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Review

The Occurrence and Diversity of Viruses Identified in Monocotyledonous Weeds

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Abstract: In crop fields, weeds are perfect hosts for plant pathogenic viruses. The effects of these viruses can range from latent infection to plant death, affecting crop quality and yield and leading to economic loss in the world. Virus infection threatens cereals used as food for most of the world's population. Weeds growing in cereal fields can compete for essential supply and act as virus reservoirs, strengthening their deteriorating effect. In this review, we collected the current information on viruses presenting in the most important monocotyledonous weeds: *Echinocloa crus-galli*, *Setaria viridis*, *Cynodon dactylon*, *Sorghum halepense* and millet species growing as weeds. Identifying plant viruses in monocotyledonous weed hosts provides more information about viral infection flow and guides the development of management strategies for safeguarding our field crops.

Keywords: cereal; *Echinochloa*; *Setaria*; *Cynodon*; sorghum; virus reservoir

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1. Introduction

Plant viruses constitute one-third of disease-causing agents, which could lead to serious crop yield losses [1]. Agricultural growth and evolution can instigate significant occurrences and variations in a plant's viral spread. This has happened in the case of plum pox virus in stone fruits; during the earliest improvement in agricultural crop production, increased and multiple spreads of this potyvirus occurred [2]. Plants are not only threatened by viruses; they also have to compete with each other for essential water and important nutrients. In fields, this competition between crops and the surrounding weeds is ongoing. Additionally, weeds could serve as reservoirs of plant pathogenic viruses and can host not only viruses but also their insect vectors, further opening up the possibility of viral transfer. Weeds play a major role in establishing novel viral infections in populations of cultivated plants through spillover activity [3,4]. The spread of viral infections from natural hosts to cultivated plant species could be exemplified best by the biogeographical study of rice yellow mottle virus (RYMV), where epidemics from Africa originate from the naturally present wild rice and *Poaceae* species [5]. Furthermore, iris yellow spot virus (IYSV), originating from native non-Allium alternate hosts, was found to be responsible for initiating significant yield losses of onions (*Allium cepa*) [6].

Weeds' role as plant viral reservoirs in crop fields could result in virus persistence and infection outbreaks, causing significant yield and quality losses in cultivated crops [7,8].

Monocotyledonous cereals are the main crops for daily food production, so monocotyledonous weeds acting as an inoculum source of plant viruses present a severe threat. In temperate regions, perennial grasses can be reservoirs of viruses that cause serious diseases [9]. Barley yellow dwarf virus (BYDV), present in pasture grasses and ryegrass, has contributed to barley yellow dwarf diseases in Latvia and other Baltic states [10].

Over the years, plant virus detection has centered on economically important crops. The use of serological assays—such as the enzyme-linked immunosorbent assay, tissue blot immunoassay [11] and lately, lateral flow strips—is common for routine testing, but these serve as an option only if virus-specific antibodies are available. The nucleic acid-based detection of pathogens with PCR-based methods has also been used, generating many sequence records for virus variants. With the above methods, only the tested pathogens can be detected, while the use of high-throughput sequencing (HTS) can detect the presence of all living organisms in the investigated plant material [12]. HTS surveys continuously reveal previously unidentified and undescribed viruses. This is why we can hypothesize that weeds could host more viruses than is currently believed and could continue to serve as fundamental sources of viral discoveries in the future.

Our understanding of viral flux from crops to weeds and from weeds to crops is far from complete and our knowledge about the role of weeds as viral reservoirs is still limited. This review collects studies investigating this question and seeks to discuss plant viral infection occurrence associated with monocotyledonous weeds, as well as their possible role as reservoirs. In addition to the classical search in publication databases, we searched the NCBI GenBank, where virus sequences described from a particular host are deposited, in the hope that in this way we will have a broader view of the current knowledge. In the current review, we provide a list of viruses that have been detected in five important weed species: *Echinocloa crus-galli*, *Setaria viridis*, *Cynodon dactylon*, *Sorghum halepense* and *Panicum* species (growing as a weed). If overwintered, these plants can pose a potential infection risk; this is why our aim is to also raise awareness of the control practices for managing plant virus reservoir weeds in crop fields.

2. Plant Viral Infections of Monocotyledonous Weeds

2.1. Viruses Which Have Been Found to Infect Echinocloa crus-galli

Barnyardgrass (*E. crus-galli*) is a weed that causes a serious threat in major cropping systems, especially in cereal fields such as rice fields. The wild grass possibly originates from tropical Asia and possesses great prowess in competing with field crops [13]. *E. crus-galli* has been identified as the host of a number of viruses, as indicated in Table 1.

Table 1. List of viruses hosted by *Echinochloa crus-galli*. GB—only GenBank record.

