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WEEDS AS RESERVOIRS OF VIRUSES IN AGROBIOCENOSIS OF CEREAL CROPS IN UKRAINE

This review examines current knowledge on the prevalence of weeds and feral grass species as possible reservoirs of plant viruses in the agroecosystems of Ukraine. Studies concerning mainly virus infection of wheat and barley and weeds distributed in the agrosystems of cereal crops and their impact on virus epidemiology have been summarized in this paper. In addition, great attention is focused on the primary sources of the main causative agents of wheat and barley viral diseases, namely Wheat streak mosaic virus (WSMV), Wheat dwarf virus (WDV), Winter wheat Russian mosaic virus (WWRMV), High Plains wheat mosaic virus (HPWMoV), Barley yellow dwarf virus (BYDV), and Brome mosaic virus (BMV) as well as the main factors contributing to the spread of these viruses in agroecosystems.

Keywords: plant viruses, weeds as reservoirs of plant viruses, vectors of cereal viruses.

Staple cereals such as wheat, maize and barley are critical to global food security as they play a critical role in human diets and are used for livestock feed worldwide [1]. Most cereals, including wheat, barley, rye, oats, rice, corn, sorghum, and millet, belong to the *Poaceae* family comprising about 700 genera and 10,000 species. Plants from this family are infected by a very large number of viruses, causing considerable economic losses to

countries around the world. Virus species that infect the *Poaceae* belong to 15 of the virus families and 36 of the virus genera currently recognized by the International Committee on Taxonomy of Viruses (ICTV) [2]. The variable epidemiological behavior of viruses that affect cereals, along with the genetic diversity of viral isolates, greatly complicates control efforts. Management of cereal viruses, in addition to diagnosis, protection

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of cultures, and breeding for virus-resistant cultivars, necessarily takes into account the possible circulation of viruses in wild plants, weeds, and surrounding crop plants. Virus-infected weeds along with wild and volunteer crop plants introduced into plantings become particularly dangerous natural foci of virus infection and, being widely disseminated by vectors, can contribute to the emergence of viral epiphytoses. Seasonal migrations of vector insects in crop rotations with a predominance of cereals, lead to the spread of viruses from wild reservoirs to agrocenoses, thus determining cereal productivity and crop quality [3, 4]. Virus infection induces metabolic reprogramming in infected cells and leads to active changes in nitrogen and carbohydrate contents, inhibition of plant growth, and significant yield losses [5]. Viruses are one of the main factors that impair grain production in Ukraine, infecting in some years more than 80% of the crop and causing average yield losses up to 63% for wheat (*Yellow dwarf virus*) and to 96% for cereals (*Wheat streak mosaic virus*) [6, 7]. In this regard, the purpose of the review was to highlight the importance to accumulate information on virus communities in wild plant and to summarize the literature data on the ecological significance of weeds in the agroecosystems of Ukraine as possible virus reservoirs of economically important cereal crops.

According to the literature data, *Wheat streak mosaic virus* (WSMV), *Barley yellow dwarf virus* (BYDV), *Wheat dwarf virus* (WDV), *Brome mosaic virus* (BMV), *High Plains wheat mosaic virus* (HPWMOV), *Barley stripe mosaic virus* (BSMV), *Winter wheat Russian mosaic virus* (WWRMV), and *Barley yellow mosaic virus* (BaYMV) have been identified in agrocenoses of Ukraine [8–13].

This review summarizes research on virus diseases of cereals, transmitted naturally by various insect vectors arresting and feeding on plants or weeds that act as reservoirs of pathogens such as *Wheat streak mosaic virus*, *Wheat*

dwarf virus, *Winter wheat Russian mosaic virus*, *High Plains wheat mosaic virus*, *Barley yellow dwarf virus*, and *Brome mosaic virus*.

Plants as reservoirs of viruses in wheat crops.

Wheat, due to its high agronomic adaptability, ease of grain storage, and unique composition, is a staple source of nutrients for around 40% of the world's population and is grown on more than 218 mln ha worldwide [1]. The global amount of wheat produced in 2021 came to about over 772 mln tons [14, 15], of these, 33 mln tons of wheat were produced in Ukraine [16]. Nevertheless, the phytosanitary state of grain crops is deteriorating every year, and the potential loss of wheat grain yield from a complex of harmful organisms (pests, pathogens, and plant viruses) is on average 25–50% [17–19]. Wheat crops are affected by many virus diseases, and wheat streak mosaic disease (WSMD) causes the second most important virus disease epidemic of wheat globally [20]. WSMD is caused by infection with *Wheat streak mosaic virus* (WSMV), which was recently described as «a century-old virus with rising importance worldwide» [21].

