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Review

Allexivirus: review and perspectives

Faten MANSOURI*, Pavel RYŠÁNEK

Department of Crop Protection, Faculty of Agrobiology, Food and Natural Resources, Czech University of Life Sciences Prague, Kamýcká 129, 165 00, Praha-Suchdol, Czech Republic
*Corresponding author. E-mail: feten.mansouri@live.fr

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Summary. *Allexivirus* (*Alphaflexiviridae*) was first described in 1970 by Razvjazkina. Since then, *Allexivirus* species have been detected in many countries. Although this genus primarily infects plants in the *Amaryllidaceae*, other hosts include plants in the *Fabaceae*, *Rosaceae* and *Orchidaceae*. Thirteen *Allexivirus* species have been assigned. Eight of these infect *Allium* hosts, and these include: shallot virus X (ShVX), garlic virus A (GarV-A), garlic virus B (GarV-B), garlic virus C (GarV-C), garlic virus D (GarV-D), garlic virus E (GarV-E), garlic virus X (GarV-X), and garlic-mite filamentous virus (GarMbFV). Five have been described from non-*Allium* hosts, including blackberry virus E (BVE), vanilla latent virus (VLV), alfalfa virus S (AVS), Arachis pintoi virus (ApV), and Senna severe yellow mosaic virus (SSYMV). This review analyzes the taxonomic positions of the thirteen recognized species and four unassigned species (Allexivirus DS-2013/CZE isolate, shallot mite-borne latent virus (SMbLV), cassia mild mosaic virus (CaMMV), and papaya virus A (PaVA)). Based on the inspection of data, we have concluded that PaVA is an *Allexivirus*, DS-2013/CZE is an isolate of GarV-D, and SMbLV is an isolate of ShVX. Current knowledge of the host ranges, symptoms, genome structure and modes of transmission of these viruses is also summarized, and control measures employed against them are outlined.

Keywords. Taxonomy, genome organization, hosts, transmission, disease management.

INTRODUCTION

Plant viruses cause major problems for agriculture, affecting crop quality and yields (Van der Vlugt, 2006). Several studies have been carried out to understand the emergence, taxonomy, and evolution of different viruses. *Allexivirus* includes thirteen species recognized by the International Committee on Taxonomy of Viruses (ICTV). Allexiviruses are considered as threats to several economically important hosts, due to their occurrence as mixed infections. To date, eight species have been described, primarily infecting alliums, and their major vector has been shown to be the eriophyid mite *Aceria tulipae* (Van Dijk *et al*., 1991). Five other *Allexivirus* species have been described from blackberry, vanilla, forage peanut alfalfa plant, and *Senna rizzinii* (syn. *Cassia chrysocarpa* var. *psilocarpa* Benth.), without their insect vectors being identified.

Allium-infecting allexiviruses were initially found infecting garlic and onion crops (Razvjazkina, 1970). Later, these viruses were described more thoroughly by Van Dijk *et al*. (1991). They were first referred to as onion mite-borne latent virus (OMbLV), shallot mite-borne latent virus (SMbLV) and garlic strain of onion mite-borne latent virus (OMbLV-G) (Van Dijk *et al*., 1991). Kanyuka *et al*. (1992) and Vishnichenko *et al*. (1993) reported the presence of a virus in shallot and named it shallot virus X (ShVX), and this virus was later considered synonymous to OMbLV and SMbLV (Van Dijk and Van der Vlugt, 1994). Allexiviruses were first assigned to *Rymovirus* (*Potyviridae*), based on their transmission by mites and the morphology of the virus particles (Barg *et al*., 1994). Subsequently, they were classified to "*Allexivirus*" within *Alphaflexiviridae*, for which ShVX is the type (Pringle, 1999).

Considerable progress has been made to characterize the genomes and expression of allexiviruses. Determining their biology and epidemiology is important, to be able to apply appropriate disease management strategies. This paper reviews the taxonomic status of *Allexivirus* through phylogenetic analyses and describes their biological properties and the impacts and management of the disease they cause. Perspectives for future research are also provided.

BIOLOGICAL PROPERTIES OF ALLEXIVIRUSES

Current taxonomy

Allexivirus has been assigned to *Alphaflexiviridae* in *Tymovirales* (Kreuze *et al*., 2020). The genus currently comprises thirteen species recognized by the ICTV, distinguished by their coat protein (CP) and replicase coding regions. According to the species demarcation criteria, members of *Allexivirus* share less than 72% nucleotide sequence identity (or 80% amino acid sequence identity) between their CP and replicase, and react differently with antisera (King *et al*., 2012).

The eight allexiviruses that have been detected in *Allium* species are ShVX, garlic virus A (GarV-A), garlic virus B (GarV-B), garlic virus C (GarV-C), garlic virus D (GarV-D), garlic virus E (GarV-E), garlic virus X (GarV-X) and garlic mite-borne filamentous virus (GarMbFV) (King *et al*., 2012). Five additional viruses were assigned to *Allexivirus* based on their genome organization and sequence identities between replicases and/or CP sequences. These viruses are blackberry virus E (BVE), vanilla latent virus (VLV), alfalfa virus S (AVS), Arachis pintoi virus (ApV), and Senna severe yellow mosaic virus (SSYMV) (Sabanadzovic *et al*., 2011; Gutiérrez Sánchez *et al*., 2016; Grisoni *et al*., 2017; Nemchinov *et al*., 2017; Alves *et al*., 2020).

In addition, new virus accessions have been shown to be related to *Allexivirus* but remain unassigned until an assessment by ICTV members. Based on sequence analyses, the unassigned viruses share a high degree of nucleotide (nt) and amino acid (aa) sequence similarity with the existing members of *Allexivirus*. The unassigned viruses comprised four species: SMbLV that was identified as ShVX isolate (GeneBank accession EU835196.1), Allexivirus DS-2013/CZE isolate (JX682826.1), and cassia mild mosaic virus (CaMMV) isolate (partial sequence GU481094.1) (Beserra *et al*. 2011). The *Senna macranthera* isolate was given the name cassia mild mosaic virus based on particle morphology and host range (J.E.A Beserra, personal communication). However, since there was no available information about the nucleotide sequence of the virus, the authors referred to the newly identified allexivirus as Senna virus X (SVX) (Beserra *et al*., 2011).

Phylogenetic analyses and taxonomic impact

Given the global distribution of allexiviruses, insights from phylogenetic analyses provides understanding of the origins and the relatedness between members of the genus. Sequence alignments were performed with MUSCLE (Edgar, 2004) and trees were constructed with nucleotide sequences of the complete genome and CP from selected allexiviruses and closely related unassigned member sequences available in NCBI (https://www.ncbi.nlm.nih.gov/). Phylogenetic trees were constructed using the neighbour-joining (NJ) method with a bootstrap value of 1000 using MEGA X (http://www.megasoftware.net/mega.php) (Kumar *et al*., 2018; Stecher *et al*., 2020) (Figure 1). Only partial sequences of GarMbFV were available in GenBank, so this virus was only included in the analysis of the CP. For the unassigned species CaMMV, only the replicase sequence was available so this species was not included in the analysis. New viruses have been deposited in GenBank as tentative *Allexivirus* species and these include: papaya virus A (PaVA; MN418120.1) (Read *et al*., 2020), garlic virus F (GarV-F; MN059330.1), garlic virus H (GarV-H; MN059332.1), garlic virus G (GarV-G; MN059331.1), garlic virus I (GarV-I; MN059334.1), and garlic yellow virus (GYV; MN059396.1). The viruses PaVA, GarV-F, -H, -G, and -I have been included in the analysis. However, GYV lacks the 42 KDa protein and is more related to *Carlavirus* (>76% nt and aa sequence identity of the CP to *Garlic latent virus*), so GYV was not considered in this review. Potato virus M (PVM, *Carlavirus*) was used

