (*Lactuca sativa* L.), pea (*Pisum sativum* L.), bean (*Phaseolus vulgaris* L.), celery (*Apium graveolens* L.), pepper (*C. annuum* L.), alfalfa (*Medicago sativa* L.), borage (*Borago officinalis* L.), tuberous comfrey (*Symphytum tuberosum* L.), cowpea (*Vigna unguiculata* (L.) Walp), mung bean (*V. mungo* (L.) Hepper), chickpea (*Cicer arietinum* L.) and tumble pigweed (*Amaranthus albus* L.) (Malor et al. 2002; Bellardi and Benni 2005; Zitikaitė and Samuitienė 2008; Fidan et al. 2012; Al-albrahim 2014).

For the *Cucumber mosaic virus* (CMV; Table 1; Fig. 4) that belongs to the genus *Cucumovirus*, it encodes five

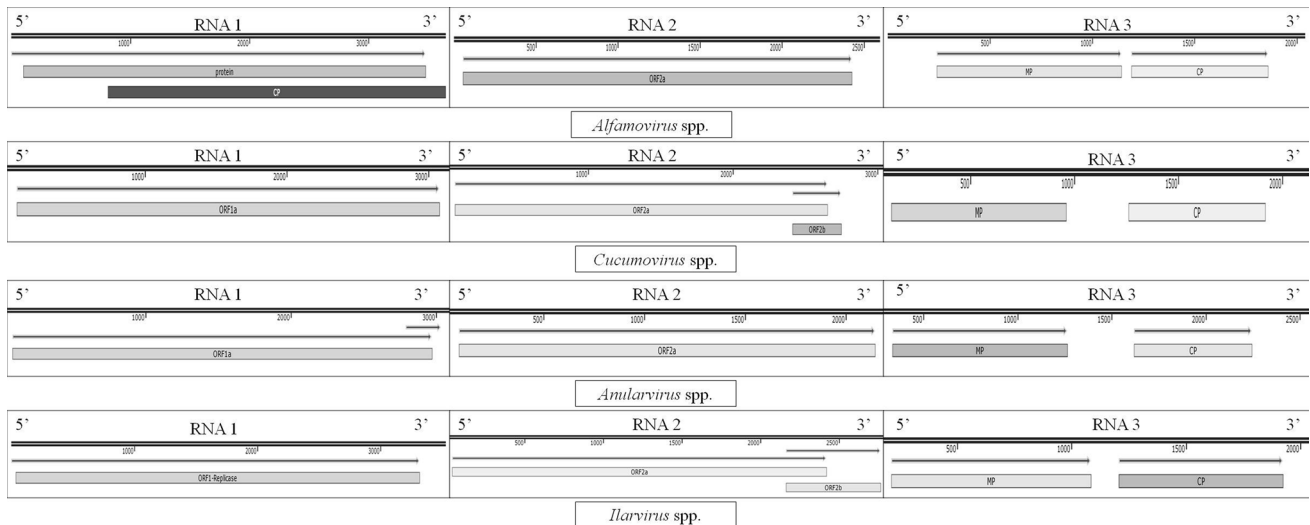


Fig. 4 Genome structure of tripartite RNA viruses from genus *Alfamovirus* (NC_001495 RNA-1; NC_002024 RNA-2; NC_002025 RNA-3), *Cucumovirus* (MG182148 RNA-1; MG182149 RNA-2;

MG182150 RNA-3), *Anulavirus* (JQ350736 RNA-1; JQ350739 RNA-2; JQ350737 RNA-3), *Ilarvirus* (FJ561302 RNA-1; FJ561303 RNA-2; FJ561301 RNA-3)

proteins (Palukaitis and Garcia-Arenal 2003). RNA 1 and 2 are for viral replication and encode the 1a and 2a proteins, respectively (Pumplin and Voinnet 2013), while RNA 4A (subgenomic RNA from RNA 2) encodes 2b protein that suppresses RNA silencing (Wang et al. 2012). RNA 3 that is translated from subgenomic RNA 4 encodes the movement protein (MP) and the coat protein (CP) (Jacquemond 2012). There are three subgroups of CMV strains (IA, II and IB) that have been categorized in which IA and II have spread globally, whereas IB is focused in Asia (Hasiów-Jaroszewska et al. 2018). According to Geetanjali et al. (2011), CMV causes damage to species under family *Solanaceae* and *Cucurbitaceae*, whereas Mochizuki and Ohki (2012) stated that CMV also caused diseases in the families *Leguminosae*, *Brassicaceae*, *Gramineae* other than *Solanaceae* and *Cucurbitaceae*.

Pelargonium zonate spot virus (PZSV; Table 1; Fig. 4) is the type member of the genus *Anulavirus* (Gioliti et al. 2014). The genome is made up of three linear positive-sense ssRNAs (RNA-1, RNA-2 and RNA-3; Fig. 4) that encode four proteins (Codoner and Elena 2006). RNA-1 encodes protein 1a, RNA-2 encodes protein 2a which consists of RNA-dependent RNA polymerase (RdRP), and RNA-3 encodes movement and coat protein (Finetti-Sialer and Gallitelli 2003). PZSV was first identified from *Pelargonium zonale* (Quacquarelli and Gallitelli 1979). Later, it was reported as causal agent of tomato diseases in Southern Italy by Gallitelli (1982) followed by identification in tomato in other countries. The distribution includes Spain, USA, Israel, Italy and France (Suresh et al. 2017). The hosts of this virus include plants from the *Solanaceae*, *Actinidiaceae*, *Brassicaceae* and *Asteraceae* (Li et al., 2014).

Ilarviruses (family *Bromoviridae*) have a genome consisting of three positive ssRNAs enclosed in quasi-spherical particles (Bratsch et al. 2019; Fig. 4). RNA-1 codes for replicase protein, and RNA-2 and RNA-3 encode replicase protein, RNA-dependent RNA polymerase, MP and CP proteins, respectively (Pallas et al. 2013). Additional tomato disease causal agents from the *ilarvirus* are *Tobacco streak virus* (TSV; Table 1; Fig. 4) discovered in USA in 1982 where the report showed global distribution (Zitter 2014). Other examples are tomato necrotic spot virus (ToNSV) and *Tomato necrotic streak virus* (TomNSV) which were discovered in California and Florida, respectively (Badillo-Vargas et al. 2016; Batuman et al. 2009). PMoV also infects plants such as *Mirabilis jalapa* and *Capsicum annuum* (Janssen et al. 2005; Parrella 2002). The expanding host range of this virus is due to the ability of it to transmit with sap extracts through physical inoculation (Aparicio et al. 2018). Thus, it can be transmitted to different families such as *Solanaceae*, *Cucurbitaceae*, *Fabaceae*, *Brassicaceae*, *Chenopodiaceae*, *Aizoaceae*, *Lamiaceae*, *Asteraceae*, *Malvaceae*, *Portulacaceae* and *Ranunculaceae* as compiled by Aparicio et al. (2018) in their review.

According to Abudurexiti et al. (2019), *Orthotospovirus* spp. (family *Tospoviridae*) which includes type virus tomato spotted wilt virus (TSWV; Table 1; Fig. 4), and capsicum chlorosis virus (CaCV), groundnut ringspot virus (GRSV), tomato chlorotic spot virus (TCSV) are classified based on the International Committee of Taxonomy of Viruses (ICTV) (Fig. 5). Other than these, the EFSA Panel on Plant Health (PLH 2012) also listed other orthotospoviruses that have infected tomato naturally and experimentally, for instance, tomato yellow ring virus (TYRV), groundnut

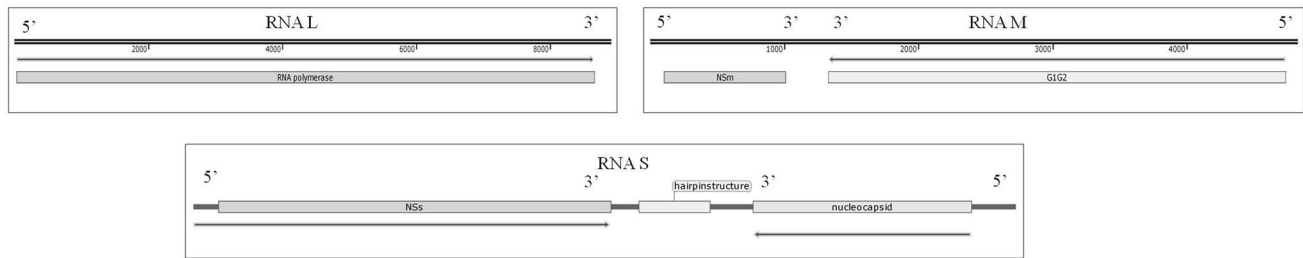


Fig. 5 *Orthotospovirus* (NC_002052 L segment; NC_002050 M segment; NC_002051 S segment)

bud necrosis virus (GBNV), tomato necrotic ringspot virus (TNRV), tomato necrotic spot virus (TNSV), tomato zonate spot virus (TZSV), alstroemeria necrotic streak virus (ANSV), chrysanthemum stem necrosis virus (CSNV), polygonum ringspot virus (PolRSV), watermelon bud necrosis virus (WBNV) and watermelon silver mottle virus (WSMoV).