Wheat streak mosaic virus belongs to *Potyviridae* family *Tritimovirus* genus and is one of the most economically devastating wheat diseases worldwide. Yield loss in wheat crops caused by WSMV-infection can surpass 60–70%. In severe cases, the virus infection leads to the plant stunting and symptoms progressing into leaf tissue necrosis and plant death. WSMV causes reductions in yield, number of productive stems as well as seed set and grain weight. Yield loss is usually correlated with the age of plant seedlings. Generally, the disease causes yield losses that reach 80–100% when the infection is widespread early in the crop life [22, 23].

Besides wheat, WSMV affects such crops as barley (*Hordeum vulgare* L.), corn (*Zea mays* L.), rye (*Secale cereale* L.), oats (*Avena sativa* L.), sorghum (*Sorghum bicolor* L. Moench), millet (*Panicum* L.), and some mostly annual grasses. Some weeds such as foxtail millet (*Setaria itali-*

ca L.), green foxtail (*Setaria* P. Beauv. spp.), cockspur grass (*Echinochloa crus-galli* (L.) P. Beauv.), feather grass (*Stipa* L. spp.), goatgrass (*Aegilops* L. spp.), crabgrass (*Digitaria* Haller. spp.), ryegrass (*Lolium* L. spp.), bromes (*Bromus* Scop. spp.), and cupgrass (*Eriochloa* Kunth spp.) can serve as WSMV reservoirs and sources of viral infection in agroecosystems (Table 1) [24–33]. In addition, there are many wild plants and weeds that can serve as alternative hosts for wheat streak mosaic virus and a «green bridge» for the virus transmission by vectors to wheat crops in the fall [31, 34]. These plants include jointed goatgrass (*Aegilops cylindrica* Host), colorado bluestem (*Elymus smithii* (Rydb.) Gould), grama grass (*Bouteloua* sp.), spiny burrgrass (*Cenchrus incertus*), smooth crabgrass (*Digitaria ischaemum* (Schreb.) Schreb. ex Muhl.), and johnson grass (*Sorghum halepense* (L.) Pers.) (Table 1) [35].

WSMV is transmitted by eriophyid mite vector — wheat curl mite (*Aceria tosichella* Keifer (another name: *Aceria tritici* Schev.)) and by mechanical transmission. The virus is seed-borne at a low level in wheat but is not seed-borne in other crops and grasses [36–38].

In Ukraine, WSMV is distributed in all wheat-growing regions and is the most harmful virus for cereals. The main host plants of WSMV are annual and perennial grasses, which are common in Ukraine, namely couch grass (*Agropyron repens* (L.) Gould), common bent (*Agrostis capillaris* L.), common wild oat (*Avena fatua* L.), japanese brome (*Bromus japonicus* Thunb.), purple false brome (*Brachypodium distachyon* (L.) P. Beauv.), and creeping soft grass (*Holcus mollis* L.) (Table 1) [24, 25, 38–40].

The main wheat yield losses in Ukraine are caused by WSMV and infestations with *Aceria tritici* Schev (*Aceria tosichella* Keifer.). Infected wheat crops, volunteer cereal plants remaining in the fields, cereal weeds surrounding fields, and wheat plants that germinate from infected seeds act as primary WSMV infection foci for the mite to acquire the virus from and then spread

it within the crop. What contributes to the development of a viral disease. Since the virus is seed-borne, infected wheat seed plays a critical role in its survival between growing seasons. Autumn sowing made soon after the previous wheat harvest allows the vectors to transmit WSMV from infected volunteer cereal plants to emerging young wheat seedlings [20, 21, 41, 42]. Winter wheat, weeds, and wild grasses are of particular importance as reservoirs of infection, since both mite and WSMV overwinter on these plants. Prediction of mite and virus infestations is often difficult, as many species of range grasses that are mite hosts grow near wheat fields. Since warm weather (above +8 °C) is a favorable condition for mite development, therefore warmer temperatures and extended wheat growing periods can also favor increased WSMV spread by its vectors. Thus, the epidemiology of WSMV is determined by many factors, among which the virus reservoirs and mite vectors are of great importance.

