Review

**Allexivirus: review and perspectives**

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**Summary.** Allexivirus (Alphaflexiviridae) was first described in 1970 by Razvajzkin. 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). Allexviruses 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.
**Phylogenetic analyses and taxonomic impact**

Given the global distribution of allexiviruses, insights from phylogenetic analyses provide 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 replicate 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 (GarVF; MN059330.1), garlic virus H (GarVH; MN059332.1), garlic virus G (GarVG; MN059331.1), garlic virus I (GarVI; MN059334.1), and garlic yellow virus (GYY; MN059396.1). The viruses PaVA, GarVF, -H, -G, and -I have been included in the analysis. However, GYY lacks the 42 KDa protein and is more related to Carlaviruses (>76% nt and aa sequence identity of the CP to Garlic latent virus), so GYY was not considered in this review. Potato virus M (PVM, Carlavirus) was used

**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 (GarVX) 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).

**Allium*-infecting allexiviruses were initially found infecting garlic and onion crops (Razvjażkina, 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.
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; Carlaviridae, 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 assignment.

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 (m7G) 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).

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...
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, ornamental...
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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.

Table 2. Geographical distribution of allexiviruses.

| Location       | Detected viruses1 | References                      |
|----------------|-------------------|---------------------------------|
| China          | GarV-A, -D, -E, -X, ShVX, GarV-B (GarV-F, GarV-J, 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                     | Klukačková 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, SMbLV3                                                | 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 = Alalfa 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).

Table 3. Location 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 allxiviruses.

| Virus species | 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. curnuam*, *A. flavum*, *A. hybridium*, *A. ledebourianum*, *A. microdictyon*, *A. moly*, *A. narcissiflorum*, *A. neapolitanum*, *A. nutans*, *A. oleraceum*, *A. ramosum*, *A. runyoni*, *A. roseum*, *A. rotundum*, *A. sativum*, *A. senescens*, *A. scabriscapum*, *A. schoenoprasum*, *A. scabriscapum*, *A. sativum*, *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. amaranthicolor*, *C. quinoa*, *Atriplex hortensis*, *C. foliitum*, *C. opulifolium*, *A. cepa*, *A. ameloprasum*, *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. curnuam*, *A. flavum*, *A. ledebourianum*, *A. hybridium*, *A. narcissiflorum*, *A. neapolitanum*, *A. nutans*, *A. oleraceum*, *A. oreypholium*, *A. sativum*, *A. schoenoprasum*, *A. scabriscapum*, *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. ameloprasum*, *A. caeruleum*, *A. angulosum*, *A. bulgaricum*, *A. carinatum*, *A. caesium*, *A. cepa L.*, *A. cyathophorum*, *A. curnuam*, *A. flavum*, *A. microdictyon*, *A. moly*, *A. narcissiflorum*, *A. neapolitanum*, *A. nutans*, *A. oleraceum*, *A. oreypholium*, *A. ranzamum*, *A. roseum*, *A. rotundum*, *A. sativum*, *A. sphaerocephalum*, *A. schoenoprasum*, *A. scabriscapum*, *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. hybridium*, *A. karataviense*, *A. macrostemon*, *A. moly*, *A. oreypholium*, *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. curnuam*, *A. flavum*, *A. sativum*, *A. sphaerocephalum*, *A. scabriscapum* | Chen and Chen, 2002; Bampi et al., 2015; Mansouri et al., 2021a |
| GarV-X        | *A. caesium*, *A. hybridium*, *A. karataviense*, *A. sativum*, *A. schubertii* | Song et al., 1998; Mansouri et al., 2021a |
| GarMbFV       | *A. caesium*, *A. cepa L.*, *A. curnuam*, *A. flavum*, *A. hybridium*, *A. karataviense*, *A. moly*, *A. oreypholium*, *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. aggregatatum*, *A. ledebourianum*, *A. hybridium*, *A. sphaerocephalum*, *A. flavum*, *A. bulgaricum*, *A. cyathophorum*, *A. curnuam*, *A. microdictyon*, *A. moly*, *A. narcissiflorum*, *A. neapolitanum*, *A. nutans*, *A. oleraceum*, *A. oreypholium*, *A. przewalskianum*, *A. ramosum*, *A. rotundum*, *A. scabriscapum*, *A. scadriscapum*, *A. sativum*, *A. thunbergii*, *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. humblottii* | 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. amaranthicolor, C. quinoa, G. globosa, S. rizzini, 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). SSVMV is mechanically transmitted to S. rizinnii, 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 GarVD 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).

Alllexiviruses 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 (Trebiani, 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 (Trebiani, 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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