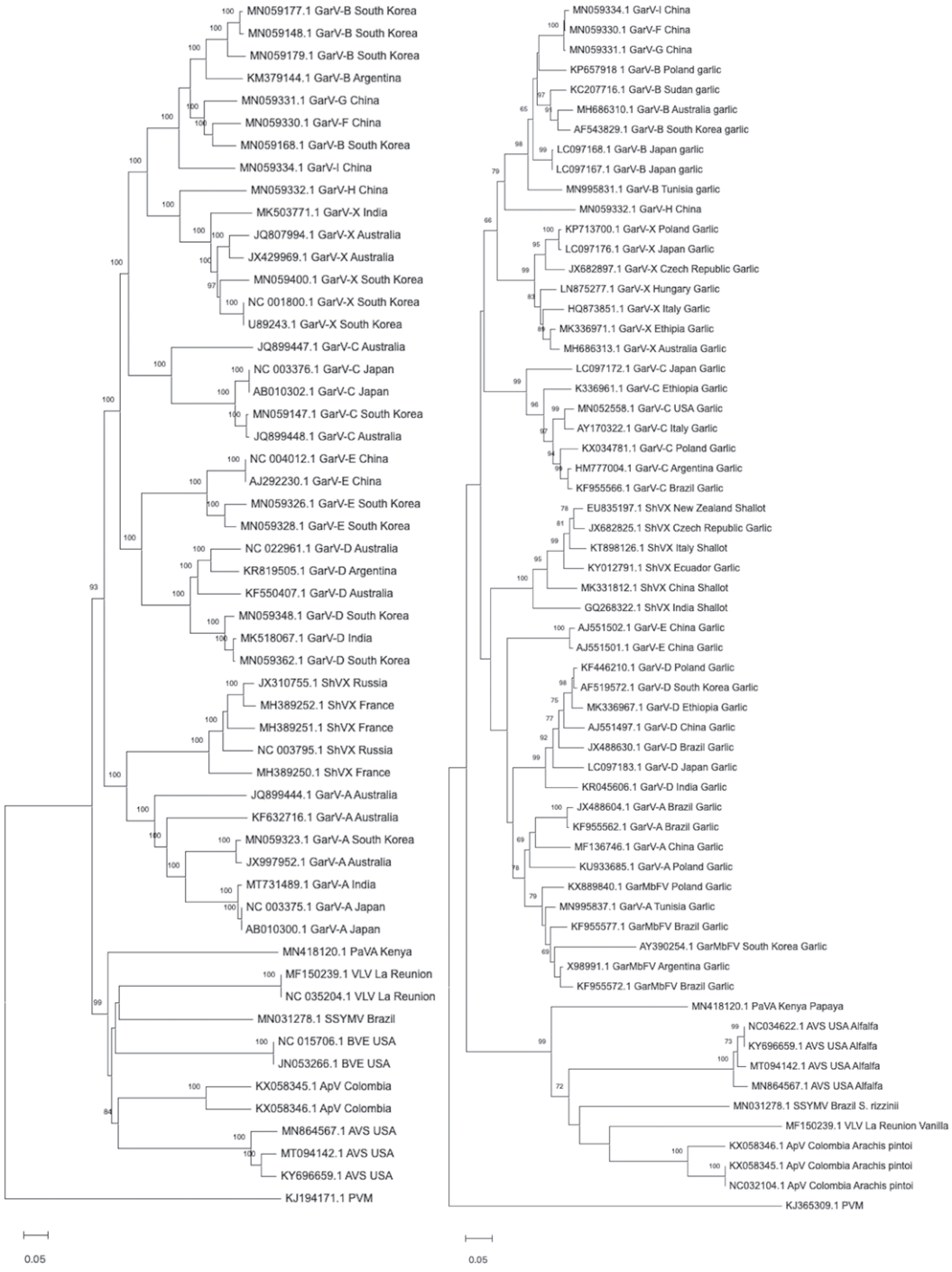

Figure 1. Phylogenetic analysis among *Allexivirus* isolates (ShVX, GarV-A, -B, -C, -D, -E, -X, -F, -G, -H, -I, GarMbFV, AVS, BVE, ApV, VLV, SSYMV, and unclassified PaVA) based on alignment of nucleotide sequences of complete genomes (**A**) and of coat proteins (**B**). Potato virus M (PVM; *Carlavirus*, *Betaflexiviridae*) was used as the outgroup. For the generation of the tree, nucleotide sequences were aligned using MUSCLE (Edgar, 2004), and the tree was constructed using MEGA x (Kumar *et al.*, 2018). The neighbour-joining method was used for the construction of the tree, and the reliability of the branches was inferred from a bootstrap analysis of 1000 replicates. Abbreviations indicated are: shallot virus X (ShVX), garlic virus A (GarV-A), garlic virus B (GarV-B), garlic virus C (GarV-C), garlic virus D (GarV-D), garlic virus E (GarV-E), garlic virus X (GarV-X), garlic mite-borne filamentous virus (GarMbFV), blackberry virus E (BVE), vanilla latent virus (VLV), alfalfa virus S (AVS) and Arachis pintoi virus (ApV), Severe yellow mosaic virus (SSYMV), garlic virus F (GarV-F), garlic virus H (GarV-H), garlic virus I (GarV-I), garlic virus G (GarV-G), and papaya virus A (PaVA). The countries of origin and the accession numbers of the selected *Allexivirus* sequences retrieved from GenBank are shown next to the virus acronyms.

as an outgroup. Sequence similarity and identity analyses were performed in BioEdit (Hall, 1999).

Whole genome phylogenetic analysis divided the allexiviruses into the *Allium* and non-*Allium*-infecting viruses (Figure 1A). Two clades were observed within the *Allium*-infecting group, separating ShVX and GarV-A from the remaining *Allium*-infecting allexiviruses. The unassigned PaVA together with the non-*Allium* allexiviruses BVE, VLV, ApV, AVS, and SSYMV, formed a monophyletic group of distant accessions. Similarly, the CP-based phylogenetic analysis showed the same two clades of the *Allium*-infecting allexivirus group and the non-*Allium* group (Figure 1B). Within the *Allium*-infecting allexivirus clade, two groups were observed: the first comprised GarV-X, -B, -I, -H, -F, -G, and -C isolates. The second group included GarV-D and -E, GarV-A and GarMbFV isolates, and grouped together with ShVX isolates. The second clade included the four non-*Allium* allexiviruses AVS, BVE, VLV, ApV, and SSYMV, while PaVA formed a very distant monophyletic isolate. In view of the high homology in the CP, and based on the phylogenetic tree, the species PaVA could be considered as new species of allexivirus.

Coat protein sequence analysis showed that the SMbLV sequence shared 90.5–97.1% nt sequence identity (97.0–98.0% aa sequence identity) to ShVX isolates (GeneBank: MH389253.1, MH389252.1, KY012791.1). Similarly, DS-2013/CZE isolate (GeneBank: JX682826.1) shared 84.2% nt sequence identity (95.0% aa sequence identity) to GarV-D isolates (GeneBank: JX682863.1, AJ551490.1). Therefore, SMbLV should be considered as an isolate of ShVX, and ShVX should be retained as an ICTV recognized species, and DS-2013/CZE isolate should be considered an isolate of GarV-D. In addition, identity pairwise comparisons of the CP gene of GarV-I, GarV-F and GarV-G showed high degrees of sequence similarity (99.1-99.6% nt sequence identity; 97.9-98.9% aa sequence identity), while GarV-H shared, respectively, 73.0%, 72.6%, and 72.5% nt sequence identity (66.1%, 65.7%, and 65.9% aa sequence identity) with, respectively, GarV-I, -G, and -F. The CP gene of GarV-I shared 85.4 to 99.5% nt sequence identity (72.7–98.9% aa sequence identity) with GarV-B isolates, but the replicase gene analysis of GarV-I identified high identity values with GarV-D isolates (92.1–95.3% nt sequence identity, 96.1-99.7% aa sequence identity). CP sequence analysis also showed that GarV-F, GarV-G, and GarV-H shared high similarity to GarV-B isolates (68.6–99.8% nt identity, 75.6–98.9% aa identity). These values suggest that GarV-F, -G, and -H are different isolates of GarV-B. Based on our analyses, these new accessions retrieved from GenBank as allexiviruses have similar structure, and they are closely related to *Allexivirus*, with evidence of recombination between the species. However, since information about these new accessions is limited, additional information is required to give accurate taxonomic assignation.

The CP and replicase genes have been used to classify species within the genus. Although this criterion has been widely used, there is growing evidence of high similarities existing between some of the *Allexivirus* species (Celli *et al*., 2018; Geering and McTaggart, 2019). For example, when available GarMbFV CP sequences were compared with GarV-A CP sequences, the identity values for CP among the isolates were 79.5 to 81.1% for nt sequences (76.6–81.8% aa sequence identity), all values of which are above the taxonomic classification criteria. Based on the phylogenetic analyses, both species formed a separate well-supported monophyletic cluster (Figure 1B), with the exception of GarV-A Tunisian isolate (GenBank: MN995837.1) that groups with GarMbFV isolates (Figure 1B). The Tunisian GarV-A shared 91.5 to 93.6% nt sequence identity (97.1–98.5% aa sequence identity) with GarMbFV isolates. Our data analysis therefore indicated that the two species are very similar and may be different isolates of the same species. The high similarity observed between the species has been clearly demonstrated by Geering and McTaggart (2019), clarifying the taxonomic position of GarMbFV and GarV-A. These authors concluded that the two species are conspecific. Additionally, since the replicase region used in taxonomic classification is absent, the risk of errors occurring in classification increases, especially in cases when only partial sequences have been determined. In view of these high proportions of sequence identity and as previously proposed (Geering and McTaggart, 2019), we suggest that GarMbFV should be considered as a strain of GarV-A species. Isolation of GarMbFV complete genome sequence is required to confirm the relationship of GarMbFV with GarV-A.