Wheat dwarf virus (WDV) affecting wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), rye (*Secale cereale* L.), and triticale (*Triticosecale* Wittm. ex A. Camus) is a member of the *Mastrevirus* genus of the *Geminiviridae* family. First, WDV was divided into wheat (WDV-W) and barley (WDV-B) forms [43–46]. Later, both forms were divided into strains A to E, and more recently into A to F [47]. It is currently believed that WDV A and F strains mainly originated from barley while B, C, D, and E — from wheat [48]. The strains of WDV can also infect some species of wild grasses and have a range of hosts within the *Poaceae* family [49]. The wheat strain of WDV was found in ovate goatgrass (*Aegilops kotschy* Boiss.), common wild oat (*Avena fatua* L.), meadow brome (*Bromus commutatus* Schrad.), wall barley (*Hordeum murinum* L.), Persian darnel (*Lolium persicum* Boiss. & Hohen.), johnsongrass (*Sorghum halepense* (L.) Pers.), and bermudagrass (*Cynodon dactylon* (L.) Pers.), while the only host of the WDV-B recognized wild barley *Hordeum spontaneum* (L.) (Table 1) [50, 51].

WDV is common on cereal crops in Asia [52–55] as well as in some European countries, including Sweden [56], France [57], and Finland [58]. It is widespread in Germany, where the sources of infection can be cereals and wild grasses such as field brome (*Bromus arvensis* L.), meadow brome (*B. commutatus* Schrad), soft brome (*B. hordeaceus* L.), japanese brome (*B. japonicus* Thunb.), barren brome (*B. sterilis* L.), and reed canary grass (*Phalaris arundinacea* L.) [49]. Since the listed plant species are also widely distributed in Ukraine, it is reasonable to assume that these plants can be reservoirs of the WDV in our country as well, despite the fact that studies on virus occurrence in weeds and volunteer plants have not yet been carried out. Wild grasses that can definitely serve as a reservoir of the *Wheat dwarf virus* in Ukraine, such as bermudagrass (*Cynodon dactylon* (L.) Pers), common wild oat (*Avena fatua* L.), wall barley (*Hordeum murinum* L.), and johnson grass (*Sorghum halepense* (L.) Pers.) are widely distributed in all areas of grain farming throughout the country (Table 1).

WDV is transmitted by the leafhopper *Psammotettix alienus* in a persistent circulative manner. The virus cannot be transmitted by mechanical inoculation, or through contact between plants, soil, pollen, or seeds [47]. Outbreaks of wheat dwarf disease in recent years have occurred regularly in some countries and are probably associated with changes in agricultural practice of early sowing of winter wheat so that virophoric insects could infect cereals seedlings as early as in autumn [59, 60]. Another cause of viral outbreaks may be extending the growth period by a long and warm autumn, which gives leafhoppers the opportunity for longer feeding on plants. Moreover, climate change may also cause changes in the biology of leafhoppers [47].

In Ukraine, WDV is distributed in Khmelnytskyi, Kyiv, Cherkasy, and Kharkiv regions [44, 61–63]. WDV was also found on wild cereals *Deschampsia* sp. in Kherson and Odesa regions [10, 64]. WDV distributed in Ukraine is a big threat to wheat crops as it significantly reduces the number of seeds per spike and decreases

Table 1. The most common weeds — reservoirs of cereal viruses

Cereal crops	Weeds	References
Wheat (<i>Triticum aestivum</i> L.), Barley (<i>Hordeum</i> L.)	<i>Wheat streak mosaic virus</i> (WSMV)	
	Cockspur grass (<i>Echinochloa crus-galli</i> (L.) P.Beauv.)	[24–28, 115]
	Feather grass (<i>Stipa</i> L. spp.)	[29–33]
	Crabgrass (<i>Digitaria</i> Haller. spp.)	[29–33]
	Smooth crabgrass (<i>Digitaria ischaemum</i> (Schreb.) Schreb. ex Muhl)	[35]
	Hairy crabgrass (<i>Digitaria sanguinalis</i> L.)	[116]
	Ryegrass (<i>Lolium</i> . L. spp.)	[29–33, 116, 117]
	Italian ryegrass (<i>Lolium mitiflorum</i> Lam.)	[116, 117]
	Rigid ryegrass (<i>Lolium rigidum</i> Gaudin)	[37]
	Slender wild oat (<i>Avena barbata</i> Pott ex Link)	[37]
	Proso millet (<i>Panicum miliaceum</i> L.)	[29, 116, 117]
	Pearl millet (<i>Pennisetum glaucum</i> L.)	[28]
	Couch grass (<i>Agropyron repens</i> (L.) Gould, <i>Elymus repens</i> L.)	[24, 25, 38–40, 115]
	Common bent (<i>Agrostis capillaris</i> L.)	[25]
	Common wild oat (<i>Avena fatua</i> L.)	[116]
Purple false brome (<i>Brachypodium distachyon</i> (L.) P. Beauv.)	[39]	
Creeping soft grass (<i>Holcus mollis</i> L.)	[115]	

