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Infection of Grasses by Barley Yellow Dwarf Viruses in California

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ABSTRACT

Barley yellow dwarf viruses (BYDVs) continue to cause losses in California cereal production. In some parts of the USA, native grasses have been implicated as reservoirs of BYDVs. This study examines the potential of native and irrigated pasture grasses as sources of BYDV inoculum in California. The effects of both natural and natural plus supplemental inoculum were examined in field trials over two growing seasons using a completely randomized design. Results were assessed by enzyme-linked immunosorbent assay (ELISA) and verified with controlled greenhouse vector transmission trials. Thirty-seven of 56 species of cool-season grasses were infected by either PAV, MAV, or RPV isolates of the BYDVs. Of the BYDV-infected grasses, only 38% displayed symptoms typically seen in infected oat (*Avena sativa* L.) and barley (*Hordeum vulgare* L.), while the others were asymptomatic. None of the plants from seven species of *Leymus*, nor plants from the majority of *Elymus* and *Elytrigia* species, had detectable BYDV infections, even though they supported aphid vector populations. A survey of common grasses from irrigated pastures showed that plants from 6 of 10 species were infected by either the PAV, MAV, or RPV isolates of BYDVs. The incidence of MAV, PAV, and RPV BYDVs were roughly equivalent for the cool-season grasses, but were highly skewed toward PAV in the irrigated pasture survey. Both cool-season and irrigated warm-season pasture grasses have the potential to serve as BYDV reservoirs in California.

THE BYDVs are common and widespread pathogens of grain and grass forage crops (Oswald and Houston, 1953; Bruehl, 1961; Plumb, 1983). The BYDVs are taxonomically separated by various characteristics such as vector transmissibility, serotype, and host ultrastructural reactions, and are designated as the PAV, MAV, SGV, RPV, and RMV types or groups (Rochow, 1984). Various BYDVs have the capacity to infect many small grains, including rice (*Oryza sativa* L.), corn (*Zea mays* L.) and many noncultivated gramineous species (Slykhuis, 1967;

Brown et al., 1984; Osler, 1984). Infection of wild hosts is of little direct economic concern; however, in some areas wild hosts have been implicated as important BYDV reservoirs, serving as overseasoning hosts that subsequently become primary inoculum sources (Bruehl, 1961; Kiesling, 1959; Plumb 1977). In other areas, wild hosts do not seem to be epidemiologically important, when compared to the mass migration of viruliferous alates from adjacent grain belt states and provinces (Slykhuis et al., 1959; Gill, 1970; Fargette et al., 1982).

In California, wheat (*Triticum aestivum* L.), barley, and oat were planted on ~400 000 hectares in 1987–1988 (Griesbach et al., 1989). Statewide BYDV survey results from 1987 and 1988 showed that various BYDVs were found throughout California and continue to cause yield losses in small grains (Griesbach et al., 1990). The primary BYDV management strategies used in California are the use of cultivars with some degree of BYDV resistance and timing planting dates so as not to subject the highly susceptible seedlings to heavy flights of viruliferous aphids (Griesbach et al., 1989). These strategies could be compromised by the presence of BYDV-infected noncultivated grasses (wild hosts) in proximity to grain fields. Where BYDV infections of wild hosts occur, environmental factors such as host senescence or vector overpopulation could force viruliferous alate aphids to move and colonize nearby grains, thereby making the noncultivated grasses important sources of primary inoculum. Also, the various BYDVs (i.e., PAV, RPV, and MAV) have been shown to be restricted in incidence to a large degree by the subfamily of wild host (Guy et al., 1987). Such type–host interaction could be important in the epidemiology of BYDV infections.

An investigation of the ability of cool-season grasses to serve as hosts of BYDVs was undertaken in the 1986–1987 and 1987–1988 growing seasons. Additionally, samples of permanent warm-season pasture grasses were collected in the summer of 1987 to identify noncultivated hosts that may serve as overwintering hosts of BYDVs and potentially become sources of primary inoculum for fall spread. Corresponding greenhouse trials of selected noncultivated

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host species were undertaken in the winter of 1987–1988 to test the ability of selected aphid species to transmit BYDVs to these grasses under controlled conditions.