During the CP and replicase gene analysis, high similarity was observed between GarV-B and GarV-X isolates. GarV-B and GarV-X isolates shared 75.4 to 78.1% nt sequences identity (84.4–89.6% aa sequence identity) between the CP sequences, and 73.4 to 74.1% nt sequences identity (81.6–82.9% aa sequence identity) between the replicase sequences, both values of which are greater than demarcation criteria of *Allexivirus* (King *et al*., 2012). Although the different accessions of both isolates are well separated in the phylogenetic analysis, GarV-B and GarV-X have enough homology to be considered as different strains of the same species. Our data analysis confirms previous results of Celli *et al*. (2018), that also indicated possible recombination events within the complete genome of *Allium*-infecting allexiviruses.

Based on the data analysis, we suggest that SMbLV is an isolate of ShVX, DS-2013/CZE is an isolate of GarV-D, while GarMbFV and GarV-A are conspecific, and GarV-B and GarV-X are also conspecific. More data are required to assess the taxonomic status of the sequences of GarV-F, -G, -H, and -I.

The genetic diversity of allexivirus populations has been reported when comparing the CP and the replicase sequences, indicating population differentiation (Chen *et al*., 2001; Melo-Filho *et al*., 2004; Mohammed *et al*., 2013). Our data indicates that phylogenetic clustering among allexivirus isolates was independent of geographical area (Figure 1B). This means that the overall variability is largely due to global trade between countries, and evolutionary forces such as virus occurrence in mixed infections and interactions between different genotypes of the same species (Melo-Filho *et al*., 2004; Mohammed *et al*., 2013). More analysis of the of allexivirus population genetics is required to allow precise understanding of their evolution and genomic diversity within virus populations.

Genome organization and virion properties

Members of *Allexivirus* are single-stranded positive-sense RNA viruses with genome sizes of approx. 9 kb (Chen *et al*., 2004). Virions are flexuous and filamentous, approx. 800 nm in length and 12 nm in diameter (Figure 2). These viruses induce granular inclusion bodies and small bundles of flexible particles in the cytoplasm of the epidermis cells of infected plants (Kang *et al*., 2007). The RNA of allexiviruses is capped at the 5' untranslated region (UTR) terminus with a 7-methylguanosine cap (m_7G) and has a polyadenylated tail at the 3' UTR terminus.

The genome organization of *Allexivirus* members is outlined in Table 1. The number of open reading frames (ORFs) varies among species. The genomes of seven *Allium*-infecting allexiviruses (GarV-A, -B, -C, -D, -E, -X, and ShVX) contains seven ORFs, whereas those of AVS, VLV, ApV and SSYMV contains six ORFs, and that of BVE contains five ORFs (Table 1), and there is no published complete genome sequence of GarMbFV. The first ORF in all *Allexivirus* species is the largest gene, which encodes a putative replicase protein with three conserved motifs: methyl transferase (MET), NTPase/helicase (HEL) and RNA-dependent RNA polymerase (RdRp) (Song *et al*., 1998). The replicase protein of ShVX and AVS contains an oxidative demethylase domain (AlkB) located between the MET and HEL domains that is present in some members of the *Alphaflexiviridae* (Van den Born *et al*., 2008; Nemchinov *et al*., 2017).

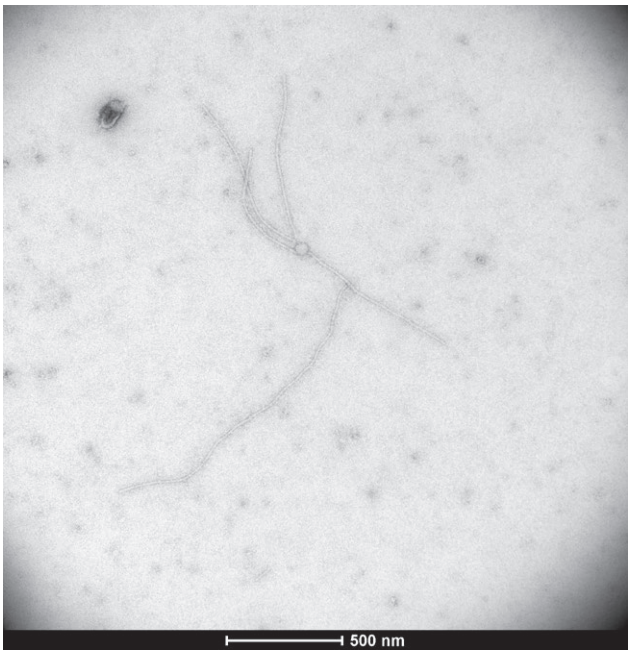

Figure 2. Transmission electron microscopy showing particles of *Garlic virus D* from garlic plants (negative staining with 1 % uranyl acetate). Particle sizes are approx. 800 nm length and 12 nm diameter. Bars represent 500 nm.

Allexiviruses also contains triple gene blocks (TGBs); TGB1 encodes helicase and TGB2 encodes virus movement domains. The two TGBs were shown to be required for viral cell-to-cell movement through plasmodesmata and systemic transport via host phloem tissues (Lezzhov *et al*., 2015). The TGB3 protein was found in all the *Allium*-infecting allexiviruses and in BVE and ApV but lacked the initiation codon. TGB3 synthesis requires a leaky ribosome scanning initiated by a TGB3 CUG initiator codon, rather than internal ribosome entry (Lezzhov *et al*., 2015). This mechanism is commonly used by RNA viruses to translate functionally multicistronic messages (Firth and Brierley, 2012). The TGB3 of the VLV, AVS, SSYMV and the unclassified virus PaVA had the initiation AUG start codon (Grisoni *et al*., 2017; Nemchinov *et al*., 2017; Read *et al*., 2020; Alves *et al*., 2020). Presumably, the TGB3 may have an accessory function alongside the TGB1 and TGB2 in cell-to-cell movement of the viruses (Morozov and Solovyev, 2003).

Another large ORF, downstream of the TGB, encoding a protein of approx. 42 KDa, is found in all allexiviruses, and this has no homology to any known protein of other genera (King *et al*., 2012). The 42 KDa protein contains a serine and threonine-rich protein and has been shown to be involved in virion assembly and act as

Table 1. Genome size, number and molecular weight of proteins encoded by the genes of each *Allexivirus*.

Virus species	GenBank accession	Genome size (nt)[1]	Number of ORF	Molecular weight (KDa)							Reference
				Replicase	TGB1	TGB2	TGB3	42K protein	CP	NABP	
GarV-A	AB010300	8660	7	183	28	11	7*	39	28	15	Sumi *et al*., 1999
GarV-B	KM379144	8327	7	168	27	12	7*	39	27	14	Celli *et al*., 2018
GarV-C	AB010302	8405	7	175	27	11	7*	41	28	15	Sumi *et al*., 1999
GarV-D	KF555653	8424	7	177	26	11	7*	40	27	15	Wylie *et al*., 2014
GarV-E	AJ292230	8451	7	176	27	11	7*	40	35	15	Chen and Chen, 2002
GarV-X	U89243	8458	7	174	26	12	7*	32	36	15	Song *et al*., 1998
ShVX	M97264	8890	7	195	26	11	7*	42	28	15	Kanyuka *et al*., 1992
BVE	JN053266	7718	5	169	27	12	11*	40	25	-**	Sabanadzovic *et al*., 2011
AVS	KY696659	8349	6	188	26	11	10	38	32	-**	Nemchinov *et al*., 2017
ApV	KX058345	7599	6	158	26	12	8	41	26	-**	Gutiérrez Sánchez *et al*., 2016
VLV	MF150239	7462	6	161	26	11	8	41	25	-**	Grisoni *et al*., 2017
SSYMV	MN031278	7829	6	164	26	11	9	37	28	-**	Alves *et al*., 2020

[1] nt= nucleotides, ORF= open reading frame, TGB = triple gene block, 42K protein = protein of unknown function, CP = Coat protein, NABP = nucleic acid binding protein, GarV-A = *Garlic virus A*, GarV-B = *Garlic virus B*, GarV-C = *Garlic virus C*, GarV-D = *Garlic virus D*, GarV-E = *Garlic virus E*, GarV-X = *Garlic virus X*, ShVX = *Shallot virus X*, BVE = *Blackberry virus E*, VLV = *Vanilla latent virus*, AVS = *Alfalfa virus S*, ApV = *Arachis pintoi virus*.