Cereal crops	Weeds	References
Wheat (<i>Triticum aestivum</i> L.), Barley (<i>Hordeum</i> L.)	Common velvet grass (<i>Holcus lanatus</i> L.)	[24, 27]
	Green foxtail (<i>Setaria viridis</i> (L.) P.Beauv.)	[24, 27]
	Foxtail millet (<i>Setaria italica</i> (L.) P.Beauv.)	[24–28, 118]
	Sorghum (<i>Sorghum bicolor</i> (L.) Moench.)	[28]
	Canada wild rye (<i>Elymus canadensis</i> L.)	[115]
	Bromes (<i>Bromus</i> Scop. spp.)	[24, 30–33]
	Rye brome (<i>Bromus secalinus</i> L.)	[27]
	Downy brome (<i>Bromus tectorum</i> L.)	[27]
	Japanese brome (<i>Bromus japonicus</i> Houtt.)	[40]
	Field brome (<i>Bromus arvensis</i> L.)	[27]
	Ripgut brome (<i>Bromus rigidus</i> L.)	[37]
	Crested wheatgrass (<i>Agropyron cristatum</i> (L.) Gaertn.)	[24]
	Jointed goatgrass (<i>Aegilops cylindrica</i> Host.)	[27]
	Slender wheatgrass (<i>Elymus trachycaulus</i> (Link) Gould ex Shinners)	[117]
	Stink grass (<i>Eragrostis cilianensis</i>)	[35]
Wheat (<i>Triticum aestivum</i> L.)	Wheat dwarf virus (WDV)	
	Field brome (<i>Bromus arvensis</i> L.)	[49]
	Meadow brome (<i>Bromus commutatus</i> Schrad)	[49, 50]
	Soft brome (<i>Bromus hordeaceus</i> L.)	[49]
	Japanese brome (<i>Bromus japonicus</i>)	[49]
	Barren brome (<i>Bromus sterilis</i>)	[49]
	Reed canary grass (<i>Phalaris arundinacea</i>)	[49]
	Ovate goatgrass (<i>Aegilops kotschyi</i>)	[50].
	Common wild oat (<i>Avena fatua</i>)	[46, 50]
	Wall barley (<i>Hordeum murinum</i>)	[50]
	Persian darnel (<i>Lolium persicum</i>)	[50]
	Johnson grass (<i>Sorghum halepense</i>)	[50]
	Bermuda grass (<i>Cynodon dactylon</i>)	[50]
	Wild barley (<i>Hordeum spontaneum</i>)	[50]
	Loose silky-bent (<i>Apera spica-venti</i> (L.) P.Beauv)	[46]
Smooth meadow-grass (<i>Poa pratensis</i> L.)	[46]	
Wheat (<i>Triticum aestivum</i> L.)	Winter wheat Russian mosaic virus (WWRMV)	
	Wild millet (<i>Setaria glauca</i> Beauv.)	[68]
	Green foxtail (<i>Setaria viridis</i> Beauv.)	[68]
Wheat (<i>Triticum aestivum</i> L.)	Wood small-reed (<i>Calamagrostis epigeios</i>)	[68]
	High Plains wheat mosaic virus (HPWMoV)	
	Rye brome (<i>Bromus secalinus</i> L.)	[74]
	Yellow foxtail, golden foxtail, wild millet (<i>Setaria pumila</i> Poir. (= <i>S. glauca</i> L.))	[74]
Wheat (<i>Triticum aestivum</i> L.)	Green foxtail, green bristlegrass, wild foxtail millet (<i>Setaria viridis</i> L.)	[74]
	Foxtail barley (<i>Hordeum jubatum</i> L.)	[72]