MATERIALS AND METHODS

Winter-Spring Field Trials. The species selected for this study included many common grasses normally found in proximity to commercial grain fields, including some wild congeners of commercial cultivars. Other species were included because they are sources of disease resistance in small grains; these included both domestic and foreign accessions. Seed sources included the Regional Plant Introduction Service, USDA, Pullman, WA, and the Department of Agronomy and Range Science, University of California, Davis. Seeds were germinated in a temperature-regulated greenhouse in the autumn of both study years. Each entry was planted three plants per pot in 10-cm diam. pots filled with soil mix. Seedlings were grown for 10 wk and then moved to a lathhouse to acclimate them to ambient conditions. Two plants of each species were transplanted to raised beds at the Armstrong Tract, University of California, Davis, in December of both study years. Entries were arranged in a completely randomized design interspersed with 'California Red' oat check plants. To increase aphid and BYDV inoculum, spreader rows of California Red oats were drilled in alternating rows between the host range species (Qualset, 1984). Reading of symptom expression (discoloration either as a yellowing or reddening in patches or blotches beginning at the distal end of leaves and progressing down the blade) were taken monthly beginning in March, until the plants senesced. In the first year of the study (1987), all infections were a result of natural field infection. In the second year (1988), BYDV-symptomatic wild oat plants (primarily *A. fatua*) infested with *Rhopalosiphum padi* L. (oat bird cherry aphid) and *Metopolophium dirhodum* Walker (rose grass aphid) from adjacent fields were scattered among the trial plants. Additionally, greenhouse oat plants infected with cultures of California MAV, PAV, and RPV BYDVs and infested with *R. padi* and *Sitobion avenae* (Fabricius) were scattered among the host range plants to increase inoculum pressure. Aphid populations were monitored in the second year of the study by direct observation of the plant with diagnoses made by hand lens.

Serological Analysis. Enzyme-linked immunosorbent assay (ELISA) tests were used to specifically assess plants for infection by the PAV, RPV, and MAV type BYDVs (Lister and Rochow, 1979; Griesbach et al., 1990). Polyclonal antisera (Pab) to NY-PAV, NY-MAV, and NY-RPV were supplied by Dr. J. Duffus, USDA, Salinas, CA. Monoclonal antibodies (Mab) of NY-PAV (MAV-3), NY-MAV (MAV-1), and NY-RPV (RPV-1, -2, and -3) were supplied by H.T. Hsu, USDA, Beltsville, MD (Hsu et al., 1984). For both the field and greenhouse trials, tissues from each replicate were collected just prior to the senescence of the earliest maturing variety. All samples were processed individually.

Samples were assayed by double antibody sandwich (DAS) ELISA using Pab for both coating and conjugation steps in 1987, and either Pab or Mab to coat plates in 1988 (Creamer and Falk, 1989). Absorbance values were assessed spectrophotometrically at 405 nm (A_{405}). Paired replicates of unknown samples, uninfected controls (2–3 per plate), and positive controls of plants infected by California isolates of PAV, MAV, and RPV (2–3 per plate) were loaded in each plate. Samples were considered positive if the A_{405} reading was greater than four times the standard deviation of the mean plus the mean of uninfected oat A_{405} values, and were also greater than the mean absorbance value of heterologous antisera reactions.

Greenhouse Virus Transmission. Several wild grass species that tested positive by ELISA in the 1987 field trial, and several species commonly found in permanent warm-season pastures were tested in the greenhouse for BYDV susceptibility. New York colonies of *R. padi* and *S. avenae* (Creamer and Falk, 1989) were used for transmission experiments. Aphids were given a 24-h acquisition access period on detached leaves of California Red oat plants infected with California isolates of PAV, RPV, and MAV. Approximately 25 viruliferous aphids from each BYDV source were then caged on each of three individually potted host plants (three replicates per treatment) for a 72-h inoculation access period. Aphids were killed with a 1 g L⁻¹ permethrin spray (3-phenoxyphenyl) methyl(1)cis, trans-ethenyl-2, 2-dimethylcyclopropane-carboxylate) and the plants were maintained in an insect-free greenhouse. Plants were tested for infection by ELISA at 30 and 180 d postinoculation, and by aphid transmission recoveries back to California Red oat plants, which were also subsequently tested by ELISA.

Irrigated Pasture Survey. Leaf samples of dominant grass species from irrigated permanent pasture areas and rice fields were collected in August of 1987 in the northern San Joaquin Valley (San Joaquin County). Samples were processed by polyclonal ELISA as above.