Genus	Virus Name	Abbreviation	Detection Method	Genbank Accession Number	Geographical Origin	Citation
Begomovirus	Tomato yellow leaf curl virus	TYLCV	PCR and amplicon sequencing	no sequence in GenBank	Republic of Korea	[14]
Tungrovirus	Rice tungro bacilliform virus	RTBV	vector transmission	no sequence in GenBank	Philippines	[15]
			RT-PCR	no sequence in GenBank	Indonesia	[16]

Table 1. *Cont.*

Genus	Virus Name	Abbreviation	Detection Method	Genbank Accession Number	Geographical Origin	Citation
Phytoreovirus	Echinochloa ragged stunt virus	ERSV	EM, serology	no sequence in GenBank	Japan	[17]
			EM, serology	no sequence in GenBank	Taiwan	[18]
	Rice black-streaked dwarf fijivirus	SRBSDV	seedling inoculation	no sequence in GenBank	Republic of Korea	[19]
	Maize rough dwarf virus	MRDV	vector transmission	no sequence in GenBank	France and Italy	[20]
Rhabdovirus	Maize Iranian mosaic virus	MIMV	Sanger sequencing	MG367447, MG242377, MG242375	Iran	[21]
Tenuivirus	Rice stripe virus	RSV	ELISA	no sequence in GenBank	Republic of Korea	[22]
Waikavirus	Rice tungro spherical virus	RTSV	vector transmission	no sequence in GenBank	Philippines	[15]
Luteovirus	Barley yellow dwarf virus	BYDV-PAV	DAS-ELISA	no sequence in GenBank	Czech Republic	[23]
			DAS-ELISA, RT-PCR	KJ816653	Turkey	[24]
	Barley virus G	BVG	small RNA HTS	PQ047243	Hungary	[25]
Polerovirus	Cereal yellow dwarf virus	CYDV	DAS-ELISA, RT-PCR	KT923457	Turkey	[24]
	Maize yellow mosaic virus	MaYMV	Sanger dideoxy sequencing/RT-PCR	OP846588, OP846589, OP846590, OP846591	China	[26]
Potyvirus	Watermelon mosaic virus	WMV	Sanger dideoxy sequencing	KP980661	Belgium	GB
	Sugarcane mosaic virus	SCMV	Sanger dideoxy sequencing	MN586599	China	GB
Tritimovirus	Wheat streak mosaic virus	WSMV		no sequence in GenBank		[27]
			TAS-ELISA and RT-PCR	no sequence in GenBank	Czech Republic	[28]
			small RNA HTS	PQ047238	Hungary	[25]
Tombusvirus	Sanya tombus-like virus	STlV	HTS	OM514394, OM514434, OM514426, OM514421	China	[29]
Narnavirus	Guiyang narna-like virus 2	GNlV2	HTS	OM514595	China	[29]
Tobravirus	Tobacco rattle virus	TRV	ELISA and bioassay	no sequence in GenBank	Germany	[30]

Table 1. *Cont.*

Genus	Virus Name	Abbreviation	Detection Method	Genbank Accession Number	Geographical Origin	Citation
Dicipivirus	Aphis glycines virus 1	ApGlV1	small RNA HTS	PQ047244	Hungary	[25]
Dicistrovirus	Ljubljana dicistrovirus	LDV	small RNA HTS	PQ047247	Hungary	[25]

Tomato yellow leaf curl virus (TYLCV) is a begomovirus that affects a wide range of host plants and causes devastating losses, particularly in tomatoes. *E. crus-galli* was reported as a TYLCV host in the Republic of Korea, where leaf and root samples of the weed were analyzed using PCR and amplicon sequencing [14].

In Indonesia, *E. crus-galli* has been reported to serve as a host for tungroviruses, including rice tungro bacilliform virus (RTBV) (caulimovirus) and rice tungro spherical virus (RTSV) (waikavirus). These viral infections cause delayed flowering times and panicle exertion in rice plants. Plants affected by tungroviruses show symptoms of reduced tillering, yellowing and stunting. RTBV and RTSV are semi-persistently spread by the green leafhopper, *Nephotettix virescens* (Distant) [16]. In fields, other *Nephotettix* species such as the *Nephotettix nigropictus* have also proven their strong relationship with and potential to disseminate RTBV and RTSV in weeds such as *E. crus-galli* through artificial inoculation [15].

E. crus-galli has also been reported to host a phytorheovirus called Echinochloa ragged stunt virus (ERSV). The first description of *E. crus-galli* as a possible host for this virus was in Taiwan in 1980, where infected plants exhibited severe dwarfing with serrated dark leaves, similar to symptoms observed in plants infected with rice-ragged stunt virus, an important rice virus causing a lot of damage in Asia [31]. Another phytorheovirus known as rice black-streaked dwarf fijivirus (SRBSDV) was reported to cause diseases in wheat, maize, barley, millet and some weed species, fueled by its viruliferous insect vectors. *E. crus-galli* was identified as the host of SRBSDV [19]. In another study about viruses that infect British grasses, *E. crus-galli* was reported to be infected with an additional phytorheovirus called maize rough dwarf virus (MRDV). Some of these viruses were believed to emanate from Europe but have hosts and associated vectors in Britain which could have devasting effects on fields [20].

Maize Iranian mosaic virus (MIMV) is a rhabdovirus that has been found to be hosted by *E. crus-galli.* MIMV has been found to infect maize, wheat, barley and weeds in Iran. Symptoms of infected plants include necrotic streaks, chlorosis and leaf stripes. In the maize-growing regions of Iran, MIMV is one of the most common plant viruses affecting maize crops [32,33]. Its whole genome sequence has been reported and in Iran, genetic diversity studies have identified three significant MIMV isolates that were also detected in *E. crus-galli* showing mosaic and chlorotic stripes [21,34,35]. Plant rhabdoviruses are not seed-transmissible and can spread through vegetative propagation and by plant-hopper vectors [21]. *E. crus-galli* population can offer the chance to sustain a persistent infection and effectively transmit viruses [36].

E. crus-galli also hosts members of the tenuivirus genus. Tenuiviruses are associated with significant disease occurrences in their hosts. Rice stripe virus (RSV), a tenuivirus is one of the most destructive viruses of rice in Japan, China and Republic of Korea. Symptoms of RSV infection in rice plants include chlorosis, weakness, necrosis and stunted growth resulting in significant yield losses [22].