* Untranslated TGB-like gene that lacks the initiator AUG codon and partially overlapping with the TGB2 genes.

** No sequence was identified.

a co-factor to facilitate the interaction of the capsid protein with genomic RNA during assembly (Vishnichenko *et al*., 2002).

The coat protein (25-36 KDa) shares the conserved structural core and evolutionary origin of some families of filamentous plant viruses and shows high similarity to carla- and potex-viruses (Kanyuka *et al*., 1992; Martelli *et al*., 2007). Only the eight viruses infecting *Allium* (ShVX, GarV-A, -B, -C, -D, -E, -X, and GarMbFV) have an additional ORF, that contains a nucleic acid binding domain (NABP). This ORF contains a small cysteine-rich protein (CRP), a basic arginine-rich domain and a zinc-finger motif at the 3'-terminal region (Song *et al*., 1998; Kanyuka *et al*., 1992). Although CRPs of many plant viruses were shown to act as RNA silencing suppressors (Senshu *et al*., 2011; Fujita *et al*., 2018), Arkhipov *et al*. (2013) did not observe this activity in ShVX. The allexivirus CPR is likely to be necessary for the regulation of virus RNA replication, together with pathogenicity determinants during allexivirus evolution and control interactions of the viruses with their plant hosts (Lukhovitskaya *et al*., 2014, Yoshida *et al*., 2018).

Various nucleotide insertions between CP and CRP genes have been observed in GarV-B, GarV-C and GarV-X. These insertions are complementary to garlic 18S ribosomal RNA (rRNA) and are probably involved in the termination-reinitiation translation mechanism (Yoshida *et al*., 2018). It is possible that GarV-B, -C, and -X utilize this mechanism to regulate the expression of virus protein, to enable adaptations to specific hosts and vectors (Gramstat *et al*., 1994).

Virus proteins are often multifunctional, and each function is essential for virus survival and can be dependent on virus species, host and/or vector. Further research is required to clarify the entire allexiviruses infection process. How these viruses avoid host defense mechanisms and what are the functional features of the virus genomes, are essential questions to allow full understanding of the expression of allexiviruses and their interactions with their hosts plants.

PATHOLOGY AND MANAGEMENT OF ALLEXIVIRUSES

Distribution, host range, and transmission

To date, *Allium*-infecting allexiviruses have been recorded in all *Allium* producing regions (Table 2), while the non-*Allium*-infecting allexiviruses have only been reported in countries where they were first described (Sabanadzovic *et al*., 2011; Gutiérrez Sánchez *et al*., 2016; Grisoni *et al*., 2017; Nemchinov *et al*., 2017; Alves *et al*., 2020). However, it is most likely that these viruses are more broadly distributed than currently is known, especially where their host plants are cultivated.

The natural host range of allexiviruses has been reported to be restricted to several cultivated, ornamen-

Table 2. Geographical distribution of allexiviruses.

Location	Detected viruses[1]	References
China	GarV-A, -D, -E, -X, ShVX, GarV-B (GarV-F, GarV-I, GarV-G, and GarV-H)[2]	Chen *et al*., 2001, 2004
Japan	GarV-A, -B, -C, -D, GarMbFV	Sumi *et al*., 1993; Yamashita *et al*., 1996
South Korea	GarV-A, -B, -C, -D, -E, -X	Kang *et al*., 2007; lee *et al*., 2007
India	GarV-A, -C, -D, -X, GarMbFV, ShVX	Mandal *et al*., 2017
Iran	GarV-A, -B, -C, -D, ShVX	Shahraeen *et al*., 2008
Russia	ShVX	Kanyuka *et al*., 1992; Vishnichenko *et al*., 1993
Turkey	GarV-B, -D, -X, GarMbFV	Fidan, 2010; Fidan *et al*., 2013
Italy	GarV-B, -D, -X, ShVX	Taglienti *et al*., 2017
Poland	GarV-A, -B, -D, -X, GarMbFV, ShVX	Bereda *et al*., 2017
France	ShVX	Marais *et al*., 2019
Greece	GarV-C, -D, GarMbFV	Dovas *et al*., 2001
Czech Republic	GarV-A, -B, -C, -D, -E, -X, GarMbFV, ShVX	Klukáčková *et al*., 2007
Slovenia	GarV-A, -B, -C, -D, -E, -X, GarMbFV, ShVX	Mavrič and Ravnikar, 2005
Spain	GarV-B, -D, -X	Tabanelli *et al*., 2004
United Kingdom	ShVX	Ryabov *et al*., 1996
Netherlands	OMBLV, SMbLV[3]	Van Dijk *et al*., 1991
Argentina	GarV-A, -B, -C	Cafrune *et al*., 2006a
Mexico	GarV-D	Rocha and Esmeralda, 2019
Brazil	GarV-A, -B, -D, -X, GarMbFV, SSYMV	Oliveira *et al*., 2014; Alves *et al*., 2020
Colombia	ApV	Gutiérrez Sánchez *et al*., 2016
Ecuador	ShVX	Granda *et al*., 2017
USA	GarV-B, -C,-D, -E, ShVX, AVS, BVE	Gieck *et al*., 2009; Sabanadzovic *et al*., 2011; Nemchinov *et al*., 2017; Wijayasekara *et al*., 2019
Sudan	GarV-A, -B, -X, ShVX	Mohammed *et al*., 2013; Hamed *et al*., 2012
La reunion	VLV	Grisoni *et al*., 2017
Ethiopia	GarV-B, -C, -D, -X	Jemal *et al*., 2015; Abraham *et al*., 2019
DR Congo	GarV-D	Majumder *et al*., 2019
New Zealand	GarV-A, -B, -D, ShVX	Ward *et al*., 2009
Australia	GarV-A, -B, -C, -D, -E, -X	Wylie *et al*., 2014; Nurulita *et al*., 2020

[1] GarV-A = *Garlic virus A*, GarV-B = *Garlic virus B*, GarV-C = *Garlic virus C*, GarV-D = *Garlic virus D*, GarV-E = *Garlic virus E*, GarV-X = *Garlic virus X*, GarV-F = *Garlic virus F* (GenBank accession MN059330.1), GarV-H = *Garlic virus H* (MN059332.1), GarV-G = *Garlic virus G* (MN059331.1), GarV-I = *Garlic virus I* (MN059334.1), GarMbFV = *Garlic-mite borne filamentous virus*, ShVX = *Shallot virus X*, BVE = *Blackberry virus E*, VLV = *Vanilla latent virus*, AVS = *Alfalfa virus S*, ApV = *Arachis pintoi virus*.
[2] Based on phylogenetic and sequence analysis, GarV-F, -H, -G, and -I are conspecific of GarV-B.
[3] Onion mite-borne latent virus (OMbLV) and shallot mite-borne latent virus (SMbLV) were the first name species given for *Allium*-infecting allexiviruses, later identified as shallot virus X (ShVX).

tal, and wild *Allium* species (Table 3). *Allium*-infecting allexiviruses, have been shown to only infect monocotyledon plants in the *Asparagales* (Van Dijk *et al*., 1991; Fidan *et al*., 2013). The only exception was detection of GarV-D on *Drimia maritima* (L.) (*Asparagaceae*), which is, to date, the only reported natural occurrence of *Allium*-infecting allexiviruses in a non-*Alliaceae* host (Fidan *et al*., 2013). The presence of *Allium*-infecting allexiviruses in *D. maritima* suggests that either the virus is expanding its host range (new host adaptation), or that it has always been present unnoticed in other host families.

ApV, AVS, BE, VLV, and SSYMV have been reported to naturally infect dicotyledonous plants in the *Rosaceae, Fabaceae, Orchidaceae* and *Caricaceae* (Table 3). The unclassified allexivirus PaVA was detected in *Carica papaya* L. (Read *et al*., 2020) and CaMMV was detected in *S. macranthera* (Beserra *et al*., 2011).

Most members of *Allexivirus* are transmissible from natural to experimental hosts by mechanical inoculation. *Allium*-infecting allexiviruses can be transmitted to several diagnostic hosts, including *Chenopodium quinoa*, *C. murale*, *C. amaranthicolor, Gomphrena globosa,*

Table 3. Natural hosts and experimental host range when mechanically inoculated with one of allexiviruses.