Cereal crops	Weeds	References
Barley (<i>Hordeum</i> L.) Wheat (<i>Triticum aestivum</i> L.), Oat (<i>Avena sativa</i> L.)	<i>Barley yellow dwarf virus</i> (BYDV)	
	Edge-flowered crested wheatgrass (<i>Agropyron dasyanthum</i> Ledeb.)	[87]
	Creeping bentgrass (<i>Agrostis stolonifera</i>)	[87, 119]
	Sweet vernal grass (<i>Anthoxanthum odoratum</i> L.)	[87]
	False oat-grass (<i>Arrhenatherum elatius</i> L.)	[87]
	Common wild oat (<i>Avena fatua</i> L.)	[87, 120]
	Rye brome (<i>Bromus secalinus</i> L.)	[87]
	Prairie grass (<i>Bromus catharticus</i> Vahl)	[87]
	Red brome (<i>Bromus rubens</i>)	[87]
	Downy brome (<i>Bromus tectorum</i> L.)	[87]
	Bermuda grass (<i>Cynodon dactylon</i> (L.) Pers)	[87]
	Cock's-foot (<i>Dactylis glomerata</i> L.)	[87]
	Large crabgrass (<i>Digitaria sanguinalis</i> L. Scop)	[87]
	Cockspur grass (<i>Echinochloa crus-galli</i> L. P.Beauv)	[87]
	Quick grass (<i>Elymus repens</i> L. Gould)	[87]
	Weeping lovegrass (<i>Eragrostis curvula</i> Schrad. Nees)	[87]
	Meadow fescue (<i>Festuca pratensis</i> Huds.)	[87]
	Tall fescue (<i>Festuca arundinacea</i>)	[87]
	Sheep's fescue (<i>Festuca ovina</i>)	[87]
	Meadow fescue (<i>Festuca pratensis</i>)	[87]
	Red fescue (<i>Festuca rubra</i>)	[87]
	Rice cutgrass (<i>Leersia oryzoides</i> L.)	[87]
	Perennial ryegrass (<i>Lolium perenne</i> L.)	[87]
	Italian ryegrass (<i>Lolium multiflorum</i> Lam.)	[87]
	Eulalia (<i>Miscanthus sinensis</i>)	[87]
	Asian rice (<i>Oryza sativa</i> L.)	[87]
	Millet (<i>Panicum miliaceum</i> L.)	[87]
	Dallisgrass (<i>Paspalum dilatatum</i>)	[87]
	Kikuyu grass (<i>Pennisetum clandestinum</i>)	[87]
	Timothy grass (<i>Phleum pratense</i> L.)	[87]
	Annual meadowgrass (<i>Poa annua</i> L.)	[87]
	Smooth meadow-grass (<i>Poa pratensis</i>)	[87]
	Foxtail millet (<i>Setaria italica</i> L. P.Beauv.)	[87]
	Sorghum (<i>Sorghum bicolor</i>)	[87]
	Johnson grass (<i>Sorghum halepense</i> (L.) Pers.)	[87]
	White clover (<i>Trifolium repens</i>)	[87]
Barley (<i>Hordeum</i> L.) Wheat (<i>Triticum aestivum</i> L.)	<i>Brome mosaic virus</i> (BMV)	
	Awnless brome (<i>Bromus inermis</i>)	[3, 96, 97]
Jointed goatgrass (<i>Aegilops cylindrica</i>)	[3, 96, 97]	

the weight of 1000 grains [61]. Its epidemiology in Ukraine is closely related to the distribution of its vector as well as to its sources in wheat crops, which can be cereals, weeds, and wild-growing herbs [65]. Currently, the economic impacts of WDV in Ukraine are rated as small due to the low abundance of the vector, but the situation may change significantly due to rapid climate change or agricultural practices. Early phytosanitary control of crops, removal of stubble, and volunteer cereal plants are of great importance in the management of the virus.

Winter wheat Russian mosaic virus (WWRMV) is a species of the genus *Nucleorhabdovirus* of the family *Rhabdoviridae*. It is transmitted by *Psammotettix alienus* Dahlbom (syn. *P. striatus* L.) and aster (six-spotted) *Macrosfeles laevis* L. Leafhoppers and significantly increases the epizootic value of the vector, which is determined by its transovarial transmission.

There is a risk of doubtful identification resulting from the transmission of this virus by the leafhopper *Psammotettix alienus*, equally the vector *Wheat dwarf virus*. However, the average time of incubation in *P. alienus* lasts about 3 weeks, WWRMV is reported to replicate in its vector excluding the presence of WDV, which is circulative in this vector [66]. In years favorable for the development of the disease, plant damage reaches 30%. In some years, especially in the case of the mass reproduction of leafhoppers, the yield losses of winter wheat due to the infection with WWRMV range from 40 to 100% [59, 60].

WWRMV is mainly found in wheat and has a very wide host range in grasses such as the bush grass (*Calamagrostis epigejos* (L.) Roth), yellow foxtail (*Setaria glauca* (L.) P. Beauv. (syn. *Setaria pumila*)), green foxtail (*S. viridis* (L.) P. Beauv.), and others (Table 1) [66–68]. In Ukraine, yellow and green foxtails grow in cultivated fields and are often found as post-harvest weeds after harvesting early winter and spring crops, as well as in late spring crops. Being natural hosts for WWRMV, these grass species can be successful

reservoirs of the virus and serve as its important source for subsequent spread to cultivated plants. The epidemiology of WWRMV is determined by reservoirs within the cereal family, including cultivated plants, weeds and wild plants, as well as virus vectors — *Psammotettix striatus* L. and *Macrostes laevis* Rib. The virus persists in overwintering crops, cereal weeds, in winter eggs and adults of striped and six-spotted leafhoppers [69]. The economic importance of the virus is greater in dry years, when the activity of cicadas increases significantly [70].