Yellow dwarf disease (YDV) can affect common wheat, barley, oats, rye, maize, millet, rice and sorghum. Barley yellow dwarf (BYD) disease is initiated by either of the closely related BYDV (luteovirus) or cereal yellow dwarf virus (CYDV) (poleovirus) [37]. The most characteristic symptoms associated with the disease include dwarfism and bright yellowish coloration. The disease causes a significant reduction in cereal grain production and yield losses of up to 80% or more over time [38–40]. Additionally, the disease is capable of infecting grasses and perennial weed plants, the majority of which belong to the *Poaceae* family [39,40]. Investigation of the presence and rate of YDV infections detected BYDV-PAV as the most virulent strain and identified CYDV-RPV as a significant cause [24]. An investigation of the association of YDVs and their over-summering and -wintering *Poaceae* weed host species in the Trakya region of Turkey revealed that *E. crus-galli* could be an important source of BYDV infections, playing a key role as reservoirs of YDV diseases [24]. The occurrence of BYDV-PAV in the tested annual grasses, including *E. crus-galli*, revealed that these weed grasses may serve as a principal source of BYDV-PAV in winter cereals, acting as a medium for BYDV [23].

An investigation identifying possible alternative hosts that may serve as virus reservoirs for common weed species reported the occurrence of maize yellow mosaic virus (MaYMV) infecting *E. crus-galli* in Zhengzhou, Henan Province, China [26].

A recent study, in which viromes of monocotyledonous weeds growing in Hungarian crop fields were investigated, identified *E. crus-galli* as a BVG host [25]. Watermelon mosaic virus (WMV) (865 bp fragment) and sugarcane mosaic virus (SCMV) (complete genome) are potyviruses that were identified and sequenced in *E. crus-galli* in Belgium and China, respectively (only GenBank records) (Table 1). Wheat streak mosaic virus (WSMV), a tritimovirus, is a serious threat to plants in the *Poaceae* family [41]. *E. crus-galli*, which belongs to the *Poaceae* family, has been confirmed to act as a reservoir for WSMV [25,28].

What is more, in a comprehensive high-throughput survey of the viromes of weeds in rice fields, 224 RNA viruses and 39 newly identified viruses were detected. *E. crus-galli* was found to host two of these: sanya tombus-like virus (STlV), a tombusvirus, and Guiyang narna-like virus 2 (GNlV2), a narnavirus. Viruses belonging to these families have positive-sense single-stranded RNA genomes [42]. Whilst tombusviruses have been reported in plant hosts, narnaviruses are mycoviruses. Their genome encodes just one polypeptide with an RNA-dependent RNA polymerase and is the simplest representative of all RNA viruses [43]. Members of the narnavirus genus have been identified in the oomycete *Phytophthora infestans* and the yeast *Saccharomyces cerevisiae*, but not in any plant host so far [43]. As identified in this study on *E. crus-galli*, it is very likely that GNlV2 originates from a fungus inhabiting the weed; however, Chao and colleagues could not exclude the possibility that the detected mycoviruses directly infected the weeds [29]. A tobravirus called tobacco rattle virus (TRV) was identified in the roots of *E. crus-galli*, which was the first weed of this species to be reported as a natural host and prospective virus reservoir in the field [30]. In addition, aphis glycines virus 1 (ApGlV1) and Ljubljana dicistrovirus (LDV) have also been reported to infect *E. crus-galli* [25].

2.2. *Cynodon dactylon* Hosted Viruses

C. dactylon is a perennial grass belonging to the *Poaceae* family. Among the several common names attributed to this weed species [44], it is most popularly referred to as the Bermuda grass. Bermuda grass is a severe, primary weed that causes varying degrees of harm in most warm climate regions in Africa, Asia, America, Australia and Southern Europe. It is a major weed in Jordan and Turkey and poses a serious threat in Iran, Israel and Lebanon in the Middle East [45,46]. Like many grasses, *C. dactylon* demonstrates great tolerance, strong establishment and high spreading abilities in different environments [47].

Mastreviruses, such as isolates of eleusine indica-associated virus (EIAV), were reported from *C. dactylon* in France [48] (Table 2).

Table 2. List of viruses hosted by *Cynodon dactylon*.

Genus	Virus Name	Abbreviation	Detection Method	Genbank Accession Number	Geographical Origin	Citation
Mastrevirus	Eleusine indica-associated virus	EIAV	Sanger sequencing	OQ211417	France	[48]
	Maize streak virus	MSV	Sanger sequencing	OQ211437, OQ211434	France	[48]
	Wheat dwarf virus	WDV	Sanger sequencing	KT958243	Iran	[49]
Tungrovirus	Rice tungro virus	RTV	Inoculation infected material	no sequence in GenBank	India	[50]
Cytorhabdovirus	Barley yellow striate mosaic virus	BYSMV	small RNA HTS	PQ047240	Hungary	[25]
Nucleorhabdovirus	Maize Iranian mosaic virus	MIMV	Sanger sequencing	MG242374	Iran	[21]
	Cynodon chlorotic streak virus	CCSV	ELISA	no sequence in GenBank	Morocco	[51]
	Cynodon rhabdovirus	CRV	Sanger sequencing	EU650683	South Africa	[52]
Nepovirus	Grapevine fanleaf virus	GFLV	ELISA and RT-PCR	no sequence in GenBank	Iran	[53]
Luteovirus	Barley yellow dwarf virus	BYDV	ELISA	no sequence in GenBank	Australia	[54]
Polerovirus	Cereal yellow dwarf virus	CYDV	ELISA	no sequence in GenBank	Australia	[54]
Tritimovirus	Wheat streak mosaic virus	WSMV	small RNA HTS	PQ047238	Hungary	[25]
Potyvirus	Sugarcane mosaic virus	SCMV	ELISA	no sequence in GenBank	Kenya	[55]
	Spartina mottle virus	SpMV	Illumina	MW314143, MW314142	USA	[56]
			Immunoelectron microscopy and RT-PCR	AF491352	Assisi, Italy	[57]
	Watermelon mosaic virus	WMV	Sanger sequencing	MN814406	Spain	[58]
Tombusvirus	Bermuda grass latent virus	BGLV	HTS/RT-PCR/Sanger sequencing	MZ671022, MZ671024, MZ671025, MZ671026, MZ671028, OK258314, OK258317, OK258318	Australia	[59]
Dicistrovirus	Ljubljana dicistrovirus	LDV	small RNA HTS	PQ047246	Hungary	[25]