RESULTS

Winter-Spring Field Trials. Positive A_{405} values averaged 1.280 for PAV, 0.541 for MAV, and 0.378 for RPV positive controls. Mean uninfected tissue readings were highest against RPV antiserum at 0.093, followed by MAV at 0.070, and PAV at 0.026. The ELISA results for the grass samples, shown as sums of both replicates (Table 1), revealed that plants from 9 of the 56 species were infected with PAV, RPV, or MAV BYDV types, either as single or mixed infections for the 1987 field trial. Plants from seven of nine species were positive for MAV, five were positive for RPV, and only one species was positive for PAV. Plants from three of nine species had mixed infections, with *Aegilops ovata* plants being infected by PAV, MAV, and RPV BYDV types.

In 1988, plants from 33 of 55 species were infected (Table 1). The PAV was detected in plants from 26 species, MAV in 16 species and RPV in 14 species. There were 17 species with plants harboring mixed infections in 1988, six of which had all three BYDV types. Comparison between the years showed that of the ten species with infected plants in 1987, six again had plants infected in 1988, plants of three species had no detectable infection, and one was not planted (Table 1).

Symptoms of virus infection were recorded in 1988, and of the 55 species planted, plants of only 14 (25.5%) species displayed gross discoloration typical of BYDV infection in oats and barley. Symptom expression generally followed generic lines, with plants from four of five *Aegilops* species, two of two *Avena* species, and two of four *Hordeum* species showing gross discoloration (Table 1). The remaining six symptomatic plants were from species dispersed among four genera.

The presence of potential aphid vector species was monitored in the field trial in 1988, and plants from all but three species tested were observed to harbor potential BYDV vectors at some time during the spring months (Table 1). The aphid species included

Table 1. Enzyme-linked immunosorbent assay results for barley yellow dwarf viruses (BYDVs) in wild-host field trials, University of California, Davis, 1987 and 1988.

Grass species	1987			1988			Symptoms	
	M	P	R†	M	P	R		
<i>Aegilops ovata</i> L.	+	+	+	+	+	+	y‡	+§
<i>Ae. ventricosa</i> Tausch	-	-	-	+	-	-	-	+
<i>Ae. triuncialis</i> L.	+	-	-	+	+	+	y	+
<i>Ae. cylindrica</i> Host	-	-	-	+	+	+	y + r	+
<i>Ae. juvenalis</i> (Thell.) Eig	+	-	+	+	+	-	y + r	+
<i>Agropyron desertorum</i> (Fisch. ex Link) Schultes	-	-	-	+	-	-	-	+
<i>Ag. bonaeapartii</i> (Spreng.) Dur. & Schinz	-	-	-	-	+	-	-	+
<i>Ag. cristatum</i> (L.) Gaertn.	-	-	-	-	-	-	-	+
<i>Avena fatua</i> L.	-	-	-	-	+	+	y + r	+
<i>Av. sativa</i> L.	-	-	+	+	+	-	r	+
<i>Brachypodium pinnatum</i> (L.) Beauv.	-	-	-	+	-	-	-	+
<i>Bra. sylvaticum</i> (Huds.) Beauv.	-	-	-	-	-	-	-	-
<i>Bra. distachyon</i> (L.) Beauv.	-	-	-	+	+	+	r	+
<i>Bra. phoenicoides</i> (L.) Roem. & Schult.	-	-	-	+	-	-	r	+
<i>Bromus hordeaceus</i> L. (syn. <i>B. mollis</i> L.)	-	-	-	-	+	-	y + r	+
<i>Bro. brizaeformis</i> Fisch. & Mey.	-	-	-	+	+	+	-	+
<i>Bro. tectorum</i> L.	-	-	-	-	-	+	r	+
<i>Bro. rubens</i> L.	-	-	-	-	+	+	-	+
<i>Deschampsia cespitosa</i> (L.) Beauv.	-	-	-	-	+	+	-	+
<i>D. flexuosa</i> (L.) Trin.	-	-	-	-	-	-	-	-
<i>Elymus canadensis</i> L.	-	-	-	-	-	-	-	+
<i>Elym. dahuricus</i> Turcz. ex Griseb.	-	-	-	-	-	-	-	+
<i>Elym. dahuricus</i> ssp. <i>excelsus</i> (Turcz. ex Griseb.) Tzvel.	-	-	-	-	-	-	-	+
<i>Elym. virginicus</i> L.	-	-	-	-	-	-	-	+
<i>Elym. sibiricus</i> L.	-	-	-	-	-	-	-	+
<i>Elym. fibrosus</i> (Schrenk) Tzvelev	+	-	-	¶	-	-	-	+
<i>Elym. trachycaulus</i> (Link) Gould ex Shinn.	+	-	-	-	-	-	-	+
<i>Elytrigia intermedia</i> ssp. <i>intermedia</i> (Host) Nevski	-	-	+	-	-	-	-	+
<i>Elyt. intermedia</i> var. <i>trichophora</i> (Link) Löve & Löve	-	-	-	-	-	-	-	+
<i>Elyt. repens</i> (L.) Nevski	-	-	-	-	-	-	-	+