TSWV is generally spherical in shape and consists of three ssRNA genomes such as small (S), medium (M) and large (L) that share the genomic features of orthotospoviruses (Turina et al. 2016; Gupta et al. 2018). The RNA-dependent RNA polymerase that is involved in RNA replication is coded by negative L RNA (Kim et al. 2013), while M RNA codes a guide for G_N/G_C glycoprotein (Whitfield et al. 2008). S RNA encodes nucleocapsid protein (Gupta et al. 2018). Furthermore, there are other proteins such as non-structural protein (NS) in the viral sense of M RNA and non-structural protein (NSs) in the viral sense of sRNA through an ambisense coding strategy (Guo et al. 2017). According to Gupta et al. (2018), one of the most detrimental viruses among the orthotospoviruses is TSWV with a host range of more than 85 families. The success of the TSWV infection in the host is achieved through the highly coordinated expression of these proteins within the hosts of tospoviruses that include tobacco, potato, pepper, groundnut, lettuce and bean other than tomato (Gupta et al. 2018).

Vector and transmission methods of plant viruses in commercial cropping system

Most plant viruses rely on insect vectors to spread to the next host (Gadhav et al. 2019). So control measures can be developed by studying the transmission vector of the viruses in order to increase the understanding of their epidemiology. Plant viruses that are spread persistently have a strong relationship with their insect vectors (Gadhav et al. 2019). *Bermisia tabaci* is the vector for both DNA and RNA viruses infecting *Begomovirus* spp., *Crinivirus* spp. and *Torradovirus* spp. Jiao et al. (2013) reported that *B. tabaci* is a natural vector that transmits viruses in a persistent and circulative manner. Chiemsombat et al. (2018) reaffirmed

that begomoviruses are spread through whiteflies *B. tabaci* in a persistent manner. In addition to *B. tabaci*, both *Crinivirus* spp. and *Torradovirus* spp. can also be transmitted by *Trialeurodes* whiteflies as their vector (Verbeek et al. 2013; Wintermantel 2004). TICV is disseminated by *T. vaporariorum*, and ToCV is disseminated by whitefly *T. abutilonea* and also *B. tabaci* (Middle East-Asia Minor 1 (MEAM1), Mediterranean (MED) and New World Group; Navas-Castillo et al. 2000; Wintermantel and Wisler 2006; de Moraes et al. 2018). *Torradovirus* spp. are transmitted by *T. Trialeurodes* and *B. tabaci* in a semi-persistent and stylet-borne manner (Verbeek et al. 2013).

For the transmission by aphids in *Cucumovirus*, *Alfamovirus* and *Potyvirus*, the transmissions of potyviruses are either through aphids, seed or contaminated living plant materials (Gibbs and Ohshima 2010). Tsedaley (2015) has also reported that PVY can be spread through mechanical means or through wounds of infected plant sap. PVY is transmitted by aphid in a non-persistent manner (Gadhav et al. 2019). A compilation has been published by Sigvald (1985) and Tsedaley (2015) on the few aphid species that have transmitted PVY, for instance, *Myzus persicae*, *Rhopalosiphum padi*, *Acyrthosiphon pisum*, *Metopolophium dirhodum*, *Cavariella aegopodi*, *Aphis* species and others.

According to Zitikaite and Samuitiene (2008), AMV is spread to the surrounding crops via at least 15 aphid species either in a stylet-borne or in a non-persistent manner. Other than that, the AMV can also be transmitted by mechanical or grafting methods (Fidan et al. 2012). In addition, CMV can also be either spread mechanically through plant saps, seeds or by aphids in a non-persistent manner (Palukaitis and Garcia-Arenal 2003). Aphids that have transmitted the CMV have been reported by Palukaitis et al. (1992) in his review where the *A. gossypii* and *M. persicae* are the most commonly associated with CMV transmission.

Other than whiteflies and aphids as vectors, thrips are also the vector for some tomato viruses. *Anulavirus*, *Ilarvirus* and *orthotospovirus* are transmitted by thrips species (Gilbertson et al. 2015; Gupta et al. 2018; Vovlas et al. 1989). According to Vovlas et al. (1989), transmission of PZSV is through seed of *Diptotaxis erucoides* and not through tomato

seed. Preliminary study also showed that thrips species carry the pollen grain of *D. erucoides* on its body in an unusual manner and transfers the virus while they feed on the flowers of tomato (Vovlas et al. 1989). Transmissions of the ilarviruses are through either seed or thrips-mediated pollen (Gilbertson et al. 2015). Orthotospoviruses can be disseminated and replicated in their thrips, tiny insects vectors, such as *Frankliniella occidentalis* (Gupta et al. 2018).

Although *Potexvirus* mainly spread from plant to plant without a vector (King et al. 2012), evidences have shown that bumblebees; fungus; and whitefly can act as the vector for PepMV (Alfaro-Fernández et al. 2009; Noëlet et al. 2014; Shipp et al. 2008). *Potexvirus* spp. can be transmitted mechanically as well (Hanssen et al. 2010). The transmission method of *Tombusvirus* is not through an insect vector but through mechanical methods, propagation material or seed and pollen (Hafez et al. 2010). Same goes to *Tobamovirus*, even though there is no vector for virus transmission, they can spread mechanically through farming process by persisting long time in contaminated soil (Candemir et al. 2012). These viruses are very stable and remain infectious for many years (Dombrovsky and Smith 2017). In damaged roots, these viruses will infect the plants (Almeida et al. 2018). In addition, they can also spread through infected seed coat which further infects the damaged roots during transplantation (Liu et al. 2014). Tobamoviruses are the seed-borne viruses (Luria et al., 2017). Moreover, these viruses can also be spreading through greenhouse design, equipments, workers' hands and ropes as well as the transportation in field (Reingold et al. 2016).

Beet leafhopper is a vector for *Curtovirus* spp. According to Jeger et al. (2017), BCTV is only transmitted through beet leafhoppers such as *Circular tenellus*. This insect can transport the virus for around 30 days but without involving virus replication (Soto and Gilbertson 2003). The *Curtovirus* spread by *C. tenellus* is in a circulative and non-propagative manner (Nusayr and Creamer 2017).

Disease spectrum of tomato viruses

The disease spectrum caused by different viruses infecting tomato as listed above consists of a wide range of symptoms and pathology. TMV the type species of tobamoviruses in family *Virgaviridae* (King et al. 2012; Scholthof et al. 2011) causes mild to severe mosaic symptoms in tomato and was also the first ever plant virus described (Mayer 1886). The viruses from the *Tobamovirus* genus not only spread globally but also adapt to different environments and cause a range of symptoms (Almeida et al. 2018). Symptoms on tomato caused by the tobamovirus ToMV include curling and deformation of leaves with inner browning, mosaic and irregular ripening (Fahim and Din 2017).

Pratapet al. (2008) described CMV as one of the most detrimental viruses infecting tomato. They are a species of the genus *Cucumovirus* whose members have a host range of more than 1200 distinct plant species within 500 genera from more than 100 families (Jacquemond 2012). Cucumber mosaic disease on tomato shows symptoms such as mosaic, necrosis, mottling, narrowing or shoes-string of leaves and stunting. Other than cucumovirus, the pepino mosaic disease caused by PepMV is a widespread pathogen that infects most of the tomato crops around the world (Hanssen and Thomma 2010). It was first described in 1980 when it infected pepino (*Solanum muricatum*) in Peru (Jones et al. 1980). In 1999, the PepMV was found infecting tomato crops in Europe (van der Vlugt et al. 2000). The significant fruit marbling symptoms make it an important and recognizable symptom of PepMV (Hanssen et al. 2008). Other symptoms are irregular or blotchy ripening of the tomato fruit, distorted young leaves, yellow angular spots on the leaves, leaf scorching, leaf mosaics and leaf blistering (Hanssen et al. 2009).

Tomato bushy stunt disease is caused by TBSV and was discovered by Smith in England in 1935 (Smith 1935). According to Martelliet al. (1988), TBSV is a soil-borne virus that can be maintained in soil, and therefore, the plant is infected in the roots locally. The infected plants will show symptoms on the fruit such as rings and lines as well as a reduction in size (Gerik et al. 1990). Other than that, distortion of leaves and fruit, necrosis, slow and thick growth pattern, chlorotic spot and wrinkling of leaf can be observed as well (Luis-Arteaga et al. 1996).