Maize crops in most African maize-growing countries have been periodically decimated by a disease known as maize streak disease (MSD), which is also caused by a mastrevirus. Maize streak virus (MSV) is the most recognized type of mastrevirus [60]. A study analyzing the abundance of mastreviruses infecting cultivated and uncultivated plants revealed *C. dactylon* as a possible host of MSV isolates [48]. Wheat dwarf virus (WDV) is also a mastrevirus which is known to infect monocotyledonous plants. Based on its primary hosts, wheat and barley, WDV disease is typically split into two distinct categories, namely the wheat dwarf virus wheat (WDV-W) and wheat dwarf virus barley (WDV-B) strains [61,62]. A phylogenetic analysis of wheat dwarf virus isolates from Iran showed that *C. dactylon* hosted the WDV-W strain of the virus [49], emphasizing the significance of monocotyledonous grasses as natural hosts of the wheat strain of WDV. Weeds infected with WDV-W have mostly been found in cereal fields and, acting as reservoirs of the virus, could have a significant impact on WDV epidemiology [62,63].

Rice-growing countries occasionally face a tungrovirus, rice tungro virus (RTV), which attacks rice crop fields. The virus has been detected and described in India, where there is a keen interest in the possible alternative hosts and insect vectors responsible for its transmission. By studying the role of weed species and rice stubbles in rice-growing fields in terms of the persistence of this virus under natural conditions, RTV was found to only be present in rice stubbles during the off-season. In addition, the viral vector *Nephotettix virescens* consumes rice as its principal food source, but when there is a lack of rice crops nearby it also feeds and grows well on some other weed species including *C. dactylon*. In this way, these weed species play an essential role in the virus vector lifecycle [50].

Rhabdoviridae is a populous family. Many of the viruses that belong to it have agricultural significance and can infect a wide range of plants [64]. For this reason, field studies could enhance our understanding of the epidemiology of these viruses in crop fields. A cytorhabdovirus, barley yellow striate mosaic virus (BYSMV), has been identified to infect *C. dactylon* in Hungary [25]. *C. dactylon* was identified as the host of several nucleorhabdoviruses, including MIMV in Iran [21]. An examination of an uncharacterized rhabdovirus infecting Bermuda grass in South Africa revealed the presence of a new virus, named Cynodon rhabdovirus (CRV), which showed the highest nucleotide sequence similarity to maize mosaic virus (MMV) and taro vein chlorosis virus (TaVCV) [52]. In addition, another rhabdovirus, the Cynodon chlorotic streak virus (CCSV), was described as infecting *C. dactylon* [51]. CCSV, which is widespread in Bermuda grasses, was found to be responsible for causing chlorotic streaks and stunting in local maize. Even though CCSV was initially thought to infect maize, it seems to be its alternative host, while its primary host seems to be Bermuda grass. CCSV resulted in chlorotic streak viral symptoms in Bermuda grasses in Morocco and was reported to be extensively dispersed in Mediterranean regions. Based on their serological, morphological and phylogenic indications, CRV and CCSV are closely related, and the former is proposed to be a strain of the latter; however, the absence of CCSV sequence information does not allow for checking this hypothesis [52].

Virus diagnostics of Bermuda grasses growing in the vicinity of a grapevine fanleaf virus (GFLV)-infected vineyard in Iran showed serological and molecular evidence of the presence of this nepovirus in this host [53]. This study suggests that the fact that Bermuda grass could be a source of GFLV propagation adds a new perspective to the virus epidemiology and suggests taking into account eliminating potential weedy reservoir virus sources during fanleaf disease management.

A survey of viral diseases in Australian pasture grasses reported BYDV and CYDV infection incidence in perennial grasses including *C. dactylon*. It was reported that these grasses could serve as substitute host reservoirs for viruses that move to neighboring crops [54,65].

The invasive nature of *C. dactylon* weeds enables the plant to spread quickly, serving as a possible host of plant viruses in crop fields. This characteristic seems to be important in wheat fields, as *C. dactylon* can be infected by WSMV [25].

Sugarcane mosaic virus (SCMV) has been reported to cause serious losses in Kenya's maize-growing districts [55]. A survey of this potyvirus using ELISA revealed its presence and natural SCMV infections in overwintering hosts, including *C. dactylon.* The presence of another potyvirus, Spartina mottle virus (SpMoV), in cordgrasses (*Spartina* sp.) was described originally in Wales and England [66], and its full genome was sequenced in Northern Germany [56,67]. For a long time, it has only been detected in *Spartina* sp. and forced viral transmission by aphid species and mechanical inoculation to other hosts proved futile [66]; however, it was later reported in *C. dactylon* in Italy and Iran [53,57]. Widely distributed weedy species such as *C. dactylon* could transmit SpMoV over large distances via vegetative propagation [56].