High Plains wheat mosaic virus, also known in the literature as *High Plains virus* (HPV), *Maize red stripe virus* (MRSV / MRStV), and *Wheat mosaic virus* (WMoV), belonging to the genus *Emaravirus*, family *Fimoviridae*, is a causal agent of High Plains disease (HPD) [71]. HPD was first identified in 1993 in wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.) in the High Plains of Texas, Kansas, Colorado, Idaho, Nebraska, and Utah [71]. HPWMoV has also been found in Israel, Chile, Argentina, Australia, and Canada [72, 73] and in different regions of Ukraine on wheat and corn [12]. It has a range of hosts that includes economically important plants such as wheat, corn, barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), rye (*Secale cereale* L.), and some weeds, including rye brome (*Bromus secalinus* L.), yellow foxtail (*Setaria pumila* (Poir.) Roem & Schult (= *S. glauca* L.), green foxtail (*Setaria viridis* L.) and foxtail barley (*Hordeum jubatum* L.)) (Table 1) [72, 74], which can be infected with wheat curl mite *Aceria tosichella* Keifer (= *Aceria tritici*) [75]. *Setaria pumila* is a good indicator of the presence of HPWMoV: 252 of 278 symptomatic plants selected in the fields within 1994–1996 were positive in enzyme-linked immunosorbent assay (ELISA) for HPWMoV [74]. All these wild cereals, *Bromus secalinus* L., *Setaria pumila* (= *S. glauca*) L., *Setaria viridis* L., and *Hordeum jubatum* L., grow throughout Ukraine in fields, pastures, cereals, and row crops and can act as reservoirs

of HPWMoV. The symptoms of HPWMoV can be confused with those caused by WSMV and can vary greatly from mild to severe, including mosaic, chlorosis, and necrosis. HPWMoV can infect plants through both mono-infection and co-infection with *Wheat stripe mosaic virus*, causing more severe symptoms leading to significant damage to crops. These viruses have a common vector; in addition, they can be transmitted by seeds. Transmission of HPWMoV by maize seeds has been confirmed [76], but further studies are needed to determine the frequency and mechanism of HPWMoV transmission by maize and wheat seeds. The main management strategy for High Plains disease relies on the management of green bridge hosts to avoid mite buildup in cereal crops and on regular seed testing for HPWMoV to ensure that HPWMoV is not imported into other countries with seeds.

Plants as reservoirs of viruses in barley crops.

Barley, along with wheat, corn, and rice, is one of the world's most important cereals for food and fodder, which is in great demand in the agricultural market. Barley could be a food source for millions of people even though currently it is mainly used for the feeding of livestock and brewing. In contrast to global trends in the growth of barley production, the interest of Ukrainian agribusiness in its cultivation has decreased slightly, as evidenced by the dynamics of the reduction of sown areas under this grain crop [77]. The total sown area of spring and winter barley decreased by almost 64%, in particular from 3.9 mln ha in 2000 to 2.5 million hectares in 2020–2021, despite the fact that winter barley ranks fourth in the structure of sown areas of Ukraine (State Statistics Service of Ukraine) [78].

Barley yellow dwarf virus (BYDV) is a type member of the genus *Luteovirus* in the family *Luteoviridae* [79]. It is now recognized as a complex of species, namely BYDV-kerII, BYDV-kerIII, BYDV-MAV, BYDV-PAS, and BYDV-PAV assigned to the *Luteovirus* genus and species that have not been assigned to a genus (BYDV-GPV and BYDV-

SGV) [80]. BYDV is considered the most economically important virus of cereals due to huge yield losses in agriculture. In wheat, BYDV can cause 5–80% grain yield losses [81]. Yield losses of barley infected with BYDV depend on such factors as virus species, environmental conditions as well as the plant growth stage at the time of infection, which is a crucial factor in the disease development. The most severe symptoms result only when annual cereals are infected on the seedling stage. At later stages of infection, when the virus has progressively less time to affect the host, the disease severity is reduced proportionately, and only the last formed leaf may show mild symptoms. In fall-sown cereals, BYDV infections increase winter killing of plants as well as reduce yields [82].

BYDV is not mechanically or seed transmissible, but it is transmitted by aphids in a circulative, nonpropagative manner [83]. BYDV-PAV can potentially use more than one aphid species for transmission (*Sitobion avenae* and *Rhopalosiphum padi*), whereas BYDV-MAV only uses *S. avenae*. Virus transmission within the pathosystem depends on the vector mobility [4, 84]. Virophoric wingless aphids can transmit BYDV over long distances, and even initial small populations of infected aphids can lead to significant economic damage [82].