Virus species[1]	Natural hosts	References	Experimental hosts (References)
GarV-A	*Allium ampeloprasum, A. angulosum, A. ascalonicum, A. anisopodium, A. caesium, A. chinense, A. bucharicum, A. carinatum, A. cyathophorum, A. cernuum, A. flavum, A. hybridum, A. ledebourianum, A. microdictyon, A. moly, A. narcissiflorum, A. neapolitanum, A. nutans, A. oleraceum, A. ramosum, A. runyonii, A. roseum, A. rotundum, A. sativum, A. senescens, A. scabriscapum, A. schoenoprasum, A. scorodoprasum, A. sphaerocephalon, A. stipitatum, A. suaveolens, A. tuberosum, A. thunbergii, A. ursinum, A. victorialis* var. *platyphyllum*, *A. vineale*	Yamashita *et al*., 1996; Ward *et al*., 2009; Park *et al*., 2011; Mansouri *et al*., 2021a	*Chenopodium murale*, *Gomphrena globosa*, *C. amaranticolor*, *C. quinoa, Atriplex hortensis, C. foliosum, C. opulifolium*, *A.cepa*, *A. ampeloprasum, Nicotiana benthamiana* (Van Dijk *et al*., 1991, Yamashita *et al*., 1996; Melo-Filho *et al*., 2004; Cafrune *et al*., 2006a; Dąbrowska *et al*., 2020)
GarV-B	*A. anisopodium, A. chinense, A. caeruleum, A. caesium, A. sphaerocephalum, A. cyathophorum, A. cernuum, A. flavum, A. ledebourianum, A. hybridum, A. narcissiflorum, A. neapolitanum, A. nutans, A. oleraceum, A. oreophilum, A. sativum, A. schoenoprasum, A. scorodoprasum, A. senescens, A. stipitatum, A. suaveolens, A. tuberosum, A. ursinum*	Ward *et al*., 2009; Bampi *et al*., 2015; Paduch-Cichal and Bereda, 2017; Mansouri *et al*., 2021a	
GarV-C	*A. ampeloprasum, A. caeruleum, A. angulosum, A. bulgaricum, A. carinatum, A. caesium, A. cepa L., A. cyathophorum, A. cernuum, A. flavum, A. microdictyon, A. moly, A. narcissiflorum, A. neapolitanum, A. nutans, A. oleraceum, A. oreophilum, A. ramosum, A. roseum, A. rotundum, A. sativum, A. sphaerocephalum, A. schoenoprasum, A. scorodoprasum, A. senescens, A. suaveolens, A. tuberosum, A. ursinum, A. vineale*	Shahraeen *et al*., 2008; Ward *et al*., 2009; Bampi *et al*., 2015 ; Mansouri *et al*., 2021a	
GarV-D	*A. atropurpureum, A. sativum, A. cepa L., A. caesium, Drimia maritima, A. ascalonicum, A. fistulosum, A. caeruleum, A. sphaerocephalum, A. angulosum, A. flavum, A. hybridum, A. karataviense, A. macrostemon, A. moly, A. oreophilum, A. scabriscapum, A. senescens, A. thunbergii*	Ward *et al*., 2009; Fidan *et al*., 2013; Bampi *et al*., 2015; Paduch-Cichal and Bereda, 2017; Mansouri *et al*., 2021a	
GarV-E	*A. caeruleum, A. cernuum, A. flavum, A. sativum, A sphaerocephalum, A. scorodoprasum*	Chen and Chen, 2002; Bampi *et al*., 2015; Mansouri *et al*., 2021a	
GarV-X	*A. caesium, A. hybridum, A. karataviense, A. sativum, A. schubertii*	Song *et al*., 1998; Mansouri *et al*., 2021a	
GarMbFV	*A. caesium, A. cepa L., A. cernuum, A. flavum, A. hybridum, A. karataviense, A. moly, A. oreophilum, A. sativum, A. schubertii*	Dovas *et al*., 2001; Mansouri *et al*., 2021a	
ShVX	*A. angulosum, A. altaicum, A. ascalonicum, A. anisopodium, A. bucharicum, A. caeruleum, A. caesium, A. sativum, A. cepa L.* var. *aggregatumA. ledebourianum, A. hybridum, A. sphaerocephalum, A. flavum, A. bulgaricum, A. cyathophorum, A. cernuum, A. microdictyon, A. moly, A. narcissiflorum, A. neapolitanum, A. nutans, A. oleraceum, A. oreophilum, A. przewalskianum, A. ramosum, A. rotundum, A. scabriscapum, A. scorodoprasum, A. stipitatum, A. suaveolens, A. tuberosum, A. ursinum, A. vineale*	Ward *et al*., 2009; Hamed *et al*., 2012; Bampi *et al*., 2015; Taglienti *et al*., 2017; Paduch-Cichal and Bereda, 2017; Mansouri *et al*., 2021a	
BVE	*Rubus* L.	Sabanadzovic *et al*., 2011	
VLV	*Vanilla planifolia, V. pompona, V. humblotii*	Grisoni *et al*., 2017	*V. planifolia*
ApV	*Arachis pintoi*	Gutiérrez Sánchez *et al*., 2016	
AVS	*Medicago sativa*	Nemchinov *et al*., 2017	
SSYMV	*Senna rizzini*	Alves *et al*., 2020	*C. amaranticolor*, *C. quinoa*, *G. globosa*, *S. rizzinii*, *S. occidentalis*

[1] GarV-A = *Garlic virus A*, GarV-B = *Garlic virus B*, GarV-C = *Garlic virus C*, GarV-D = *Garlic virus D*, GarV-E = *Garlic virus E*, GarV-X = *Garlic virus X*, GarMbFV = *Garlic-mite borne filamentous virus*, ShVX = *Shallot virus X*, BVE = *Blackberry virus E*, VLV = *Vanilla latent virus*, AVS = *Alfalfa virus S*, ApV = *Arachis pintoi virus*.

Nicotiana occidentalis and *Atriplex hortensis* (Van Dijk *et al*., 1991; Yamashita *et al*., 1996). VLV is mechanically transmitted to its natural vanilla host (*Vanilla planifolia*) (Grisoni *et al*., 2017). SSYMV is mechanically transmitted to *S. rizzinii*, *S. occidentalis, C. amaranticolor*, *G. globosa*, and the unassigned CaMMV is transmitted mechanically to *S. macranthera, Phaseolus vulgaris*, and *G. globosa* (Beserra *et al*., 2011; Alves *et al*., 2020).

Allium-infecting allexiviruses are transmitted by their major vector, the eriophyid mite *Aceria tulipae* Keifer (Van Dijk *et al*., 1991). The *Allium*-infecting allexiviruses have been successfully transmitted to leek plants (*Allium ampeloprasum*) by *A. tulipae* (Dąbrowska *et al*., 2020; Mansouri *et al*., 2021b). The transmission characteristics of these viruses, including acquisition time, inoculation time, persistence in the vector, and effectiveness of the transmission, have been recently described as semipersistent (Mansouri *et al*., 2021b). Studies on other mite-transmitted viruses indicated a similar mode of transmission (Gispert *et al*., 1998; Kulkarni *et al*., 2002).

Potential vectors of the non-*Allium* allexiviruses have not yet been identified and are different to the those of other allexiviruses, because *A. tulipae* was shown to be restricted to alliums (Kiedrowicz *et al*., 2017). Dissemination of these viruses probably takes place through the distribution of infected propagative materials, which is a major mode for the long-distance dissemination of allexiviruses (King *et al*., 2012). In addition, detailed studies on the transmission of the non-*Allium* allexiviruses are required to understand and prevent their dissemination.

Economic impacts and disease management

The *Allium*-infecting allexiviruses are responsible for important economic impacts, although they only cause mild host symptoms (mild mosaic, yellow stripes, stunted growth) in natural infections (Kang *et al*., 2007). These viruses have been reported to cause yield losses and reduce quality of several *Allium* crops (Cafrune *et al*., 2006b). Single infection with either GarV-C or GarV-A resulted in decreased garlic bulb weight (approx. 15% reduction) and diameter (approx. 5%) (Cafrune *et al*., 2006a; Perotto *et al*., 2010). Single infection with GarV-D caused a 12% reduction in garlic bulb weight and 7% of bulb quality (Celli *et al*., 2016). Although infections of garlic crops by one of the *Allium*-infecting allexiviruses alone could result in diseases, yield losses were considerably more severe when allexiviruses occurred in mixed infections, especially in the presence of *Potyvirus* and *Carlavirus* species (Conci *et al*., 2003). Little research has been reported on the non-*Allium* allexiviruses since their discovery, suggesting that they have low prevalence on their host crops. Although BVE and ApV cause mild host symptoms (e.g., chlorosis and vein yellowing), it is possible that these symptoms are exhibited due to mixed virus infections (Sabanadzovic *et al*., 2011; Martin and Tzanetakis, 2015; Gutiérrez Sánchez *et al*., 2016).