Genetic diversity studies of another potyvirus, watermelon mosaic virus (WMV), and its prevalence in agricultural ecosystems reported WMV infection incidence in *C. dactylon* in Spain [58].

A combination of HTS and RT-PCR revealed the existence of a new virus of *C. dactylon*, Bermuda grass latent virus (BGLV), in the United States, which has tentatively been assigned to the panicovirus genus of the *Tombusviridae* family [68]. BGLV surveys conducted in Australia, using recently developed universal panicovirus primers in RT-PCR tests, revealed prevalent infection by this virus in a wide range of cultivars of Bermuda grass in New South Wales and Queensland [59]. More interestingly BGLV was also diagnosed in two accessions of sterile hybrid Bermuda grass, sampled from different study locations in South East Queensland but originating from the USA [69]. This research raises the possibility of autonomous virus acquisition from local sources after the grass' first introduction into Australia. Representing the second recorded incidence of BGLV after the USA, these results suggest the possibility of the existence of more natural BGLV weed hosts awaiting identification [59]. LDV has also been found to infect this host [25].

2.3. Plant Viral Disease Incidence in Setaria viridis

S. viridis is commonly known as "green foxtail." This weed is a kind of annual grass originating from Eurasia. It belongs to the *Poaceae* family and is regarded as an invasive plant that can be found in most regions of the globe. This is because *S. viridis* produces a large number of seeds and can develop fast from the vegetative stage to flowering [70,71]. This weed is mostly found growing in pastures, fallow fields, crop fields and gardens [71,72]. Due to its capacity to sprout in late spring or early summer, elude early cultivation and finish its life cycle quickly, green foxtail is highly suited for survival in conventional cropping systems [71].

S. viridis has been reported as an alternate host for several insect vectors and plant viruses that attack crops [71,73]. Iris yellow spot virus (IYSV) is a serious pathogen in onion bulbs and seed crops [74]. In addition to onions and other susceptible crops, weeds could be potential IYSV hosts and reservoir sources, as found in *S. viridis* [75] (Table 3).

Table 3. List of viruses hosted by *Setaria viridis*. GB—only GenBank record.

Genus	Virus Name	Abbreviation	Detection Method	Genbank Accession Number	Geographical Origin	Citation
Tospovirus	Iris yellow spot virus	IYSV	DAS-ELISA, RT-PCR	FJ652594	USA	[75]
Potexvirus	Foxtail mosaic virus	FoMV	EM, serology	no sequence in GenBank	USA	[76]
Luteovirus	Barley yellow dwarf virus	BYDV	DAS-ELISA	no sequence in GenBank	USA	[77]
Polerovirus	Maize yellow mosaic virus (Sv-ZZ-1, ZZ-2)	MaYMV	RT-PCR/Sanger sequencing	OP871831, OP871832	China	[26]
Tritimovirus	Wheat streak mosaic virus	WSMV		no sequence in GenBank		[27]
			small RNA HTS	PQ047238	Hungary	[25]
Potyvirus	Sugarcane mosaic virus (S-SCMV)	SCMV	Sanger sequencing	MN586598	China	GB
	Maize dwarf mosaic virus	MDMV	seedling inoculation	no sequence in GenBank	USA	[78]
Panicovirus	Thin paspalum asymtpomatic virus	TPAV	seedling inoculation	no sequence in GenBank	USA	[79]

In 1967 in the United States, foxtail mosaic virus (FoMV) was detected in *S. viridis* using electron microscopy and serology [76]. Although this potexvirus has been found to affect a broad host range of grasses, it has not been associated with any detrimental yield loss [76]. BYDV was also found in *S. viridis* using DAS-ELISA in New York, USA [77]. Moreover, other important plant viruses of economic concern—such as MaYMV, a polerovirus, in China [26], wheat streak mosaic virus (WSMV) [25,27] and two potyviruses, sugarcane mosaic virus (SCMV) in China and maize dwarf mosaic virus (MDMV) in Mississippi, USA [78]—have been detected in *S. viridis* (Table 3). SCMV disease was found to significantly affect crop growth, resulting in reduced production and consequently, serious economic losses [80].

Thin paspalum asymptomatic virus (TPAV) has been described from a metagenomic survey in Osage County, Oklahoma, USA, where *S. viridis* was identified as the host producing symptomless infections. TPAV is a panicovirus known to affect plants in the *Poaceae* family [79].

2.4. Viruses Infecting *Sorghum halepense*

Johnsongrass (*S. halepense*) is indigenous to the Mediterranean region of Europe and Africa and is extensively present in North America and Southwestern Asia [81,82]. Due to its international introduction, the weed has expanded its borders significantly across warm temperate climates [46]. It is a warm-season perennial grass and one of the most invasive and harmful weeds [83]. *S. halepense* belongs to the *Poaceae* family, together with several prevalent and challenging-to-control weeds. Moreover, this plant family also includes cereals, corn, sugarcane and sorghum, which are susceptible to infections by plant viruses [84,85].

WDV has been identified in Iran from a *S. halepense* host [49]. In addition, another mastrevirus, sorghum arundinaceum-associated virus (SAAV), was described in *S. halepense* from Ecuador (Table 4).