The host range of BYDV is restricted by *Poaceae* species and includes the range of cereal crops (wheat, barley, oats, triticale maize, rye) and over 150 species of cultivated, lawn, weed, pasture, and range grasses [85]. Many annual and perennial lawn and weed pasture species have been reported to be naturally infected with BYDV and therefore can serve as a virus inoculum for annual species and emerging agricultural crops and thus contribute to further pathogen distribution [86]. The pasture crops that are mostly affected include ryegrass (*Lolium perenne* L., *Festuca perennis* Lam. (syn. *Lolium multiflorum*)), *Festuca* spp., *Bromus* spp., cocksfoot (*Dactylis glomerata* L.), phalaris (*Phalaris aquatica* L.), and timothy grass (*Phleum pratense* L.) [87].

In Ukraine, BYDV occurs in all cropping regions and dominates among wheat and barley viruses [88]. The non-cultivated grass species, which include perennial ryegrass, bromes, cock's-foot, bulbous canarygrass, and timothygrass (*Phleum pratense* L.) are widely distributed in Ukrainian agrocenosis and can play an important role in disease incidence [89] (Table 1). *Barley yellow dwarf virus* overseasons in grass hosts, fall-sown cereals, and viruliferous adult aphids. In spring, the virus is introduced to a new crop by migrating viruliferous aphids (primary infection). Under the favorable to aphid development and spread weather conditions, the BYDV spreads in the crop (secondary infection). The worst epidemics develop when the spring and early summer weather is cool and moist [82, 86].

The epidemiology of BYDV is certainly closely related to the virus circulation in cereal crops and surrounding wild grasses as well as among the aphid vectors [90]. BYDD epidemics depend on the weather conditions that promote early accumulation of aphid vectors in alternative aphid and BYDV hosts and their large-scale migration to wheat crops at an early growth stage. Because the interaction among the vectors, host plant, and BYD viruses is complex, the disease prediction seems to be a rather difficult task. Data on the mean daily rainfall and temperature before sowing allow predictions of infection incidence and losses and provide decision support over insecticide applications to kill aphid vectors [41, 91].

Brome mosaic virus (BMV) is a type member of the genus *Bromovirus* in the family *Bromoviridae*. It is widely distributed globally, and it has been reported in the United States, Canada, South Africa, Russia, Poland, Czechoslovakia, Estonia, Great Britain, and Finland [92]. In Ukraine, *Brome mosaic virus* is sporadically detected in the commercial fields under cereals. The virus was most often found in winter wheat and spring barley plants in Kyiv, Vinnytsia, and Odesa regions [93]. The results of a field survey on winter wheat in Vinnytsia, Khmelnytskyi,

Kyiv, Chernihiv and Cherkasy regions conducted in 2020 did not confirm the occurrence of BMV there, despite the plants showed characteristic symptoms [61].

BMV is considered a pathogen of minor economic value. However, infection of different cereal species at early growth stages leads to severe losses of grain yield reaching 35—65%. Early infection of winter and spring barley, wheat, or oat may lead to total loss of crops [93]. BMV has a wide host range (162 species are known currently) including wheat, oats, barley, rye, corn, sorghum, fescue, couch grass, various species of ryegrass, meadow ryegrass, timothy, smooth meadow-grass as well as dicotyledonous plants (beans, cucumbers, datura, etc.) belonging to seven families [94, 95]. In nature perennial weeds such as smooth brome (*Bromus inermis* Leys.), and triticum cylindrical (*Aegilops cylindrica* Host) harbor BMV and serve as virus reservoirs [3, 96, 97]. Since these grasses are widespread in Ukraine, one can assume their important role in the accumulation of viral infection and the spreading of BMV in natural ecosystems. BMV transmission in plants is not well characterized, it can be transmitted in the field by human activities and in laboratory settings — by mechanical inoculation. The virus was efficiently transmitted by the barley flea beetle, *Phyllotreta vittula*, in the laboratory [98]. In the field, it is transmitted mainly mechanically or through seeds [99—101]. Greenhouse experiments have also been described with wheat and barley as hosts with low rates of transmission by Russian wheat aphid (*Diuraphis noxia*), flea beetle (*Altica foliaceae*), dagger nematode (*Xiphinema spp.*), cereal leaf beetle (*Oulema melanopus*), and bird cherry-oat aphid (*Rhopalosiphum padi*) [102, 103].