PVY potyvirus disease was placed in the top five most important viruses causing global loss in tomato plants by Scholthof et al. (2011). The genus *Potyvirus* from the family *Potyviridae* found worldwide and infect both monocot and dicot plants (Gibbs and Ohshima 2010) and was first described in the 1920s by Kenneth Smith in the UK (Smith 1931). Another species of *Potyvirus*, TEV, was discovered by Valleau and Johnson (1928) in Kentucky. Symptoms such as necrosis, mottling on leaf, wrinkle and leaf distortion can be seen on potyvirus TEV-infected tomato plants. In addition, symptoms such as fruit mottling are also observed (Zitter 1991). For the crinivirus infections, yellow interveinal and thick mature leaves are some of the symptoms seen. Fruits may show no specific symptom, although they can be smaller, lesser and earlier in ripening (Dalmon et al. 2009).

Based on Panagopoulos (2000), tomato double-streak disease is caused by the mixed infection of two types of virus which are the PVX and ToMV. Otsuki and Takebe (1976) observed that the two were able to interact and replicate in the same cell. Tomato crops grown in infected potato fields often have a high chance of being infected by PVX whose primary host is the potato crops (Cerkauskas 2005). Generally, tomato double-virus streak disease causes dwarf plant, curl leaves, long brown to dark streaks on the leafstalk, veins

and the stalk; on the other hand, the uneven brown gangrene spots of different sizes will be seen in infected fruits as well as irregular ripening (Zitter and Provvideti 1984). Both viruses are economically important on their own causing severe yield losses.

For the torrado virus disease, the initial symptoms of the infection are light green or yellowing below the leaflets surrounding the necrotic spots. Later, severe necrosis will be seen in the leaves and fruit resulting in diminishing growth (Verbeek et al. 2007). Pelargonium zonate spot disease shows symptoms such as chlorotic and necrotic rings as well as line patterns on the leaves and fruit, which result in plant stunting, leaf malformation and fruit reduction, subsequently causing death (Gallitelli 1982). *Parietaria motile virus* (PMoV), which causes ilarvirus disease, was first found infecting *Parietaria officinalis* L. in Italy (Caciagli et al. 1989). A few years later, PMoV infecting tomato was reported in Piedmont, Italy by Ramasso et al. (1997). The symptoms of PMoV can be observed in two stages, initial infection and later infection (Aparicio et al. 2018). During the early stage of the infection, symptoms such as necrosis of leaves, stem and apex can be seen, while in the later stage, plants will show necrotic mosaic symptoms on the newly emerging shoot, while corky rings and brown patches of scars will be formed on the fruit, followed by the distortion and color changes on the fruit (Aparicio et al. 2018).

For the disease caused by *Orthotospovirus* spp., the viruses have been found infecting tomato plants throughout Asia, Middle East and Australia (Dong et al. 2008). Despite this, Orthotospoviruses are also found in South Africa and South America (de Avila et al. 1993), USA (Webster et al. 2011) as well. The incidence of infection by *Orthotospovirus* spp. has risen with the increase in the population of the western flower thrips (*Frankliniella occidentalis*; Rojas and Gilbertson 2008). TSWV was first identified in 1915, but it was only in 1930 that it was recognized as the causal agent of this disease (Oliver and Whitfield 2016). The disease symptoms first appear in the foliage stage, where the leaflets show small and dark green chlorotic lesions, and later the chlorotic lesions will combine to and give a bronze necrotic appearance resulting in wilting necrosis spreads to the terminal shoots (Melzer et al. 2012). On the other hand, if the mature plants are infected, the distinguishable symptoms are discolored blotches or concentric rings on the fruits (Melzer et al. 2012).

Alfalfa mosaic disease caused by AMV is a global pathogen and causes infection in wide range of plant species (Loebenstein et al. 2001). According to Zitikaite and Samuitiene (2008), alfalfa seems to be the overwintering host of AMV where the infected tomatoes farm is generally near alfalfa fields. Fruits and the interveinal region of the leaves on the infected tomato plants showed bright yellow mottle symptoms, and later, the leaf will turn yellowing followed

by plant stunting and leaflet distortion (Zitikaite and Samuitiene 2008).

Geminiviruses which include the *Curtovirus* and *Begomovirus* affect the photosynthetic process of infected plants by invading the phloem cells which subsequently causes starch declination and flower and fruit disruption (Rojas 2004). The symptoms of begomoviruses include retarded growth, wrinkling, twisted leaf, mottle, thick and yellow vein and small leaves (Inoue-Nagata et al. 2016), whereas symptoms of curtovirus disease include retarded plant growth, wrinkling, yellowing and swelling vein, phloem hyperlasia and twisted leaf (Hosseini 2010).

Control strategies

Basic control strategy of plant virus diseases starts with conventional good farming practices. Islam (2017) has suggested several methods to handle virus disease at the farmer stage which included crop rotation to prevent the planting of similar host, selection of healthy cuttings or seeds; removal of the disease infected plants from the farm; and removal of weeds or hosts that are potential reservoir of the virus or its vector. Additionally, the use of appropriate insecticides to eradicate the vector insects, soil fumigation, use of resistant variety and last but not least to provide education on good practices to the farmers is vital (Islam 2017). Rojas et al. (2018) reported that the use of resistant varieties was an effective strategy in controlling the tomato yellow leaf curl disease. Biswa et al. (2011) also suggested methods such as organic farming and cross-protection which have been used to control ToMV.

The rapid adaptive nature and ability to utilize resources in host plants for their replication make viruses a challenge to the crop industries. Additionally, plant viruses generally do not spread itself instead it relies on vectors such as insect, fungus, nematode or arthropod to reach their target plants (Dietzgen et al. 2016). Understanding that genome of viruses reveals the multifunctional features of their proteins (Sanfacon 2017). Generally, to express the functions of the proteins in virus, interplay of plant proteins with viral proteins is needed (Nagy 2016). Thus, identifying the necessary factors that the hosts need for survival and the host factors that the virus needs for infection and their interactions is the key step in controlling virus disease (Garcia-Ruiz 2018).

During the replication cycle, translation of the viral proteins is necessary for replication, assembly and lastly movement of the virus to the adjacent cells (Garcia-Ruiz 2018). Movement of viruses necessitates plant cellular factors and virus proteins (Wan et al. 2015). For example, with the help of plant cellular factors, MP of plant viruses enables them to enlarge the plasmodesmata path and therefore able to move through cell to cell (Heinlein 2015). This understanding has led to multiple approaches in genetically engineering of

plants some of which are produced to remove or deactivate the factors that are necessary for virus infection, importantly without affecting the development of the plants (Pyott et al. 2016).

Genetic plant defense mechanism through RNA interference (RNAi) appears to be an efficient mechanism for counteracting pathogens in many plants (Duan et al. 2012). RNAi is a mechanism where the dsRNA leads to the post-transcriptional gene silencing (PTGS) to inhibit the gene expression (Kim and Rossi 2007). According to Almeida and Allshire (2005), transcription and translation were restrained by corresponding mRNAs which are initiated by dsRNA to silence the target genes. RNAi is also known for the ability to promote resistance towards diseases caused by viruses through virus-induced gene silencing (Ding 2010). Unlike bacteria and fungi, virus multiplies inside the host, which makes the role of RNAi important (Wang et al. 2012). There is direct silencing of the genome of the virus through siRNA that has been demonstrated (Ruize-Ferrer and Voinnet 2009). Bioinformatic research also proposes that miRNAs have the capacity for antiviral mechanism by aiming genomes of virus (Perez-Quintero et al. 2010). Significant examples include the development of transgenic tomato lines constructed with hpRNAi by Mahmoudieh et al. (2019) to induce RNAi pathway and then activate gene silencing. Fuentes et al. (2016) on the other hand showed the resistance of RNAi transgenic tomato plants towards TYLCV.

The precise and early detection of plant pathogens in-field is also critical in light of the rapid changes in the pathogen population due climate change, vector evolution and farm practice (Donoso and Valenzuela 2018). Early detection not only lowers the disease outbreak but also enables farmers to take appropriate control methods rapidly (Pallas et al. 2018). To date, many reviews of available technologies or techniques have been published. Other than the conventional immunological (Martinelli et al. 2014) and morphological techniques (Capote et al. 2012), molecular approaches have been widely utilized, including the use of polymerase chain reaction (PCR)-based techniques such as RT-PCR, real-time PCR, isothermal PCR, ELISA PCR, multiplex PCR and nested PCR (Capote et al. 2012). According to Martinelli et al. (2014), PCR-based techniques provide more advantages than immunoassays based on cost, time and efficiency. PCR-based methods not only faster and cheaper but also manage to detect single target in multiple targets, as well as detect the pathogens that are not able to culture such as bacteria, phytoplasma and viruses (Martinelli et al. 2014). Other technologies include loop-mediated isothermal amplification (LAMP) assay, recombinase polymerase amplification, multiplex immunodetection, microsphere immunoassays (MIA), aptamer-based diagnosis or portable nanopore sequencing; detailed reviews of these can be retrieved from Donoso and Valenzuela (2018). Moreover, Pallas et al. (2018) have also

written a review on next-generation sequencing (NGS), multiplex and hybridization technologies for virus detection. Constantly checking for pathogen at its early phase is important as some of the plants will not show symptoms in the early phase; therefore, high-throughput, accurate and highly sensitive technologies are needed (Donoso and Valenzuela 2018).