Table 4. List of viruses hosted by *Sorghum halepense*. GB—only GenBank record.

Genus	Virus Name	Abbreviation	Detection Method	Genbank Accession Number	Geographical Origin	Citation
Mastrevirus	Wheat dwarf virus	WDV	Sanger sequencing	KT958235	Iran	[49]
	Sorghum arundinaceum-associated virus	SAAV	HTS	PP461403	Ecuador	GB
Begomovirus	Papaya leaf curl virus	PaLCuV	Sanger sequencing	MZ041266	India	GB
	Tomato leaf curl Palampur virus	ToLCPalV	Sanger sequencing	MZ041256	India	GB
Endornavirus	Johnsongrass virus	JVG	HTS	MW756210, MW756211	Turkey	GB
Tenuivirus	Maize stripe tenuivirus	MSpV	ELISA	no sequence in GenBank	India	[86]
Potyvirus	Maize dwarf mosaic virus	MDMV	PCR	FM883224, FM883214, FM883193, FM883174	Hungary	[87]
			Sanger sequencing	MN615724	USA	[88]
			HTS	OK149210-14	Spain	GB
			HTS	MZ188925	Spain	GB
	Iranian Johnsongrass mosaic virus	IJMV	Sanger sequencing	KU746860, KU746862	Iran	[89]
	Sugarcane mosaic virus	SCMV	Sanger sequencing	KX430773, KX430774	Iran	[89]
	Johnsongrass mosaic virus	JGMV		NC_003606.1		[90]
Tombusvirus	Maize chlorotic mottle virus	MCMV	Sanger sequencing	KX824059, KX824060	Spain	[91]
	Johnsongrass umbra-like virus 1	JgULV	HTS	OM937760	Ecuador	[92]
	Johnsongrass chlorotic stripe mosaic virus	JCSMV	HTS	MT682309	Iran	GB
Dicipivirus	Aphis glycines virus 1	ApGlV1	small RNA HTS	PQ047244	Hungary	[25]

Infection from isolates of two begomoviruses of Indian origin—papaya leaf curl virus (PaLCuV) and tomato leaf curl Palampur virus (ToLCPalV)—and an endornavirus from Turkey—Johnsongrass virus—in *C. dactylon* have only been registered as GenBank records thus far. In a study where plant samples from multiple farmed fodder and weed hosts were tested for the presence of maize stripe tenuivirus (MSpV), wheat and *S. halepense* showed positive ELISA reactions. The disease manifests in short panicles and chlorotic stripes, which is also a common symptom in virus-infected sorghum plants [86].

MDMV could propagate mechanically through contaminated seeds or by feeding insect vectors, such as aphids, by non-persistent means [93]. Whilst maize is considered to be the main host of MDMV, the host range of this potyvirus includes Johnsongrass, which is a significant overwintering virus reservoir for MDMV [87,94,95]. Examining

the genetic diversity and population structure of MDMV from maize and Johnsongrass in eight distinct Spanish maize-growing regions revealed that, except for Andalucia, the high prevalence of MDMV in *S. halepense* confers great potential for genetic variation because this host is infected for extended periods [96]. Johnsongrass is a common weedy grass serving as a reservoir for MDMV and offering possible viral transmission in crop fields [97]. This report found it critical to look out for Johnsongrass growing close to cornfields, especially if there were any telltale signs of MDMV infections, such as yellow or chlorotic leaf streaks [85]. Gene expression studies of MDMV in maize [88] also revealed that Ohio-collected Johnsongrass was infected with MDMV. The cloned Johnsongrass-derived MDMV isolate (MDMV OH-5) was fully sequenced. There are also isolates of MDMV identified in *S. halepense* from Spain, but these only exist as GenBank records (Table 4).

Iranian Johnsongrass mosaic virus (IJMV) is a pervasive potyvirus causing maize mosaic disease in Iran [98]. Phylogenetically, IJMV clusters to the same subgroup to which other potyviruses, such as MDMV, Johnsongrass mosaic virus (JGMV), SCMV and sorghum mosaic virus (SrMV) belong [89,98–101]. The presence of these viruses in sugarcane, sorghum, maize and other monocotyledonous plants has resulted in substantial yield losses [102]. The Iranian case study provides interesting findings about IJMV's evolution and host diversity. Although, in an ecological context, Johnsongrass is considered a key natural host with a recorded incidence of IJMV, this virus can infect other hosts like sugarcane, threatening its cultivation and the Iranian industry. The principal source of primary maize, sorghum and sugarcane IJMV infection could be attributed to Johnsongrass as a perennial grass host [89].

The maize chlorotic mottle virus (MCMV) was first identified and supposedly originated in Peru, where it then spread to other countries such as central USA and China. It has also been detected in eastern Sub-Saharan Africa. Depending on the condition and the age of the plant upon infection, symptoms might range from a slight chlorotic mottling to yellowing, necrosis and plant death [103–105]. This tombusvirus genome is a single-stranded positive-sense RNA transmitted by beetles and thrips as its primary vectors [104,106]. Sugarcane, maize and sorghum could all be infected by MCMV [107,108]. MCMV and sugarcane mosaic virus (SCMV, potyvirus) coinfection results in synergistic, collaborative lethal necrotic disease (LND) [109]. A similar effect was reported in viral MCMV and SCMV infections [110]. Monocot crop species and other weedy grasses have been confirmed to be vulnerable to MCMV. To ascertain the presence of MCMV in Spain, weed grasses, including *S. halepense*, showing characteristic symptoms were sampled and investigated using RT-PCR. An MCMV variant from *S. halepense* showed the highest affinities with American and African isolates, respectively, indicating the first report of remarkable MCMV detection in a perennial host [91].