Allexiviruses present distinct challenges for control and management of their spread and emergence in several crops. These viruses are not seedborne, but they have been introduced in different countries via infected plant material. Disease control methods, including diagnosis, sanitation, sanitary certification, host resistance and vector management, are all likely to be key factors for the effective management of these diseases. Other approaches, such as conventional host breeding, transgenic methods, and gene silencing strategies, have been used to control RNA viruses (Chaudhary, 2018). It is therefore important that the biology of viruses is fully understood so that these methods can be utilized to limit the spread of viruses.

The use of healthy planting material is one of the most effective methods for controlling viruses and maintaining good crop yields (Torres *et al*., 2000; Salomon, 2002). *In vitro* tissue culture techniques, such as micropropagation, meristem culture, thermotherapy, chemotherapy, cryotherapy, and somatic embryogenesis, have been used for production of virus-free garlic plants (Ghaemizadeh *et al*., 2014; Manjunathagowda *et al*., 2017). Although these techniques have been used successfully in the elimination of allexiviruses in alliums, these viruses remain major problems because these crops are easily re-infected once they are planted in fields. Re-infections occur from vector transmission from nearby infected crops, such as garlic and onion (Taglienti *et al*., 2017). Regular crop inspection for vectors and strict pest control management are essential throughout crop growth.

There have been no reports of *in vitro* sanitation and control management for BVE, ApV, AVS, VLV and the newly unassigned viruses. However, the use of virus-free planting material can effectively control these viruses. Development of transgenic berry crops and legumes has been reported to limit damaging viruses in different families (Hill *et al*., 1991; Divakaran *et al*., 2008; Martin and Tzanetakis, 2015). Therefore, the use of host resistance and transgenic varieties may be worthwhile strategies for management of allexiviruses. Although limited effectiveness has been reported, further research is required on the modes of transmission of the non-allium allexiviruses.

PERSPECTIVES

Plant viruses are major problems in many vegetable and ornamental crops, causing economic losses as high as 50 billion euros per year (Zhao *et al*., 2017), especially in crops for which no virus-resistant varieties are available. Allexiviruses continue to be threats to *Allium* production. Key areas for future research are: i) the understanding of basic allexivirus biology, including how their genomes contribute to infection processes; and ii) the underlying mechanisms governing their interactions with host plants, and their vectors.

The trade of infected plant material locally, regionally, and globally has been the most important factor in dissemination of allexiviruses, causing high yield losses. Improved techniques for rapid detection and diagnosis, including the use of molecular and serological tools such as enzyme-linked immunosorbent assay (ELISA), reverse transcription polymerase chain reaction (RT-PCR), and RT quantitative PCR (RT-qPCR), are essential to assist effective disease management decisions. In addition to the use of traditional cultural practices, especially control of nearby infected crops and vector hosts, management tactics must also account for climate change. Use of high phytosanitary standards for exchanged plant material, grower, and public education about these viruses their management, are all important to avoid crop yield losses.

Climate change poses a new challenge that may affect the distribution and survival of plant viruses and their vectors, and is likely to aggravate virus epidemics (Jones, 2014; 2018). Climate change can also affect virulence and pathogenicity of plant viruses including allexiviruses, by increasing disease and insect pest outbreaks (Trebicki, 2020). Outbreaks of severe epidemics, coupled with increased long-distance pathogen and vector dispersal through the exchange of infected plant material, will lead to yield losses. Therefore, understanding of *Allexivirus* epidemiology is required to anticipate challenges ahead, and to develop effective strategies to secure global food production for the future (Trebicki, 2020).

The use of sensitive methods, such as transcriptomic analysis and RNA sequencing (RNAseq), may provide valuable insights into host factors that differentially interact with viruses (Kamenetsky *et al*., 2015; Khandagale *et al*., 2020). These methods can enhance understanding of host-virus interaction mechanisms and can lead to the discovery of genes involved in plant defense responses. One recent addition to genetic engineering is the development of the characteristic clustered regularly interspaced short palindromic repeats-associated 9 (CRISPR/Cas9) protein, that has emerged as a potent genome-editing tool to confer resistance against viruses (Khan *et al*., 2018). Implementation of CRISPR/Cas9 to modify host plants and introduce effective resistance against allexiviruses and their vectors could be worthwhile (Khandagale *et al*., 2020). These host modification techniques will complement traditional resistance breeding strategies to achieve improve levels of virus resistance.

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LITERATURE CITED

Abraham A.D., Kidanemariam D.B., Holton T.A., 2019. Molecular identification, incidence and phylogenetic analysis of seven viruses infecting garlic in Ethiopia. *European Journal of Plant Pathology* 155:181–191.

Alves T.M., Silva de Novaes Q., de Paula A., Camelo-García V. M., Nagata T., … Kitajima E.W., 2020. Near-complete genome sequence and biological properties of an *Allexivirus* found in *Senna Rizzinii* in Brazil. *Archives of Virology* 165: 1463–1467.

Arkhipov A.V., Solovyev A.G., Vishnichenko V.K., 2013. Reproduction of *Shallot virus X* in absence of its own active suppressor protein of RNA silencing. *Russian Agricultural Sciences* 39: 218–221.

Bampi D., Reinsel M.D., Hammond J., 2015. Viruses present in ornamental *Allium* in the United States. In: *Proceedings of the APS Annual Meeting 1st-5th August, Pasadena, California,* USA, 513.

Barg E., Lesemann D.E., Vettren H.J., Green S.K., 1994. Identification, partial characterization and distribution of viruses infecting *Allium* crops in South and Southeast Asia. *Acta Horticulturae* 358: 251–258.

Bereda M., Paduch-Cichal E., Dąbrowska E., 2017. Occurrence and phylogenetic analysis of allexiviruses identified on garlic from China, Spain and Poland commercially available on the Polish retail market. *European Journal of Plant Pathology* 149: 227–237.

Beserra J.E.A., de Carvalho M.G., Barguil B.M., Murilo Zerbini F., 2011. Partial genome sequence of a Potyvirus and of a virus in the order Tymovirales found in *Senna macranthera* in Brazil. *Tropical Plant Pathology* 36: 116–120.

Cafrune E.E., Perotto M.C., Conci V.C., 2006a. Effect of two *Allexivirus* isolates on garlic yield. *Plant Disease* 90: 898–904.

Cafrune E.E., Balzarini M., Conci V.C., 2006b. Changes in the concentration of an *Allexivirus* during the crop cycle of two garlic cultivars. *Plant Disease* 90: 1293–1296.

Celli M.G., Perotto M.C., Buraschi D., Conci V.C., 2016. Biological and molecular characterization of *Garlic virus D* and its effects on yields of garlic. *Acta Horticulturae* 1143: 193–200.

Celli M.G., Perotto M.C., Luciani C.E., Pozzi E.A., Conci V.C., 2018. Molecular characterization of the *Garlic virus B* genome and evidence of *Allexivirus* recombination. *European Journal of Plant Pathology* 153: 307–316.

Chaudhary K., 2018. CRISPR/Cas13a targeting of RNA virus in plants. *Plant Cell Reports* 37: 1707–1712.

Chen J., Chen J., 2002. Genome organization and phylogenetic tree analysis of *Garlic virus E*, a new member of genus *Allexivirus*. *Chinese Science Bulletin* 47: 33–37.

Chen J., Chen J., Adams M.J., 2001. Molecular characterization of a complex mixture of viruses in garlic with mosaic symptoms in China. *Archives of Virology* 146: 1841–1853.

Chen J., Zheng H.Y., Antoniw J.F., … Lin, L., 2004. Detection and classification of allexiviruses from garlic in China. *Archives of Virology*, 149: 435–44.

Conci V. C., Canavelli, A., Lunello, P., Di Rienzo, J., Nome, S. F., Zumelzu, G., Italia, R., 2003. Yield losses associated with virus-infected garlic plants during five successive years. *Plant Disease* 87: 1411–1415.

Dąbrowska E., Lewandowski M., Koczkodaj S., Paduch-Cichal E., 2020. Transmission of Garlic virus B, Garlic virus C, Garlic virus D and Garlic virus X by *Aceria tulipae* (Keifer) in leek. *European Journal of Plant Pathology* 157: 215–222.

Divakaran M., Pillai G.S., Babu K.N., Peter, K.V., 2008. Isolation and fusion of protoplasts in Vanilla species. *Current Science* 94:115–120.

Dovas C.I., Hatziloukas E., Salomon R., Barg E., Shiboleth Y., Katis N.I., 2001. Incidence of viruses infecting *Allium* spp. in Greece. *Journal of Phytopathology* 149: 1–7.

Edgar R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.