Conclusion and future perspective

The review of viral diseases in tomato has shown the widespread effects of the diverse pathogens on tomato production in different parts of the world. One reason why viral diseases are of great concern to farmers is because of its diversity and range, fast replication and ease of spread through vectors which enhances its evolution and adaptation towards natural selection pressure (Hanssen et al. 2010). According to Hanssen et al. (2010), the rapid appearance of new viruses could be related to climate change, introduction of new host plants, vectors evolution and cultural practices. The simplicity of its genome is one of the reasons why viruses adapt to the varying environments easily (Jones 2016). The change in climate is thought to be a major causal reason for deteriorating economic production when associated with virus diseases (Pallas et al. 2018). Eastburn et al. (2011) have also reported that the environment plays crucial roles on virus spread and behavior as well as susceptibility of the host. Moreover, climate change also results in alteration of phenology, physiology and morphology of the vectors in addition to affecting host plants (Jones 2016), thus increasing the knowledge on interplays and interactions between pathogen and its antagonist; physiology and ecology of plants and the intermediate vectors are critical for developing strategies for plant protection (Tsitsigiannis et al. 2008). Undeniably, being familiar with the biochemical and molecular structures that consolidate these interplays and interactions is important to unearth effective control methods. On the other hand, the development of simplified and cost-efficient technology has actually facilitated the identification and discovery of the biological properties of the virus and subsequently results in understanding their structure and mechanisms. However, there are still substantive gaps in knowledge as not all of the viruses have been adequately studied due to their large population and high variation among each group, especially under different environmental conditions, stresses, climate and cultural conditions. Studies have shown that through better understanding of these interactions, resistant plant cultivars have been successfully developed in tomato that is resistant to TYLCV, ToTV and ToMarV (Hanssen et al. 2010). For example, introduction of genes controlling resistance to the *Begomovirus* spp. (*Ty* genes) from the wild *Solanum* species (Hanssen et al. 2010). Vidavski et al. (2008) have shown

that the *Ty* resistance genes may interact with each other and results in hybrid plants that have higher resistance than their parental line. The host–virus relationship is governed by a complicated network of interactions. With the increasing availability of genome wide data and big omics data for many of the hosts, pathogens and vectors, the opportunity for elucidating new information on these interactions is growing exponentially. Ultimately the combination of the laboratory research to the application in the field is an approach that should be driven by both researchers and farmers in order to develop sustainable and holistic strategies to limit the spread of virus diseases in this crop.

Compliance with ethical standards

Conflict of interest The authors declared no conflict of interest.

References

- Abdalla OA, Mohamed SA, Eraky AI, Fahmy FG (2015) Genetic comparison between coat protein gene of *Alfalfa mosaic virus* isolate infecting potato crop in Upper Egypt and worldwide isolates. *Int J Virol* 11:112–122
- Abudurexiti A, Adkins S, Alioto D et al (2019) Taxonomy of the order *Bunyavirales*: update 2019. *Arch Virol* 164:1949–1965
- Agirrezabala X, Méndez-López E, Lasso G, Sánchez-Pina MA, Aranda M, Valle M (2015) The near-atomic cryoEM structure of a flexible filamentous plant virus shows homology of its coat protein with nucleoproteins of animal viruses. *eLife* 4:e11795
- Aguilar JM, Hernandez-Gallardo MD, Cenis JL, Lacasa A, Aranda MA (2002) Complete sequence of the *Pepino mosaic virus* RNA genome. *Arch Virol* 147(10):2009–2015
- Al-Abraham JS (2014) Molecular identification of *Alfalfa Mosaic Virus* isolated from naturally infected Alfalfa (*Medicago sativa*) crop in Saudi Arabia. *Int J Plant Animal Environ Sci* 4(1):348–352
- Alfaro-Fernández A, Córdoba-Sellés C, Cebrián-Micó MC, Font M, Juárez V, Median A, Lacasa A, Sánchez-Navarro JA, Pallas V, Jordá-Gutiérrez C (2007) Advances in the study of tomato “Torrado” or “Cribado” syndrome. *Boletín de Sanidad Vegetal Plagas* 33(1):99–109
- Alfaro-Fernández A, Córdoba-Sellés MC, Herrera-Vásquez JA, Cebrián MC, Jordá C (2009) Transmission of *Pepino mosaic virus* by the fungal vector *Olpidium virulentus*. *J Phytopathol* 158(4):217–226
- Almeida R, Allshire RC (2005) RNA Silencing and genome regulation. *Trends Cell Biol* 15(5):251–258
- Almeida JEM, dos Reis FA, PdeSG D, Lucas MA, Alencar NE (2018) Procedure for detecting tobamovirus in tomato and pepper seeds decreases the cost analysis. *Plant Prot* 77:590–598
- Al-Saleh MA, Amer MA (2013) Biological and molecular variability of *Alfalfa mosaic virus* affecting alfalfa crop in Riyadh region. *Plant Pathol J* 29(4):410–417
- Amari K, Gonzalez-Ibeas D, Gomez P, Sempere RN, Sanchez-Pina MA, Aranda MA (2008) *Tomato torrado virus* is transmitted by *Bermisia tabaci* and infects pepper and eggplant in addition to tomato. *Dis Notes* 92(7):1139
- Ammara UE, Mansoor S, Sæed M, Amin I, Briddon RW, Al-Sadi AM (2015) RNA interference-based resistance in transgenic tomato plants against *Tomato yellow leaf curl virus*-Oman (TYLCV-OM) and its associated betasatellite. *Virol J* 12:38
- Andou T, Yamaguchi A, Kawano S, Kawabe K, Ueda S, Onuki M (2010) *Ageratum yellow vein virus* isolated from tomato plants with leaf curl on Ishigaki Island, Okinawa. *Jpn J Gen Plant Pathol* 76(4):287–291
- Aparicio F, Aramburu J, Soler S, Galipienso L, Nuez F, Pallás V, López C (2009) Immunodiagnosis of *Parietaria mottle virus* in tomato crops using a polyclonal antiserum against its coat protein expressed in a bacterial system. *J Phytopathol* 157:511–513
- Aparicio F, Aramburu J, Herranz MC, Pallas V, Lopez C (2018) *Parietaria mottle virus*: a potential threat for tomato crops? *Acta Hort* 1207:261–268
- Arinaitwe W, Ochwo-ssamakula M, Mbewe WK, Sseruwagi P, Kyamanywa S, Erbaugh M, Miller S, Qu F (2018) Molecular characteristics of *Tomato mosaic virus* infecting tomato in Uganda. *Afr Crop Sci J* 26:433–445
- Artelli GP, Russo M, Rubbino M (2001) Tomato bushy stunt virus A.A.B. *Descript Plant Virus* 71:382
- Badillo-Vargas IE, Baker CA, Turechek WW, Frantz G, Mellinger HC, Funderburk JE, Adkins S (2016) Genomic and biological characterization of *Tomato necrotic streak virus*, a novel subgroup 2 ilarvirus infecting tomato in Florida. *Plant Dis* 6:1046–1053
- Barker RF, Jarvis NP, Thompson DV, Loesch-Fries LS, Hall TC (1983) Complete nucleotide sequence of alfalfa mosaic virus RNA3. *Nucleic Acids Res* 11(9):2881–2891
- Batuman O, Miyao G, KuoY-W C-F, Davis RM, Gilbertson RL (2009) An outbreak of a necrosis disease of tomato in California in 2008 was caused by a new ilarvirus species related to *Parietaria mottle virus*. *Plant Dis* 93:546
- Baulcombe DC (1996) RNA as a target and an initiator of posttranscriptional gene silencing in transgenic plants. *Plant Mol Biol* 32:79–88
- Bellardi MC, Benni A (2005) The occurrence of alfalfa mosaic virus in *Symphytum tuberosum*. *J Plant Pathol* 87(1):75–76
- Bennett CW (1971) The Curly Top Disease of Sugar Beet and Other Plants. *Am Phytopa Soc* 7:0569–6992
- Biswa KK, Kumari S, Tarafdar A (2011) Present scenario of management strategies of plant viral diseases. *Insect Pest and Disease Management*. https://www.academia.edu/8538737/Prese-nt_scenario_of_management_strategies_of_plant_viral_diseases. Accessed 20 Mar 2019
- Blystad D-R, van der Vlugt R, Alfaro-Fernandez A et al (2015) Host range and symptomatology of *Pepino mosaic virus* occurring in Europe. *Eur J Plant Pathol* 143:43–56
- Bolok Yazdi HR, Heydarnejad J, Massumi H (2008) Genome characterization and genetic diversity of *Beet curly top Iran virus*: a geminivirus with a novel nonanucleotide. *Virus Genes* 36:539–545
- Bratsch S, Grinstead S, Creswell T, Ruhl GE, Mollov D (2019) Characterization of *Tomato necrotic spot virus*, a subgroup 1 ilarvirus causing necrotic foliar, stem, and fruit symptoms in tomatoes in the United States. *Plant Dis* 103(6):1943–7692
- Caciagli P, Boccardo G, Lovisolo O (1989) *Parietaria mottle virus*, a possible new ilarvirus from *Parietaria officinalis* (*Urticaceae*). *Plant Pathol* 38:577–584
- Candemir F, Kutluk-Yilmaz ND, Gülser C (2012) The effect of tobacco waste application on *Tobacco mosaic virus* (TMV) concentration in the soil. *ŽemdirbystėAgriculture* 99(1):99–104
- Cantu-Iris M, Pastor-Palacios G, Mauricio-Castillo JA et al (2019) Analysis of a new begomovirus unveils a composite element conserved in the CP gene promoters of several *Geminiviridae* genera: clues to comprehend the complex regulation of late genes. *PLoS ONE* 14(1):e0210485
- Capote N, Pastrana AM, Aguado AS, Anchez-Torres P (2012) Molecular tools for detection of plant pathogenic fungi and fungicide resistance. In: Cumagun CJR (ed) *Plant pathol*. InTech, London, pp 151–202