Umbraviruses are non-encoding coat protein viruses that rely on helper viruses or multiple simultaneous infections for plant-to-plant vector-borne transmission [111]. In a study in Ecuador, two umbravirus-like associated RNA (ulaRNA) viral entities were described in maize and Johnsongrass, respectively. For coherent expediency, the new ulaRNA from maize was referred to as maize umbra-like virus (MULV), while that from Johnsongrass was known as Johnsongrass umbra-like virus (JgULV) [92]. Johnsongrass chlorotic stripe mosaic virus (JgCSMV), a tombusvirus, has also been detected in *S. halepense* from Iran. Recently, *S. halepense* has been identified as a potential new ApGlV1 host in Hungary [25].

2.5. Viruses Hosted by Different Millet Species

Millets are a group of annual grasses that have unique botanical varieties. Foxtail (*Setaria italica*), proso (*Panicum miliaceum*), finger (*Eleusine coracana*) and pearl (*Pennisetum glancum*) millets are some of the most significant varieties [112]. These different millets have distinct characteristics in terms of their optimal growing seasons, grain consistency, soil needs and sizes. They show tolerance to drought and high temperatures [113,114]. Millets are widely consumed as staple foods and are also used to make traditional beverages. They are cultivated in warm, tropical regions of the world including Africa, Asia and Eastern and Southern Europe. Millets are widely grown for fodder in the United States, Australia, Brazil and South Africa. Pearl millet is being produced in greater quantities for chicken feed. Their consumption is also expanding in specialized diets [115].

Recently, it has been reported that, with the increase in crop production, millet may become a precarious weed in crop fields. With the capacity to host plant viruses and serve as a reservoir, the plant could easily be dispersed and found in wheat, maize and other crop fields [116,117]. Millet species could be infected with several different viruses. In this work, infections where GenBank records were available for the millet-infecting strain have been collected and reviewed.

A study of streak disease in pearl millet led to the description of a possible mastrevirus: millet streak virus (MSV). MSV was identified in Africa during the surveying of a collection of streak viruses of pearl millet originating from Nigeria [118] (Table 5).

Table 5. List of viruses with GenBank records regarding their infection of different millet species. GB—only GenBank record.

Genus	Virus Name	Abbreviation	Detection Method	Genbank Accession Number	Geographical Origin	Species	Citation
Mastrevirus	Millet streak virus	MSV	PCR	X86705	UK	*Pennisetum glaucum*	[118]
Cytorhabdovirus	Barley yellow stripe mosaic virus = Cytorhabdovirus hordei strain	BYSMV	Small RNA HTS	MT260881, MT260882, MT260883, MT260884, PQ047240	Hungary	*Panicum milaceum*	[25,117]
			HTS, RT-PCR	MN434075, MN434076, MN434077	China	*Setaria italica*	[119]
Tenuivirus	Rice stripe virus	RSV	ELISA, RT-PCR	JN245627, JN245628	South Korea	*Panicum milaceum*; *Setaria italica*	[120]
Tymovirus	Maize rayado fino virus	MRFV	SIA	GU068591, HM133581, HM133582	USA	*Panicum virgatum*	[121]
	Switchgrass mosaic virus	SwMV	PCR	NC_015522 = JF727261	USA	*Panicum virgatum*	[122]
	Pennisetum glaucum marafivirus	PGMV	HTS, Sanger sequencing	MZ305310	Burkina Faso	*Cenchrus americanus*	[123]
Luteovirus	Barley yellow dwarf virus	BYDV-PAV	PCR	KR259156, KR259157	Pakistan	*Cenchrus americanus*	GB

Table 5. *Cont.*

Genus	Virus Name	Abbreviation	Detection Method	Genbank Accession Number	Geographical Origin	Species	Citation
Polerovirus	Maize yellow mosaic virus	MaYMV	Sanger sequencing	MF622081	Republic of Korea	*Panicum miliaceum*	[124]
	Barley virus G	BVG	JTS	MF960779	Netherlands	*Panicum virgatum*	[125]
			Small RNA HTS, Sanger sequencing	MT260885, PQ047241, PQ047242	Hungary	*Panicum milaceum*	[25,117]
	Panicum distortion mosaic virus	PDMV	PCR	LC424839	Republic of Korea	*Panicum milaceum*	GB
Tritimovirus	Wheat streak mosaic virus	WSMV	Small RNA HTS, Sanger sequencing	MT260879, MT780552, MT780553, PQ047238, PQ047239	Hungary	*Panicum milaceum*	[25,117]
Potyvirus	Sugarcane mosaic virus	SCMV	SIA	HM133587	USA	*Panicum virgatum*	[121]
			DAS-ELISA, RT-PCR	KM926613, KM926614, KM926615, KM926616	Kenya	*Eleusine coracana*	[110]
	Johnsongrass mosaic virus	JGMV	PTA-ELISA, HTS	KT289893	Brazil	*Panicum maximum*	[126]
Tombusvirus	Maize chlorotic mottle virus	MCMV	DAS-ELISA, RT-PCR	KM926617, KM926618	Kenya	*Eleusine coracana*	[110]
Dicistrovirus	Ljubljana dicistrovirus	LDV	small RNA HTS	PQ047246	Hungary	*Panicum milaceum*	[25]