(continued)

(in decreasing order of abundance) *R. padi*, *M. dirhodum*, *Schizaphis graminum* (Rondani), and *S. avenae*. Plants from those grass species that did not support aphids, despite infestation with aphids, included *Brachypodium sylvaticum*, *Deschampsia flexuosa*, and *Festuca dolichophylla*. Additionally, plants from these three species tested negative for BYDVs.

Greenhouse Virus Transmission. Greenhouse aphid transmissions were verified by ELISA and aphid recovery with transmission to California Red oats from four of 14 grass species inoculated (Table 2). The ELISA results at 30 d postinoculation were positive for two or more types of BYDVs in seven grasses, and in all the California Red oat check plants tested. Seven species were negative for all BYDVs by ELISA, and were not subjected to further testing. Aphid recoveries from the 30-d ELISA-positive plants were successful for *Aegilops ovata*, *Ae. triuncialis*, *Bromus mollis*, and *Festuca arizonicus* (Table 2). Additionally, plants of these four species tested positive for BYDVs by ELISA at 180 d. Neither *Hordeum brevi-*

Table 1 (continued).

Grass species	1987			1988			Symptoms	
	M	P	R†	M	P	R		
<i>Eragrostis curvula</i> (Schröd.) Nees	-	-	-	-	-	-	-	+
<i>Festuca rubra</i> L.	-	-	-	-	+	-	-	+
<i>F. dolichophylla</i> Presl.	-	-	-	-	-	-	-	-
<i>F. arizonica</i> Vasey	+	-	-	-	+	-	-	+
<i>F. tenuifolia</i> Sibth.	-	-	-	-	-	-	-	+
<i>F. elatior</i> many authors, not L. (syn. <i>F. pratensis</i> Huds.)	-	-	-	-	+	-	-	+
<i>F. megalura</i> Nutt. [Syn. <i>Vulpia megalura</i> (Nutt.) Rydb.]	-	-	-	+	+	+	-	+
<i>F. arundinacea</i> Schreb. (Syn. <i>F. elatior</i> L.)	-	-	-	+	+	-	-	+
<i>F. ovina</i> L.	-	-	-	-	+	-	y + r	+
<i>F. longifolia</i> Thuill.	-	-	-	-	+	-	-	+
<i>F. idahoensis</i> Elmer	-	-	-	-	+	-	-	+
<i>Hordeum jubatum</i> L.	-	-	-	-	+	+	y + r	+
<i>H. brevisubulatum</i> (Trin.) Link ssp. <i>violaceum</i> (Boiss. & Hohen.) Tzvelev.	+	-	+	-	-	-	-	+
<i>H. brachyantherum</i> Nevski (syn. <i>H. californicum</i>)	-	-	-	-	+	+	y	+
<i>H. muticum</i> Presl.	-	-	-	-	+	-	-	+
<i>Leymus angustus</i> (Trin.) Pilger	-	-	-	-	-	-	-	+
<i>L. arenarius</i> (L.) Hochst.	-	-	-	-	-	-	-	+
<i>L. racemosus</i> (Lam.) Tzvelev	-	-	-	-	-	-	-	+
<i>L. condensatus</i> (Presl.) A. Löve	-	-	-	-	-	-	-	+
<i>L. mollis</i> (Trin.) Pilger	-	-	-	-	-	-	-	+
<i>L. triticoides</i> (Buckl.) Pilger	-	-	-	-	-	-	-	+
<i>Lolium multiflorum</i> Lam.	-	-	-	-	+	-	-	+
<i>Pascopyrum smithii</i> (Rydb.) A. Löve	-	-	-	+	-	+	-	+
<i>Paspalum dilatatum</i> Poir.	-	-	-	+	+	-	-	+
<i>Poa annua</i> L.	-	-	-	+	+	-	r	+

† ELISA samples were considered positive (+) if the A_{405} of the sample mean was greater than the mean plus four times the standard deviation of the uninfected mean, and were also greater than the mean of heterologous cross-reacting antisera, and included MAV (M), PAV (P), and RPV (R) antisera.

‡ Symptoms were assessed by gross discoloration typical for BYDV infections on barley and oat and are expressed as yellow (y) and/or red (r).