- Cerkauskas R (2005) Potato virus X (PVX). AVRDC The World Vegetable Center Fact Sheet. https://203.64.245.61/web_crops/tomato/PVX.pdf.
- Chiemsombat P, Srikamphung B, Yule S (2018) Begomoviruses associated to pepper *Yellow leaf curl disease* in Thailand. *J Agric Res* 3:000183
- Codoner FM, Elena SF (2006) Evolutionary relationships among members of the *Bromoviridae* deduced from whole proteome analysis. *Arch Virol* 151:299–307
- Cornelissen BJ, Brederode FT, Moormann RJ, Bol JF (1983a) Complete nucleotide sequence of *Alfalfa mosaic virus* RNA 1. *Nucleic Acids Res* 11(5):1253–1265
- Cornelissen BJ, Brederode FT, Veeneman GH, van Boom JH, Bol JF (1983b) Complete nucleotide of *Alfalfa mosaic virus* RNA 2. *Nucleic Acids Res* 11(10):3019–3025
- Chung BYW, Miller WA, Atkins JF, Firth AE (2008) An overlapping essential gene in the *Potyviridae*. *Proc Natl Acad Sci USA* 105(15):5897–5902
- Dalmon A, Fabre F, Guilbaud L, Lecoq H, Jacquemond M (2009) Comparative whitefly transmission of *Tomato chlorosis virus* and *Tomato infectious chlorosis virus* from single or mixed infections. *Plant Pathol* 58(2):221–227
- De Avila AC, de Haan P, Kormelink R, Resende RO, Goldbach RW, Peters D (1993) Classification of tospoviruses based on phylogeny of nucleoprotein gene-sequences. *J Gen Virol* 74:153–159
- De Haan P, Wagemakers L, Peters D, Goldbach R (1990) The S RNA segment of tomato spotted wilt virus has an ambisense character. *J Gen Virol* 71:1001–1007
- De Haan P, Kormelink R, de Oliveira RR, van Poelwijk F, Peters D, Goldbach R (1991) *Tomato spotted wilt virus* L RNA encodes a putative RNA polymerase. *J Gen Virol* 72:2207–2216
- De Moraes LA, Muller C, de Freitas Bueno RCO et al (2018) Distribution and phylogenetics of whiteflies and their endosymbiont relationships after the Mediterranean species invasion in Brazil. *Sci Rep* 8:14589
- Diaz-Pendon JA, Sanchez-Campos S, Fortes IM, Moriones E (2019) *Tomato yellow leaf curl Sardinia virus*, a *Begomovirus* species involving by mutation and recombination: A challenge for virus control. *Viruses* 11(1):45
- Dietzgen RG, Mann KS, Johnson KN (2016) Plant virus-insect vector interactions: current and potential future research directions. *Viruses* 8(11):303
- Ding SW (2010) RNA-based antiviral immunity. *Nat Rev Immunol* 10(9):632–644
- Dombrovsky A, Smith E (2017) Seed transmission of Tobamoviruses: Aspects of global disease distribution. *Adv Seed Biol* 12:234–260
- Dong JH, Cheng XF, Yin YY, Fang Q, Ding M, Li TT, Zhang LZ, Su XX, McBeath JH, Zhang ZK (2008) Characterization of *Tomato zonate spot virus*, a new *Tospovirus* in China. *Arch Virol* 153(5):855–864
- Donoso A, Valenzuela S (2018) In-field molecular diagnosis of plant pathogen: recent trends and future perspectives. *Plant Pathol* 67(4):1451–1461
- Duan CG, Wang CH, Guo HS (2012) Application of RNA silencing to plant disease resistance. *Silence* 3:5
- Eastburn DM, McElrone AJ, Bilgin DD (2011) Influence of atmospheric and climatic change on plant–pathogen interactions. *Plant Pathol* 60:54–69
- Edwardson JR (1974) Some properties of the *Potato virus Y* group. Florida Agriculture Experiment Station Monograph Series 4:225
- EFSA Panel on Plant Health (PLH) (2012) Scientific Opinion on the pest categorisation of the tospoviruses. *EFSA J* 10(7):2772
- Fahim M, Din N (2017) Evaluation of tomato genotypes against *Tomato mosaic virus* (ToMV) and its effect on yield contributing parameters. *Pal J Bot* 49:1585–1592
- FAOSTAT (2019) Statistics Division of the Food and Agricultural Organization of the United Nations. <https://www.fao.org/faostat/en/#data/QC>. Accessed 12 Feb 2019.
- Fauquet MC, Mayo MA (1999) Abbreviations for plant virus names. *Arch Virol* 144(6):1249–1273
- Fidan H, Adak NA, Konuksal A, Akerzurumlu E, Yılmaz MA (2012) Occurrence of *Alfalfa mosaic virus* (AMV) diseases on potato crops in Northern Cyprus. *Acta Hort (ISHS)* 960:341–346
- Finetti-Sialer M, Gallitelli D (2003) Complete nucleotide sequence of *Pelargonium zonate spot virus* and its relationship with the family *Bromoviridae*. *J Gen Virol* 84:3143–3151
- Gadhve KR, Dutta B, Coolong T, Srinivasan R (2019) A non-persistent aphid-transmitted *Potyvirus* differentially alters the vector and non-vector biology through host plant quality manipulation. *Sci Rep* 9(1):2503
- Gallitelli D (1982) Properties of tomato isolate of *Pelargonium zonate spot virus*. *Ann Appl Biol* 100(3):457–466
- García-Arenal F, Fraile A, Malpica JM (2001) Variability and genetic structure of plant virus populations. *Annu Rev Phytopathol* 39:157–186
- García-Ruiz H (2018) Susceptibility genes to plant viruses. *Viruses* 10(9):484
- Geetanjali AS, Kumar R, Srivasta PS, Mandal B (2011) Biological and molecular characterization of two distinct tomato strains of *Cucumbr mosaic virus* based on complete RNA-3 genome and subgroup specific diagnosis. *Indian J Virol* 22(2):117–126
- Gibbs A, Ohshima K (2010) Potyviruses and the digital revolution. *Annu Rev Phytopathol* 48:205–223
- Gibson KE (1967) Possible incidence of curly top in Iran: A new record. *Plant Dis Rep* 51:976–977
- Gerik JS, Duffus JE, Perry R, Stenger DC, Van Maren AF (1990) Etiology of tomato plant decline in California desert. *Phytopathol* 80:1352–1356
- Gilbertson RL, Batuman O, Webster CG, Adkins S (2015) Role of the insect super-vectors *Bemisia tabaci* and *Frankliniella occidentalis* in the emergence and global spread of plant viruses. *Annu Rev Virol* 2(1):67–93
- Giolitti F, Bejerman N, Nome C, Visintin G, de Breuil S, Lenardon S (2014) Biological and molecular characterization of an isolate of *Pelargonium zonate spot virus* infecting sunflower in Argentina. *J Plant Pathol* 96(1):189–194
- Guo Y, Liu B, Ding Z, Li G, Liu M, Zhu D, Sun Y, Dong S, Lou Z (2017) A distinct mechanism for the formation of the ribonucleoprotein complex of the Tomato *spotted wilt virus*. *J Virol* 91:e00892–e917
- Gupta R, Kwon S-Y, Kim ST (2018) An insight into the *Tomato spotted wilt virus* (TSWV), tomato and thrips interaction. *Plant Biotech Rep* 12(3):157–163
- Gutierrez C (2002) Strategies for geminivirus DNA replication and cell cycle interference. *Physiol Mol Plant P60(5):219–230*
- Hafez ESE, Saber GA, Fattouh FA (2010) *Tomato bushy stunt virus* (TBSV) infecting *Lycopersicon esculentum*. *Z Naturforsch* 65(9–10):619–626
- Harvey M, Quilley S, Beynon H (2002) Exploring the Tomato. Transformations of nature, society, and economy. Edgar, Cheltenham
- Hanssen IM, Thomma BPHJ (2010) *Pepino mosaic virus*: a successful pathogen that rapidly evolved from emerging to endemic in tomato crops. *Mol Plant Pathol* 11(2):179–189
- Hanssen IM, Paeleman A, Wittemans LPF, Goen K, Lievens B, Bragard C, Vanachter ACRC, Thomma BPHJ (2008) Genetic characterization of *Pepino mosaic virus* isolates from Belgian greenhouse tomatoes reveals genetic recombination. *Eur J Plant Pathol* 121(2):131–146
- Hanssen IM, Paeleman A, Vandewoestijne E, Van Bergen L, Bragard C, Lievens B, Vanachter ACRC, Thomma BPHJ (2009) *Pepino*