Although BMV is known as a model for the biology of an RNA virus, very little information is available on its economic impact on wheat production, and even more so on the importance of wild grasses in viral epidemiology.

However, with a rapidly changing climate and redistribution of areas for cultivation of crops, the importance of the grasses-reservoirs of BMV must not be overlooked.

Barley stripe mosaic virus (BSMV), the genus *Hordeivirus* type member, is the most intensely studied virus that has a narrow host range, predominantly affecting two major monocot crops, wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) [104]. Yield reductions in barley of 20–50% were recorded when crops were infected with BSMV. The decrease in grain weight is mainly due to the number of seeds per spike, the number of heads per plant, and kernel weight reduction in infected plants [105].

BSMV has a worldwide distribution, it occurs in North America, Europe, Japan, the former Soviet Union, China, and Australia [106–108]. There are no known vectors to transmit the virus. BSMV is transmitted by mechanical inoculation, by seed (90–100%) and pollen to the pollinated plant. The seed transmission rate depends on the host species, virus strain, infection stages, and environmental conditions. In barley seeds, the virus can persist for many years, and plants grown from infected seeds are usually dwarf, a significant part of them die before they reach the soil surface.

In the field, BSMV is easily transmitted from infected to healthy plants through contact, when leaves rub together as a result of wind, hail, or animals [104]. BSMV has a narrow host range and predominantly affects barley but it can also infect wheat. Under experimental conditions, BSMV was mechanically transmitted to the range of *Poaceae* (more than 250 species) in particular corn (*Zea mays* L.), oats (*Avena sativa* L.), herbs of the genus *Brachypodium spp.*, and some dicotyledonous plants (spinach, beetroot, and tobacco) [109–112].

In the epidemiology of the virus, transmission through seeds is a significant factor, but accumulation of the pathogen in reservoir plants, such as common wild oat (*Avena fatua* L.) and

bristle grasses of *Poaceae* family can also be of great importance [113]. Currently, BSMV is present at a low level in all barley germplasm collections around the world [114].

Thus, the rate of BSMV spread is dependent on the amount of virus initially present in the seed, the virus strain-host combination, and the subsequent spreading by mechanical means. As the virus can be spread by mechanical inoculation, it is also important to consider its possible movements out of the infected area of crop or plantreservoirs resulting in the secondary infection of commercial fields. Wind and rain may also be factors affecting secondary spread, because they would increase contact between infected and healthy plants. Since there are no known natural vectors of BSMV, weeds and wild grasses do not have a decisive influence on the epidemiology of this virus.

Discussion. In the present work, we have analyzed the possible significance of weeds growing in Ukraine as a virus inoculum for annual species and emerging agricultural crops as well as for spreading cereal viruses. Unfortunately, our knowledge and understanding of the role and influence of weeds and wild or volunteer plants on the virus distribution in ecosystems and natural plant communities can be considered incomplete at best. This situation is largely due to the fact that the efforts of plant virologists have been largely focused on crops and the viruses that affect them. Despite the fact that the virus and vectors can be found in agricultural and unmanaged habitats in the same region, however, the movement of vectors throughout habitats and the role of each of the participants, that is, the virus, the vectors, and the host (alternative host or reservoir of viral infection), have not yet well understood. In view of the facts that many grass species remain unexamined for their ability to host cereal viruses, and new hosts continue to be identified, virologists need to study more closely the possible role of wild plants and weeds in the epidemiology of plant virus diseases.

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БУР'ЯНИ — РЕЗЕРВАТОРИ ВІРУСІВ В АГРОБІОЦЕНОЗАХ ЗЕРНОВИХ УКРАЇНИ

В огляді наведено аналіз даних літератури щодо поширеності бур'янів та дикорослих злаків в агроекосистемах України як можливих резерваторів вірусів. У статті узагальнено дослідження вірусної інфекції пшениці та ячменю, а також бур'янів, поширених в агросистемах зернових культур, та їх впливу на вірусну епідеміологію. Крім того, велика увага приділена першоджерелам основних збудників вірусних хвороб пшениці та ячменю, а саме вірусу смугастої мозаїки пшениці (ВСМП), вірусу карликовості пшениці (ВКП), вірусу російської мозаїки озимої пшениці (ВРМОП), вірусу мозаїки пшениці Високих рівнин (ВМПВР), вірусу жовтої карликовості ячменю (ВЖКЯ) та вірусу мозаїки бромусу (ВМБ), а також основним факторам, що сприяють поширенню цих вірусів в агроценозах.

Ключові слова: віруси рослин, бур'яни-резерватори вірусів рослин, вектори вірусів зернових культур.