§ All plants had aphids capable of vectoring BYDV feeding on them during the monitoring period (+) except for those marked (-).

¶ *Elym. fibrosus* was not planted in 1988.

subulatum (Trin.) Link. ssp. *violaceum* (Boiss. et Hohen.) Tzvelev or *Elytrigia intermedium* (Host.) Nevski tested positive by ELISA in greenhouse transmission, yet plants of these two species were positive for at least 1 yr in the field trials.

Irrigated Pasture Survey. Six of ten species from samples of summer annual and perennial grasses (represented by 64 total samples) tested positive for BYDVs (Table 3). Reactions for PAV were predominant, being found in 20 (31.3%) of 64 samples. One sample tested positive for MAV, and one sample reacted positively for a RPV-PAV mixed infection.

DISCUSSION

The accuracy of BYDV host studies is dependent on several factors, including sufficient quantity (inoculum pressure) and quality (aphid species and virus isolate) of inoculum. The importance of inoculum

Table 2. Susceptibility of selected grasses to Barley Yellow Dwarf Viruses under greenhouse conditions as verified by enzyme-linked immunosorbent assay (ELISA) and aphid acquisition.†

Host plants	ELISA 30 d pi‡				Aphid recovery from§			ELISA 180 d pi¶			
	CK	MAV	PAV	RPV	MAV	PAV	RPV	MAV	PAV	RPV	CK
					proportion						
<i>Avena sativa</i> cv. California Red	—††	3/3	3/3	3/3	2/2	2/2	2/2	3/3	3/3	3/3	0/1
<i>Aegilops ovata</i> L.	—	3/3	3/3	3/3	3/3	3/3	3/3	2/3	0/3	2/3	0/1
<i>Ae. triuncialis</i> L.	—	1/3	1/3	3/3	1/1	1/1	1/3	1/3	0/3	1/3	0/1
<i>Bromus rubens</i> L.	—	—	1/3	2/3	—	—	—	—	—	—	—
<i>B. mollis</i> L.	—	3/3	2/3	3/3	3/3	1/1	2/2	—	1/3	1/3	0/1
<i>Digitaria sanguinalis</i> (L.) Scop.	—	1/3	2/3	3/3	0/1	0/2	0/3	0/3	2/3	0/3	0/1
<i>Festuca arizonica</i> Vasey	—	2/3	1/3	1/3	1/2	1/1	0/1	0/3	1/3	0/3	0/1
<i>Poa annua</i> L.	—	—	1/3	2/3	—	0/1	0/2	—	—	—	—
<i>Echinochloa crus-galli</i> (L.) Beauv.	—	—	—	—	—	—	—	—	—	—	—
<i>Leptochloa dubia</i> (H.B.K.) Nees	—	—	—	—	—	—	—	—	—	—	—
<i>Hordeum brevisubulatum</i> (Trin.) Link	—	—	—	—	—	—	—	—	—	—	—
<i>Elytorgia intermedia</i> (Host) Nevski	—	—	—	—	—	—	—	—	—	—	—
<i>Setaria lutescens</i> (Weigel) Hubb.	—	—	—	—	—	—	—	—	—	—	—
<i>Cynodon dactylon</i> (L.) Pers.	—	—	—	—	—	—	—	—	—	—	—
<i>Phalaris arundinacea</i> L.	—	—	—	—	—	—	—	—	—	—	—

† Plants of 15 gramineous species were exposed to either viruliferous *Rhopalosiphum padi* or *Sitobion avenae* carrying California MAV, PAV, or RPV; or to nonviruliferous aphids (CK). Each treatment was replicated three times.

‡ Plants from 8 of 15 species were positive by ELISA at 30 d post infection (pi) for at least two BYDV types. Values indicate the number out of three replicates that tested positive. A (—) indicates all samples were ELISA negative.

§ With the exception of all *Digitaria sanguinalis* inoculations, and the RPV inoculation of *Festuca arizonica*, those still living of ELISA positives at 30 d were verified by subsequent aphid acquisition and transmission to California Red oat trap plants. Double minus signs (—) denote samples that died or senesced. The numerator is the number of BYDVs infections reacquired and transmitted to bait plants, and the denominator is the number of recoveries attempted from originally infected grass species.

¶ 180 d ELISA indicates the BYDVs detected in the original plants, at 180 d pi.

†† Samples negative by ELISA (—) at 30 d pi were not included in the recovery test.