- mosaic virus* isolates and differential symptomatology in tomato. *Plant Pathol* 58(3):450–460
- Hanssen IM, Lapidot M, Thomma BPHJ (2010) Emerging viral diseases of tomato crops. *America Phytopa Soc* 23(5):539–548
- Hasiów-Jaroszewska B, Budzyńska D, Rymelska N, Korpys P, Borydnyko-Filas N (2018) Phylogenetic evidence of natural reassortants in the *Cucumber mosaic virus* population in Poland. *Can J Plant Pathol* 40(4):1715–2992
- Hassan I, Orilio AF, Fiallo-Olive E, Briddon RW, Navas-Castillo J (2016) Infectivity, effects on helper viruses and whitefly transmission of the deltasatellites associated with sweepviruses (genus *Begomovirus*, family *Geminiviridae*). *Sci Rep* 6:30204
- Hassani-Mehraban A, Saaijer J, Peters D, Goldbach R, Kormelink R (2005) A new tomato-infecting *Tospovirus* from Iran. *Phytopathol* 95:852–858
- Hearne PQ, Knorr DA, Hillman BI, Morris TJ (1990) The complete genome structure and synthesis of infectious RNA from clones of tomato bushy stunt virus. *Virology* 177(1):141–151
- Heinlein M (2015) Plant virus replication and movement. *Virology* 479–480:657–671
- Hosseini S (2010) Interaction between the chromatin of Beet curly top virus and TFL2 protein. Master thesis, Swedish University of Agricultural Sciences.
- Inoue-Nagata AK, Lima MF, Gilbertson RL (2016) A review of *Geminivirus* (*Begomovirus*) diseases in vegetables and other crops in Brazil: current status and approaches for management. *Hortic Bras* 34:008–018
- Ishibashi K, Ishikawa M (2016) Replication of tobamovirus RNA. *Annu Rev Phytopathol* 54:55–78
- Islam W (2017) Management of plant virus diseases; farmer's knowledge and our suggestions. *Hosts Viruses* 4(2):28–33
- Jacquemond M (2012) Cucumber mosaic virus. *Adv Virus Res* 84:440–491
- Janssen D, Saez E, Segundo E, Martín E, Gil F, Cuadrado IM (2005) *Capsicum annum*—a new host of *Parietaria mottle virus* in Spain. *Plant Pathol* 54(4):567
- Jaspars EMJ (1985) Interaction of alfalfa mosaic virus nucleic acid and protein. In: Davies JW (ed) *Molecular plant virology*. CRC Press, New York, pp 155–221
- Jeger M, Bragard C, Caffier D et al (2017) Scientific Opinion on the pest categorisation of *Beet curly top virus* (non-EU isolates). *EFSA J* 15:4998
- Jiao X, Gong H, Liu X, Xie Y, Zhou X (2013) Etiology of *Ageratum yellow vein* diseases in South China. *Plant Dis* 97(11):1497–1503
- Jones RAC (2016) Future scenarios for plant virus pathogens as climate change progresses. *Adv Virus Res* 95:87–147
- Jones RAC, Koenig R, Lesemann DE (1980) *Pepino mosaic virus*, a new potexvirus from pepino (*Solanum muricatum*). *Ann Appl Biol* 94(1):61–68
- Kenyon L, Kumar S, Tsai W-S, da Hughes J (2014) Virus diseases of peppers (*Capsicum* spp.) and their control. *Adv Virus Res* 90:297–354
- Kim DH, Rossi JJ (2007) Strategies for silencing human disease using RNA interference. *Nat Rev Genet* 8(3):173–184
- Kim J-H, Kim Y-S, Jang S-W, Jeon Y-H (2013) Complete genome sequence of *Tomato spotted wilt virus* from paprika in Korea. *Int J Phyto* 2(3):121–136
- King AMQ, Adams MJ, Carstens EB, Lefkowitz EJ (2012) Potexvirus, in virus taxonomy, classification and nomenclature of viruses. In: King AMQ, Adams MJ, Carstens EB, Lefkowitz EJ (eds) *Ninth report of the international committee on taxonomy of viruses*. Elsevier Academic Press, London, UK, pp 912–915
- Kiss ZA, Medina V, Falk BW (2013) Crinivirus replication and host interactions. *Front Microbiol* 4:1–11
- Kormelink R, de Haan P, Meurs C, Peters D, Goldbach R (1992) The nucleotide sequence of the M RNA segment of tomato spotted wilt virus, a bunyavirus with two ambisense RNA segments. *J Gen Virol* 73:2795–2804
- Krenz B, Bronikowski A, Lu X, Ziebell H, Thompson JR, Perry KL (2015) Visual monitoring of *Cucumber mosaic virus* infection in *Nicotiana benthamiana* following transmission by the aphid vector *Myzus persicae*. *Gen Virol* 96:2904–2912
- Lam N, Creamer R, Rascon J, Belfon R (2009) Characterization of a new curtovirus, *Pepper yellow dwarf virus*, from Chile pepper and distribution in weed hosts in New Mexico. *Arch Virol* 154(3):429–436
- Lapidot M, Guenoune-Gelbart D, Leibman D, Holdengreer V, Davidovitz M, Machbash Z, Klieman-Shoval S, Cohen S, Gal-On A (2010) *Pelargonium zonate spot virus* is transmitted vertically via seed and pollen in tomato. *Phytopathol* 100(8):798–804
- Lee Y-J, Kil E-J, Kwak H-R, Kim M, Seo J-K, Lee S, Choi H-S (2018) Phylogenetic characterization of *Tomato chlorosis virus* population in Korea: evidence of reassortment between isolates from different origins. *Plant Pathol J* 34(3):199–207
- Li YY, Wang CL, Xiang D, Li RH, Liu Y, Li F (2014) First report of *Tomato mottle mosaic virus* infection of pepper in China. *Plant Dis* 98:1447
- Li Y, Wang Y, Hu J, Xiao L, Tan G, Lan P, Liu Y, Li F (2017) The complete genome sequence, occurrence and host range of *Tomato mottle mosaic virus* Chinese isolate. *Virology* 14:15
- Liu HW, Luo LX, Li JQ, Liu PF, Chen XY, Hao JJ (2014) Pollen and seed transmission of *Cucumber green mottle mosaic virus* in cucumber. *Plant pathol* 63(1):72–77
- Loebenstein G, Berger PH, Brunt AA, Lawson RH (2001) *Virus and virus-like diseases of potatoes and production of seed potatoes*. Kluwer Academic, Netherlands
- Lozano G, Moriones E, Navas-Castillo J (2004) First report of sweet pepper (*Capsicum annum*) as a natural host plant for *Tomato chlorosis virus*. *Plant Dis* 88:224
- Luis-Arteaga M, Rodriguez-Cerezo E, Fraile A, Sae E, Garcia-Arenal F (1996) Different *Tomato bushy stunt virus* strains that cause disease outbreaks in solanaceous crops in Spain. *Phytopathol* 86:535–542
- Luria N, Smith E, Reingold V et al (2017) A new Israeli *Tobamovirus* isolate infects tomato plants harboring *Tm-22* resistance genes. *PLoS ONE* 12:e0170429
- Mahmoudieh MK, Mohamad Roff MN, Harikrishna JA, Othman RY (2016) *Ageratum yellow vein virus*-Malaysia [Malaysia-Tomato leaf curl- 2011] genome has a betasatellite and is a begomovirus infecting *Solanum lycopersicum* in Malaysia. *Unpublished*.
- Mahmoudieh M, Noor MRM, Harikrishna JA, Othman RY (2019) Tomato *Solanum lycopersicum* expressing the overlapping regions of three begomovirus genes exhibit resistance to *Ageratum yellow vein Malaysia virus*. *Physiol Mol Plant P* 108:101425
- Mallor C, Luis-Arteaga M, Cambra MA, Fernandez-Cavada S (2002) Natural infection of field-grown borage (*Borago officinalis*) by *Alfalfa mosaic virus* in Spain. *Plant Dis* 86(6):698
- Martelli GP, Gallitelli D, Russo M (1988) *Tombusviruses*. *Plant Viruses* 3:13–72
- Martinelli F, Scalenghe R, Davino S et al (2014) Advanced methods of plant disease detection a review. *Agron Sustain Dev* 35(1):1–25
- Martinez F, Rodrigo G, Aragones V, Ruiz M, Lodewijk I, Fernandez U, Elena SF, Daros J-A (2016) Interaction network of Tobacco etch potyvirusNla protein with the host proteome during infection. *BMC Genom* 17:87
- Mayer A (1886) Concerning the mosaic disease of tobacco. *Versionstn, Landwirtschaft*
- McMicheal LA, Persley DM, Thomas JE (2002) A new *Tospovirus* serogroup IV species infecting capsicum and tomato in Queensland Australia. *Australas Plant Pathol* 31(3):231–239