Fidan H., 2010. *Detection of Main Virus Diseases on Garlic, Onion and Leek Plants and Determination of Reaction of Taşköprü 56 Garlic Types Against to Common Virus Diseases in Turkey*. (Doctoral dissertation, Çukurova University)

Fidan H., Çaglar B.K., Baloglu S., Yilmaz M.A., 2013. *Urginea maritima (L.)* is a new host of *Allexivirus* group on onion and garlic plants in Turkey. *Acta Horticulturae* 1002: 309–312.

Firth A.E., Brierley I., 2012. Non-Canonical Translation in RNA Viruses. *Journal of General Virology* 93: 1385–1409.

Fujita N., Komatsu K., Ayukawa Y., Matsuo Y., Hashimoto M., … Arie T., 2018. N-terminal region of cysteine-rich protein (CRP) in carlaviruses is involved in the determination of symptom types. *Molecular Plant Pathology* 19: 180–90.

Geering A.D.W., Mctaggart A.R., 2019. Questions surrounding the taxonomic validity of the species Garlic miteborne filamentous virus (genus *Allexivirus*). *Archives of Virology* 164: 2367–2370.

Ghaemizadeh F., Dashti F., Khodakaramian G., Sarikhani H., 2014. Combination of stem-disc dome culture and thermotherapy to eliminate Allexiviruses and *Onion yellow dwarf virus* from garlic (*Allium sativum* cv. Hamedan). *Archives of Phytopathology and Plant Protection* 47: 499–507.

Gieck S.L., Hamm P.B., David N.L., Pappu H.R., 2009. First report of *Garlic virus B* and *Garlic virus D* in garlic in the Pacific Northwest. *Plant Disease* 93: 431.

Gispert C., Oldfield, G.N., Perring, T.M., Creamer, R., 1998. Biology of the transmission of peach mosaic virus by *Eriophyes insidiosus* (Acari: Eriophyidae). *Plant Disease* 82: 1371–1374.

Gramstat A., Prüfer D., Rohde, W., 1994. The nucleic acid-binding zinc finger protein of potato virus M is translated by internal initiation as well as by ribosomal frameshifting involving a shifty stop codon and a novel mechanism of P-site slippage. *Nucleic Acids Research* 22: 3911–3917.

Granda R., Landázuri G., Arkhipov A.V., 2017. First Report of *Shallot virus X* in Garlic in Ecuador. *Plant Disease* 101: 1066.

Grisoni M., Marais A., Filloux D., Saison A., Faure C., … Candresse T., 2017. Two novel *Alphaflexiviridae* members revealed by deep sequencing of the Vanilla (*Orchidaceae*) virome. *Archives of Virology* 162: 3855–3861.

Gutiérrez Sánchez P.A., Jaramillo Mesa H., Marin Montoya M., 2016. Next generation sequence analysis of the forage peanut (*Arachis pintoi*) virome. *Revista Facultad Nacional de Agronomía* 69: 7881–7891.

Hall T.A., 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/ NT. *Nucleic Acids Symposium Series* 41: 95–98.

Hamed K., Menzel W., Mohamed M. E., Dafallah G., Gadelseed A.M.A., Winter S., 2012. First Report of *Shallot virus X* in Onion in Sudan. *Plant Disease* 96: 1075–1075.

Hill K., Jarvis-Eagan N., Halk E., Krahn K.J., Liao L.W., … Loesch-Fries L.S., 1991. The Development of Virus-Resistant Alfalfa, Medicago sativa L. *Biotechnology* 9: 373–377.

Jemal K., Abraham A., Feyissa T., 2015. The Occurrence and Distribution of Four Viruses on Garlic (Allium sativum L.) in Ethiopia. *International Journal of Basic and Applied Sciences* 4: 5–11.

Jones R.A.C., 2014. Plant virus ecology and epidemiology: Historical perspectives, recent progress and future prospects. *Annals of Applied Biology* 164: 320–347.

Jones R.A.C., 2018. Future Scenarios for Plant Virus Pathogens as Climate Change Progresses. *Advances in Virus Research* 95: 87–147.

Kamenetsky R., Faigenboim A., Mayer E.S., Michael T.B., Gershberg C., … Sherman A., 2015. Integrated transcriptome catalogue and organ-specific profiling of gene expression in fertile garlic (*Allium sativum* L.). *BMC Genomics* 16: 12.

Kang S.G., Bong J.K., Eun T.L., Moo U.C., 2007. *Allexivirus* transmitted by eriophyoid mites in garlic plants. *Journal of Microbiology and Biotechnology* 17: 1833–1840.

Kanyuka K.V., Vishichenko V.K., Levy K.E., Zavriev S.K., 1992. Nucleotide sequence of *shallot virus X* RNA reveals a 5'-proximal cistron closely related to those of potexviruses and a unique arrangement of the 3'-proximal cistrons. *Journal of General Virology* 73: 2553.

Khan M.Z., Amin I., Hameed A., Mansoor S., 2018. CRISPR–Cas13a: Prospects for Plant Virus Resistance. *Trends in Biotechnology* 36: 1207–1210.

Khandagale K., Krishna R., Roylawar P., Ade1 A.B., Benke A., … Rai A., 2020. Omics approaches in Allium research: Progress and way ahead. *PeerJ* 8: 1–34.

Kiedrowicz A., Szydło W., Skoracka A., 2017. Population growth rate of dry bulb mite, Aceria tulipae (Acariformes: Eriophyidae), on agriculturally important plants and implications for its taxonomic status. *Experimental Applied Acarology* 73: 1–10.

King A.M.Q., Adams M.J., Carsten E.B., Lefkowitz E.J., 2012. Virus Taxonomy: Classification and Nomenclature of Viruses. Ninth Report of the International Committee on Taxonomy of Viruses. Elsevier Inc.

Klukáčková J., Navratil M., Duchoslav M., 2007. Natural infection of garlic (*Allium sativum* L.*)* by viruses in the Czech Republic. *Journal of Plant Diseases* 114: 97–100.

Kreuze, J.F., Vaira, A.M., Menzel, W., Candresse, T., Zavriev, S K., Hammond, J., Ryu, K.H., 2020. ICTV virus taxonomy profile: *Alphaflexiviridae*. *Journal of General Virology* 101: 699–700.

Kulkarni N.K., Kumar, P.L., Muniyappa, V., Jones, A.T., Reddy, D.V.R., 2002. Transmission of Pigeon pea sterility mosaic virus by the Eriophyid Mite, *Aceria cajani* (Acari: Arthropoda). *Plant Disease* 86: 1297–1302.

Kumar S., Stecher G., Li M., Knyaz C., Tamura K., 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549.

Lee E.T., Koo B.J., Jung J.H., Chang M.U., Kang S.G., 2007. Detection of allexiviruses in the garlic plants in Korea. *Journal of Plant Pathology* 23: 266–271.

Lezzhov A.A., Gushchin V.A., Lazareva E.A., Vishnichenko V.K., Morozov S.Y., Solovyev A.G., 2015. Translation of the *Shallot virus X* TGB3 gene depends on non-AUG initiation and leaky scanning. *Journal of General Virology* 96: 3159–3164.

Lukhovitskaya N.I., Vetukuri R.R., Sama I., Thaduri S., Solovyev A.G., Savenkov E.I., 2014. A viral transcription factor exhibits antiviral RNA silencing suppression activity independent of its nuclear localization. *Journal of General Virology* 95: 2831–2837.

Majumder S., Mbay, K., Singh, J., 2018. First report of garlic virus D in garlic from D.R. Congo. *Journal of Plant Pathology* 100: 143.

Mandal B., Rao G.P., Baranwal V.K., Jain R.K., 2017. *A Century of Plant Virology in India*. Springer Nature Singapore Pte Ltd.

Manjunathagowda D.C., Gopal J., Archana R., Asiya K.R., 2017. Virus Free Seed Production of Garlic (*Allium sativum* L.*). Status and Prospects* 6: 2446–2456.

Mansouri F., Krahulec F., Duchoslav M., Ryšánek P., 2021a. Newly identified host range of viruses infecting species of the genus *Allium* L. and their distribution in six habitats in the Czech Republic. *Plant Pathology* 70: 1496–1507.

Mansouri F., Richert-Pöggeler K.R., Lewandowski M., Ryšánek, P., 2021b. Transmission characteristics of allexiviruses by the eriophyid mite, *Aceria tulipae* (Keifer) (Acari: Eriophyidae) from naturally mixed infected garlic (*Allium sativum* L.). *European Journal of Plant Pathology* 160(4): 789–796.

Marais A., Faure C., Theil S., Candresse, T., 2019. Characterization of the virome of shallots affected by the

shallot mild yellow stripe disease in France. *PLoS ONE* 14: 1–15.