In studying natural viral infections, small RNA HTS was used to investigate the presence of viruses in weedy proso millet in Hungary [117]. In this study, important wheat- and cereal-infecting viruses, such as WSMV, BYSMV and BVG, have been found to infect this host, sometimes via multiple infections. The buildup to this study revealed more recent findings describing proso millet as a potential new host of LDV [25]. Isolates of barley yellow stripe mosaic virus (BYSMV) have also been detected in foxtail millet from China [119], where viral infections in this millet are a major concern. Foxtail millet varieties exhibiting virus-associated symptoms were found to be infected with this cytorhabdovirus, which showed a similar identity to an isolate identified from wheat [119]. The study concluded that it is crucial to develop a plan that will effectively monitor, prevent and manage BYSMV. BYSMV was discovered to infect wheat and rice in China, but it was first linked to Italy [127,128]. Proso millet and foxtail millet plants showing yellow stripe symptoms in Korea were sampled from areas where rice was affected by an outbreak of rice stripe virus (RSV). The diseased plants tested positive for RSV using an ELISA, and the presence of viral infection was validated with RT-PCR [120].

Maize rayado fino virus (MRFV) is a widespread tymovirus with increasing significance in maize-growing regions in America. The disease caused by the virus is characterized by chlorotic stripes on the leaves and can cause endemic yield losses. Surveying the presence of RNA viruses through sequence-independent amplification revealed an MRFV isolate in switchgrass, emphasizing the need to study the impact of this isolate on cultivated cereals [121]. The complete genomic sequence of another newly described marafivirus, switchgrass mosaic virus (SwMV), has also been reported. The virus was described as being closely related to MRFV but possessing unique features, including associated mosaic

symptoms on switchgrass leaves [122]. An additional, currently tentative marafivirus, pennisetum glaucum marafivirus (PGMV), was discovered in pearl millet using HTS in Burkina Faso, where it is extensively grown and cultivated [123]. Pearl millet can also host BYDV-PAV, according to a GenBank record originating from Pakistan (Table 5).

MaYMV is a possible novel polerovirus that has been discovered in maize in China and Brazil [129,130]. It has also been reported to infect grasses and sugarcane crops in Africa [131]. The first report of MaYMV in South Korea revealed an isolate of MaYMV infecting *P. miliaceum*, identifying this plant as a new host of the virus [124]. Barley virus G is a polerovirus that has been detected in foxtail millet in the Korean Republic [132], in *P. miliaceum* samples in Hungary [117] and in switchgrass from the Netherlands [125]. According to GenBank records, there is another polerovirus, Panicum distortion mosaic virus (PDMV), that has been reported to infect *P. milliaceum* in South Korea (Table 5). Potyviruses can also infect millet species. Sugarcane mosaic virus (SCMV) was found in switchgrass plants in the USA [121]. Surveying its alternate hosts in Kenya, SCMV was detected in finger millet [110]. In a study exploring biological, serological and molecular assays, leaf samples from *P. maximum* cv. Mombaca exhibiting mosaic symptoms revealed infection with a Brazilian isolate of JGMV [126]. In Kenya, isolates of MCMV have been detected and described in finger millet using serological methods and RT-PCR [110].

3. Ways of Viral Transfer Between Crops and Weeds: The Role of Vectors

Crop production output is threatened by weeds, which reduce the available nutrients and act as reservoirs of vector-borne viral diseases [133]. These weeds are virus reservoirs only if their infecting virus is further transmitted to other hosts. Insect vectors play a significant role during this transmission. They can carry viral pathogens across geographical distances, helping their survival during climatic variations in the ecological system [134]. Weeds could also provide an avenue enabling the accumulation of vector populations in crop fields [135].

Common insect vectors associated with plant viral infection and transmission include thrips, aphids and whiteflies. Thrips are polyphagous insect vectors accountable for the transmission of significant plant viruses of agricultural concern, including tospoviruses [136]. Thrips, including the most effective vector, the western flower thrip (*Frankliniella occidentalis*), obtain and disperse viruses in a persistent, propagative manner [137,138]. Aphids are direct parasites to crops that act as vectors of viral diseases [139]. The most destructive and all-pervasive aphid species in plant viral pathogen transmission is the green peach aphid (*Myzus persicae*) [140]. Typically found on the underside of leaves, whiteflies are among the noxious agricultural insect vectors [141]. The rapid propagation of the sweet potato whitefly (*Bemisia tabaci*) constantly enhances its vector competency and insecticide resistance [142]. Some vectors can spread viruses more efficiently from infected weeds to nearby crops than during crop-to-crop transmission [143]. Studies have shown that some insect vectors have a strong affinity for weed hosts, improving vector prolificacy and prolonged existence [143]. Non-native plants and insects may also broaden their terrestrial avenues or habitats and settle in areas where they were previously absent. These species may serve as reservoir hosts or vectors with the potential to cause epidemics among adjacent crops [144].

4. Conclusions

Analyzing weed hosts of plant viruses and their diversity is crucial in unearthing virus ecology and epidemiology in crop fields. Recently, experts have started investigating the virus reservoir role of weeds on a metagenome scale. Viruses can persist in weed

populations in crop fields; this is why it is important to raise awareness among farmers and crop producers regarding effective weed management and disease control practices.

In addition to acting as virus reservoirs, weeds can also house the vectors responsible for viral transmission. Analyzing vector populations and their viral diseases can help in choosing adequate management practices. Improved virus diagnostic assays can reveal all presenting viruses in the investigated sample and meet the changing needs in identifying emerging viruses. However, research on plant viruses in weeds around cultivated crop fields should be continued in order to improve management and obtain greater yields.

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