- Melzer MJ, Tripathi S, Matsumoto T, Keith L, Sugano J, Borth WB, Wieczorek A, Gonsalves D, Hu JS (2012) Tomato Spotted Wilt. *Plant Dis* 81:1220
- Mochizuki T, Ohki ST (2012) *Cucumber mosaic virus*: viral genes as virulence determinants. *Mol Plant Pathol* 13(3):217–225
- Moreno-Pérez MG, Pagán I, Aragón-Caballero L, Cáceres F, Fraile A, García-Arenal F (2014) Ecological and genetic determinants of *Pepino mosaic virus* emergence. *J Virol* 88:3359–3368
- Moriones E, Navas-Castillo J, Díaz-Pendón JA (2011) Emergence of begomovirus diseases. In: Caranta C, Aranda MA, Tepfer M, López-Moya JJ (eds) *Caister Academic*: Norfolk, VA, USA, pp 301–320
- Moyle R, Pretorius L-S, Shuey LS, Nowak E, Schenk PM (2018) Analysis of the complete genome sequence of *Cucumber mosaic virus* strain K. *Genome Announc* 6(7):e00053–e118
- Nagy PD (2016) Tombusvirus-host interactions: co-opted evolutionarily conserved host factors take center court. *Annu Rev Virol* 3:491–515
- Nasir M, Idrees M, Zaidi SSH, Chisti SA, Ayub M, Aamrao L (2016) *Tomato bushy stunt virus* and tomato advanced lines/cultivars. *Pak J Phyto* 28(2):283–286
- Navas-Castillo J, Camero R, Bueno M, Moriones E (2000) Severe yellowing outbreaks in tomato in Spain associated with infections of *Tomato chlorosis virus*. *Plant Dis* 84(8):835–837
- Nawaz HH, Umer M, Bano S, Usmani A, Naseer M (2014) A research review on *Tomato bushy stunt virus* disease complex. *J Nat Sci Res* 4(5):2224–3186
- Noël P, Hance T, Bragard C (2014) Transmission of the *Pepino mosaic virus* by whitefly. *Eur J Plant Pathol* 138:23–27
- Nusayr T, Creamer R (2017) A novel *groel* gene from the endosymbiont of beet leafhopper, *Candidatus Sulcia muelleri*. *Afr J Microbiol Res* 11:1586–1599
- Oliver JE, Whitfield AE (2016) The genus *Tospovirus*: emerging bunyaviruses that threaten food security. *Annu Rev Virol* 3:101–124
- Otsuki Y, Takebe I (1976) Double infection of isolated tobacco mesophyll protoplasts by unrelated viruses. *J Gen Virol* 30(3):309–316
- Palukaitis P, Garcia-Arenal F (2003) Cucumoviruses. *Adv Virus Res* 62:241–323
- Palukaitis P, Roossinck MJ, Dietzgen RG, Francki RIB (1992) Cucumber mosaic virus. *Adv Virus Res* 41:281–348
- Pallas V, Aparicio V, Herranz MC, Sanchez-Navarro JA, Scott SW (2013) The molecular biology of ilarviruses. *Adv Virus Res* 87:139–181
- Pallas V, Sanchez-Navarro JA, James D (2018) Recent advances on the multiplex molecular detection of plant viruses and viroids. *Front Microbiol* 9:2087
- Parrella G (2002) First report of *Parietaria mottle virus* in *Mirabilis jalapa*. *Plant Pathol* 51(3):401
- Panagopoulos CG (2000) Diseases of vegetable crops. In: *Vegetable disease*, Stamoulis, Athens, pp 15–189 (In Greek).
- Perez-Quintero A, Neme R, Zapata A, Lopez C (2010) Plant microRNAs and their role in defense against viruses: A bioinformatics approach. *BMC Plant Biol* 10:138
- Pratap D, Kumar S, Raj SK (2008) First molecular identification of a *Cucumber mosaic virus* isolate causing shoestring symptoms on tomato in India. *Australas Plant Dis Notes* 3(1):57–58
- Pumplin N, Voinnet O (2013) RNA silencing suppression by plant pathogens: defence, counter-defence and counter-counter-defence. *Nat Rev Microbiol* 11(11):745–760
- Pyott DE, Sheehan E, Molnar A (2016) Engineering of CRISPR/Cas9-mediated potyvirus resistance in transgene-free arabidopsis plants. *Mol Plant Pathol* 17(8):1276–1288
- Quacquarelli A, Gallitelli D (1979) Three virus diseases of Pelargonium in Apulia. *Phytopathol Mediterr* 18:61–70
- Raiola A, Rigano MM, Calafiore R, Frusciante L, Barone A (2014) Enhancing the human-promoting effects of tomato fruit for bio-fortified food. *Hindawi Pub Corp Mediators Inflamm* 40:1–6
- Ramasso E, Roggero P, Dellavalle G, Lisa V (1997) Necrosi apicale del pomodoro causata da un ilarvirus. *Infotore Fitopato* 11: 71-77
- Rashid TS, Sijam K, Awla HK, Saud HM, Kadir J (2016) Pathogenicity assay and molecular identification of fungi and bacteria associated with diseases of tomato in Malaysia. *Am J Plant Sci* 7(6):949–957
- Reingold V, Lachman O, Belausov E, Koren A, Mor N, Dombrovsky A (2016) Epidemiological study of *Cucumber green mottle mosaic virus* in greenhouses enables reduction of disease damage in cucurbit production. *Ann Appl Biol* 168(1):29–40
- Rojas A (2004) A complex of begomoviruses affecting tomato crops in Nicaragua. Ph.D. thesis, University of Agricultural Sciences
- Rojas MR, Gilbertson RL (2008) Chapter 3, Emerging plant viruses: a diversity of mechanisms and opportunities. In: Roossinck MJ (ed) *Plant Virus Evolution*. Springer, Berlin, pp 27–51
- Rojas M, Hagen C, Lucas W, Gilbertson R (2005) Exploiting chinks in the plant's armor: Evolution and emergence of geminiviruses. *Annu Rev Phytopathol* 43:361–394
- Rojas MR, Macedo MA, Maliano MR et al (2018) World management of geminiviruses. *Annu Rev Phytopathol* 56:637–677
- Rondon SI, Roster MS, Hamlin LL, Green KJ, Karasev AV, Crosslin JM (2016) Characterization of *Beet curly top virus* Strains circulating in Beet Leafhoppers (Hemiptera: Cicadellidae) in North-eastern Oregon. *Plant Dis* 100:8
- Ruiz-Ferrer V, Voinnet O (2009) Role of plant small RNAs in biotic stress responses. *Annu Rev Biol* 60:485–510
- Sanfaçon H (2017) Grand challenge in plant virology: understanding the impact of plant viruses in model plants, in agricultural crops and in complex ecosystems. *Front Microbiol* 8:860
- Sanfaçon H, Wellink J, Le Gall O, Karasev A, van der Vlugt R, Wetzel T (2009) *Secoviridae*: A proposed family of plant viruses within the order *Picornavirales* that combines the families *Sequiviridae* and *Comoviridae*, the unassigned genera *Cheravirus* and *Sadwavirus*, and the proposed genus *Torradovirus*. *Arch Virol* 154(5):899–907
- Scholthof HB, Morris TJ, Jackson AO (1993) The capsid protein gene to tomato bushy stunt virus is dispensable for systemic movement and can be replaced for localized expression of foreign genes. *Mol Plant Microbe In* 6:309–322
- Scholthof HB, Scholthof KBG, Jackson AO (1995) Tomato bushy stunt virus spread is regulated by two nested genes that function in cell-to-cell movement and host-dependent systemic invasion. *Virology* 213(2):425–438
- Scholthof KG, Adkins S, Czosnek H et al (2011) Top 10 plant viruses in molecular plant pathology. *Mol Plant Pathol* 12(9):938–954
- Scorza R, Callahn A, Levy L, Damsteegt V, Webb K, Ravelonandro M (2001) Post-transcriptional gene silencing in plum pox virus resistant European plum containing the plum pox potyvirus coat protein gene. *Transgenic Res* 10(3):201–209
- Sharma P, Sahu AK, Verma RK, Mishra R, Choudhary DK, Gaur RK (2014) Current status of *Potyvirus* in India. *Arch Phytopathol Plant Protect* 47(8):906–918
- Shipp JL, Buitenhuis R, Stobbs L, Wang K, Kim WS, Ferguson G (2008) Vectoring of *Pepino mosaic virus* by bumble-bees in tomato greenhouses. *Ann Appl Biol* 153(2):149–155
- Sigvald R (1985) Mature-plant resistance of potato against potato virus Y^o (PVY^O). *Potato Res* 28:135–143
- Smith KM (1931) On the composite nature of certain potato virus diseases of the mosaic group as revealed by the use of plant indicators and selective methods of transmission. *Proc R Soc* 109:251
- Smith KM (1935) Strains of *Tomato bushy stunt virus*. *Ann Appl Biol* 22:731–741