Martelli G.P., Adams M.J., Kreuze J.F., Dolja V.V., 2007. Family *Flexiviridae*: A Case Study in Virion and Genome Plasticity. *Annual Review of Phytopathology* 45: 73–100.

Martin R.R., Tzanetakis I.E., 2015. Control of Virus Diseases of Berry Crops. *Advances in Virus Research* 91: 271–309.

Mavrič I., Ravnikar M., 2005. A carlavirus serologically closely related to Carnation latent virus in Slovenian garlic. *Acta Agriculturae Slovenica* 85: 343–349.

Melo-Filho P., Nagata T., Dusi A.N., Buso J.A., Torres A.C., Eiras M., Resende R.O., 2004. Detection of three *Allexivirus* species infecting garlic in Brazil. *Pesquisa Agropecuaria Brasileira* 39: 735–740.

Mohammed S.H., Zicca S., Manglli A., Mohamed M.E., El Siddig M.A.R., … Tomassoli L., 2013. Occurrence and phylogenetic analysis of potyviruses, carlaviruses and allexiviruses in garlic in Sudan. *Journal of Phytopatology* 161: 642–650.

Morozov S.Y., Solovyev A.G., 2003. Triple gene block: Modular design of a multifunctional machine for plant virus movement. *Journal of General Virology* 84: 1351–1366.

Nemchinov L.G., Grinstead S.C., Mollov D.S., 2017. *Alfalfa virus S*, a new species in the family *Alphaflexiviridae*. *PLoS ONE* 12: e0178222.

Nurulita S., Geering A.D.W., Crew K.S., Harper S., Thomas J.E., 2020. First report of garlic virus E in Australia. *Australasian Plant Disease Notes* 15: 1–3.

Oliveira M.L., De Marchi B.R., Mituti T., Pavan M.A., Krause-Sakate R., 2014. Identification and sequence analysis of five allexiviruses species infecting garlic crops in Brazil. *Tropical Plant Pathology* 39: 483–489.

Paduch-Cichal E., Bereda M., 2017. Viruses infecting ornamental *Allium* species in Poland. *Journal of Plant Pathology* 99: 509–512.

Park S.J., Nam M., Kim J.S., Lee Y.H., Lee J.B., … Lee S.H., 2011. First Report of the Virus Diseases in Victory Onion (*Allium victorialis* var. *platyphyllum*). *Research in Plant Disease* 17: 66–74.

Perotto M.C., Cafrune E.E., Conci V.C., 2010. The effect of additional viral infections on garlic plants initially infected with Allexiviruses. *European Journal of Plant Pathology* 126: 489–495.

Pringle, C.R., 1999. Virus Taxonomy at the XIth International Congress of Virology in Sydney, Australia. *Archives of Virology* 144: 421–429.

Razvjazkina G.M., 1970. Das Zwiebelmosaikvirus und seine Verbreitung im Freiland. *Tagungs-Berichte der Deutschen Akademie der Landwirtschaftswissenschaften* 115: 69–76.

Read D.A., Muoma J., Thompson G.D., 2020. Metaviromic analysis reveals coinfection of papaya in western Kenya with a unique strain of Moroccan watermelon mosaic virus and a novel member of the family *Alphaflexiviridae*. *Archives of Virology* 165: 1231–1234.

Rocha A., Esmeralda A., 2019. *Identificación e Incidencia de Virus Patógenos en el Cultivo de Ajo (Allium sativum L.) en Aramberri, Nuevo León*. Maestría thesis, Universidad Autónoma de Nuevo León. (Doctoral dissertation, Universidad Autónoma de Nuevo León)

Ryabov E.V., Generozov E.V., Vetten H.J., Zavriev S.K., 1996. Analysis of the 30-region of the mite borne filamentous virus genome testifies its relation to the shallot virus X group. *Molecular Biology* 30: 103–110.

Sabanadzovic S., Ghanem-Sabanadzovic N.A., Tzanetakis I.E., 2011. *Blackberry virus E*: An unusual *Flexivirus*. *Archives of Virology* 156: 1665–1669.

Salomon R., 2002. Virus diseases in garlic and propagation of virus free plants. In: *Allium Crop Sciences (*H.D. Rabinowitch, L. Currah, Ed), CAB Internacional, Wallingford, United Kingdom, 311–328.

Senshu H., Yamaji Y., Minato N., Shiraishi T., Maejima K., … Namba S., 2011. A Dual Strategy for the Suppression of Host Antiviral Silencing: Two Distinct Suppressors for Viral Replication and Viral Movement Encoded by Potato Virus M. *Journal of Virology* 85: 10269–10278.

Shahraeen N., Lesemann D.E., Ghotbi T., 2008. Survey for viruses infecting onion, garlic and leek crops in Iran. *EPPO Bulletin* 38: 131–135.

Song S.I., Song J.T., Kim C.H., Lee J.S., Choi Y.D., 1998. Molecular characterization of the *garlic virus X* genome. *Journal of General Virology* 79: 155–159.

Stecher G., Tamura K., Kumar S., 2020. Molecular Evolutionary Genetics Analysis (MEGA) for macOS. *Molecular Biology and Evolution* 37: 1237–1239.

Sumi S., Matsumi, T., Tsuneyoshi, T., 1999. Complete nucleotide sequences of garlic viruses A and C , members of the newly ratified genus Allexivirus. *Archives of Virology* 144: 1819–1826.

Tabanelli D., Bertaccini A., Bellardi M.G., 2004. Molecular detection of filamentous viruses infecting garlic from different geographic origins. *Journal of Plant Pathology* 86: 335–335.

Taglienti A., Tiberini, A., Manglli, A., Rea, R., Paoletti, S., Taviani, P., Tomassoli, L., 2017. Molecular identification of allexiviruses in a complex mixture of garlic viruses in Latium (Central Italy). *European Journal of Plant Pathology* 150: 797–801.

Torres A.C., Fajardo T.V., Dusi A.N., 2000. Shoot tip culture and thermotherapy for recovering virus-free plants of garlic. *Horticulture* 18: 192–195.

Trebicki P., 2020. Climate change and plant virus epidemiology. *Virus Research* 286.

Van den Born E., Omelchenko M.V., Bekkelund A., Leihne V., Koonin V.E. … Falnes P., 2008. Viral AlkB proteins repair RNA damage by oxidative demethylation. *Nucleic Acids Research* 36: 5451–5461.

Van der Vlugt R.A.A., 2006. Plant viruses in European agriculture: current problems and future aspects. In: *Virus Diseases and Crop Biosecurity,* NATO Security through Science Series, Springer, Dordrecht, 33–44.

Van Dijk P., and Van der Vlugt R.A.A., 1994. New mite-borne virus isolates from rakkyo, shallot and wild leek species. *European Journal of Plant Pathology* 100: 269–277.

Van Dijk P., Verbeek M., Bos L., 1991. Mite-borne virus isolates from cultivated *Allium* species, and their classification into two new rymoviruses in the family *Potyviridae*. *European Journal of Plant Pathology* 97: 381–399.

Vishnichenko V.K., Konareva T.N., Zavriev S.K., 1993. A new filamentous virus in shallot. *Plant Pathology* 42: 121–126.

Vishnichenko V.K., Stel'mashchuk V.Y., Zavriev S.K., 2002. The 42K protein of *shallot virus X* participates in formation of virus particles. *Molecular Biology* 36: 879–882.

Ward L.I., Perez-Egusquiza Z., Fletcher J.D., Clover G.R.G., 2009. A survey of viral diseases of *Allium* crops in New Zealand. *Australasian Plant Pathology* 38: 533–539.

Wijayasekara D., Ferguson C., Ali A., 2019. First Report of Garlic virus C, Occurring on Garlic Plants (*Allium sativum*) with Various Mosaic-Like Symptoms, in the United States. *Plant Disease* 103: 12.

Wylie S.J., Li H., Saqib M., Jones M.G.K., 2014. The global trade in fresh produce and the vagility of plant viruses: A case study in garlic. *PLoS ONE* 9: e105044.

Yamashita K., Sakai J., Hanada K., 1996. Characterization of a new virus from garlic (*Allium sativum L.*), *garlic mite-borne mosaic virus*. *Annual Phytopathology Society* 62: 483–489.

Yoshida N., Shimura H., Masuta C., 2018. Allexiviruses may have acquired inserted sequences between the CP and CRP genes to change the translation reinitiation strategy of CRP. *Archives of Virology* 163: 1419–1427.

Zhao L., Feng C., Wu K., Chen W., Chen Y., Hao X., Wu, Y., 2017. Advances and prospects in biogenic substances against plant virus: A review. *Pesticide Biochemistry and Physiology* 135: 15–26.