- Soto MJ, Gilbertson RL (2003) Distribution and rate of movement of the *curtovirus* *Beet mild curly top virus* (family *Geminiviridae*) in the beet leafhopper. *Phytopathol* 93(4):478–484
- Srivastava A, Kumar S, Raj SK (2015) Molecular characterization of a begomovirus and betasatellite causing yellow vein net disease of *Ageratum houstonianum*. *Plant Dis* 99:627–631
- Suresh LM et al (2017) Tomato disease field guide. *Seminis Vegetable Seeds*. <https://seminis-us.com/resources/disease-guides/tomatoes/>. Accessed 14 Apr 2020
- Trigiano TN, Windham MT, Windham AS (2003) *Plant pathology: concepts and laboratory exercises*. CRC Press, Boca Raton (FL)
- Tsai W, Shih S, Green S, Hanson P, Liu H (2004) First report of the occurrence of Tomato chlorosis virus and Tomato infectious chlorosis virus in Taiwan. *Plant Dis* 88:311
- Tsedaley B (2015) A review paper on *Potato virus Y* (PVY) biology, economic importance and its management. *J Biol Agricul Healthcare* 5(9):2224–3208
- Tsitsigiannis DI, Antoniou PP, Tjamos SE, Paplomatas EJ (2008) Major diseases of tomato, pepper and eggplant in greenhouses. *Eur J Plant Sci Biotech* 2:106–124
- Turina M, Ricker MD, Lenzi R, Masenga V, Ciuffo M (2007) A severe disease of tomato in the Culiacan area (Sinaloa, Mexico) is caused by a new picorna-like viral species. *Plant Dis* 91:932–941
- Turina M, Kormelink R, Resende RO (2016) Resistance to tospoviruses in vegetable crops: epidemiological and molecular aspects. *Annu Rev Phytopathol* 54:347–371
- Usha Rani T, Laxmi Devi V, Jalali S, Krishna Reddy M (2009) Molecular characterization and complete nucleotide sequence of *Tobacco streak virus* infecting pumpkin in India. Unpublished.
- Valleau WD, Johnson EM (1928) Some virus diseases of tobacco in Kentucky. *Phytopathol* 18:132–133
- Van der Vlugt RAA, Stijger CCMM, Verhoeven JJJ, Lesemann DE (2000) First report of *Pepino mosaic virus* on tomato. *Plant Dis* 84:103
- Varma A, Malathi VG (2003) Emerging geminivirus problems: A serious threat to crop production. *Ann Appl Biol* 142(2):145–164
- Verbeek M, Dulleman AM, van den Heuvel JFJM, Maris PC, van der Vlugt RAA (2007) Identification and characterisation of *Tomato torrado virus*, a new plant picorna-like virus from tomato. *Arch Virol* 152(5):881–890
- Verbeek M, Dulleman AM, van den Heuvel JFJM, Maris PC, van der Vlugt RAA (2008) *Tomato marchitez virus*, a new plant picorna-like virus from tomato related to *Tomato torrado virus*. *Arch Virol* 153:127–134
- Verbeek M, van Bekkum PJ, Dulleman AM, van der Vlugt RAA (2013) Torradoviruses are transmitted in a semi-persistent and stylet-borne manner by three whitefly vectors. *Virus Res* 186:55–60
- Verchot-Lubicz J, Chang-Ming Y, Bamunusinghe D (2007) Molecular biology of potexviruses: recent advances. *J Gen Virol* 88:1643–1655
- Vidavski F, Czosnek H, Gazit S, Levy D, Lapidot M (2008) Pyramiding of genes conferring resistance to *Tomato yellow leaf curl virus* from different wild tomato species. *Plant Breed* 127:625–631
- Vovlas C, Gallitelli D, Conti M (1989) Preliminary evidence for an unusual mode of transmission in the ecology of *Pelargonium zonate spot virus* (PZSV). 4th Plant Virus Epidemiology Workshop. France, Montpellier, pp 302–305
- Wan J, Basu K, Mui J, Vali H, Zheng H, Laliberte JF (2015) Ultrastructural characterization of turnip mosaic virus-induced cellular rearrangements reveals membrane-bound viral particles accumulating in vacuoles. *J Virol* 89:12441–12456
- Wang M-B, Masuta C, Smith NA, Shimura H (2012) RNA silencing and plant viral disease. *America Phytopa Soc* 25:1275–1285
- Webster CG, Reitz SR, Perry KL, Adkins S (2011) A natural MRNA reassortant arising from two species of plant- and insect-infecting bunyaviruses and comparison of its sequence and biological properties to parental species. *Virol* 413:216–225
- Whitfield AE, Kumar NKK, Rotenberg D, Ullman DE, Wyman EA ZC, Willis DK, German TL (2008) A soluble form of the *Tomato spotted wilt virus* (TSWV) glycoprotein G(N) (G(N)-S) inhibits transmission of TSWV by *Frankliniella occidentalis*. *Phytopathol* 98:45–50
- Wintermantel WM (2004) Emergence of greenhouse whitefly (*Trialeurodes vaporariorum*) transmitted criniviruses as threats to vegetable and fruit production in North America. *APSnet Feature Articles*. <https://doi.org/10.1094/APSnetFeature-2004-0604>
- Wintermantel WM, Wisler GC (2006) Vector specificity, host range and genetic diversity of *Tomato chlorosis virus*. *Plant Dis* 90:814–819
- Wintermantel WM, Wisler GC, Anchleta AG, Liu H-Y, Karasev AV, Tzanetakis IE (2005) The complete nucleotide sequence and genome organization of tomato chlorosis virus. *Arch of Virol* 150(11):2287–2298
- Wisler GC, Duffus JE, Lui HY, Li RH (1998) Ecology and Epidemiology of whitefly transmitted closteroviruses. *Plant Dis* 82(3):270–280
- Zerbini F, Briddon RW, Idris A et al (2017) ICTV Virus Taxonomy Profile: Geminiviridae. *J Gen Virol* 98(2):131–133
- Zhou X (2013) Advances in understanding begomovirus satellites. *Annu Rev Phytopathol* 51:357–381
- Zitikaite I, Samuitiene M (2008) Identification and some properties of Alfalfa mosaic alfamovirus isolated from naturally infected tomato crops. *Biologija* 54(2):83–88
- Zitter TA (1991) Potato virus Y and Tobacco etch virus. In: Jones JB, Jones JP, Stall RE, Zitter TA (eds) *Compendium of Tomato diseases*. American Phytopathological Society, St. Paul, MN, pp 36–38
- Zitter TA (2014) Diseases caused by viruses. In: Jones JB, Zitter TA, Momol TM, Miller SA (eds) *Compendium of Tomato Diseases and Pests*, 2nd edn. American Phytopathological Society, St. Paul, MN, pp 71–79
- Zitter TA, Provvidenti R (1984) Virus diseases and disorders of tomato. *Cornell Cooper Exten Veg Horti Crops Fact Sheet* 735:40
- Zubair M, Zaidi SS, Shakir S, Farooq M, Amin I, Scheffler JA, Scheffler BE, Mansoor S (2017) Multiple begomoviruses found associated with cotton leaf curl disease in Pakistan in early 1990 are back in cultivated cotton. *Sci Rep* 7:680

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.