Table 3. Enzyme-linked immunosorbent assay (ELISA) detection of Barley Yellow Dwarf Viruses (BYDVs) in irrigated pasture grasses in the northern San Joaquin Valley of California.†

Species	N‡	RPV	MAV	PAV	P + R§
					no.
<i>Leptochloa uninervia</i> (Presl.) Hitchc. & Chase	8	0	0	2	0
<i>L. fascicularis</i> (Lam.) A. Gray.	8	0	0	0	0
<i>Paspalum dilatatum</i> Poir.	12	0	0	10	0
<i>Digitaria ischaemum</i> (Schreber) Schreb. ex Muhlenberg	4	0	0	2	1
<i>Lolium multiflorum</i> Lam.	8	0	0	3	0
<i>Echinochloa crus-galli</i> (L.) Beauv.	8	0	1	0	0
<i>Phalaris paradoxa</i> L.	8	0	0	3	0
<i>Eriochloa contracta</i> Hitchc.	8	0	0	0	0

† ELISA samples were considered positive if the A_{405} of the sample mean was greater than the uninfected control mean plus four times the standard deviation of the uninfected mean, and were also greater than the mean of any heterologous, cross-reacting antisera and included MAV, PAV, and RPV antisera.

‡ N is the number of samples tested; other numbers are the total positives for each BYDV.

§ P + R is a mixed infection of PAV and RPV.

pressure was dramatically revealed here by the difference in proportion of species infected in the two study years. In 1987, when the inoculum was natural, only 21% of the grass species tested positive. In contrast, when inoculum was supplemented in the plots in 1988, 76% of the species tested positive, with more than half of these being infected by two or more BYDV types. As such, surveys of wild hosts infected by natural inoculum must be interpreted carefully. These data were supported in part by controlled green-

house transmission and recovery experiments, where plants from approximately 6 of the 14 species tested were able to serve as inoculum sources for BYDV aphid transmission, and tested positive by ELISA at 6 mo postinfection. Such a lengthy infection period suggests that, under favorable conditions such as summer irrigation, they could serve as long-term reservoirs of BYDVs.

Shulke et al. (1987) reported two types of resistance to BYDVs in species of *Agropyron*. The first of these appears to be an inability to support vector feeding as observed on *Ag. smithii*. The second is observed as the ability of the plant to resist detectable virus replication while supporting viruliferous aphids, as observed with *Ag. intermedium*. Three species from this study; *Brachypodium sylvaticum*, *Deschampsia flexuosa*, and *Festuca dolichophylla*; were not observed to support any aphid populations and tested negative by ELISA in both years of the study. All species of *Leymus* and *Elymus* (excluding those species synonymized from the genus *Agropyron*) exhibited resistance to BYDVs even though vector aphid species were seen to feed on them. These results suggest that both types of resistance observed by Shulke et al. (1987) appeared to be present in the grassy weed species screened in this study.

The resistance observed in *Elymus* and *Leymus* in this study has been previously reported by other researchers (Sharma et al., 1984; Edwards et al., 1988) indicating that species from these genera may be sources of durable resistance to BYDVs. In fact, *Elymus mollis* already has been utilized in hybrid crosses

with barley as a source of tolerance to BYDVs (Schooler, 1980; Schooler and Franckowiak, 1981). Interestingly, the resistance shown by *Elymus* and *Leymus* species in this study is to three BYDV types, not just to PAV types, as appears to be primarily the case with the *yd₂* gene in barley (Griesbach and Falk, 1988).

Other factors reported to influence the susceptibility of wild hosts to BYDV infection involved BYDV type specificity. Guy et al. (1987) have shown that BYDV type (i.e., PAVs and RPVs) frequency in wild hosts may be affected by the subfamily of the host. They reported that members of the subfamily Poacoideae (= Festucoideae) were predominantly infected with PAVs in nature (with the exception of *Poa pratensis* and *Dactylis glomerata*), while members of the Panicoideae and Arundinoideae were predominantly hosts to RPVs. The great majority of the species in the present study are of the Poacoideae and as previously mentioned, about half were able to support mixed infections. However, 15 species supported only single infections; of these, seven were PAVs, five were MAVs, and three were RPVs alone. Therefore, there was no apparent trend in BYDV type specificity in the Poacoideae under these test conditions.

The relative frequencies of BYDV types in summer annual and perennial grasses commonly found in irrigated pastures showed that PAV types were the most frequent, followed by MAV and RPV types. This distribution is similar to the distribution of BYDV types seen in commercial small grains in California (Griesbach et al., 1990). The relatively high percentage of RPV and mixed infections in these species make non-cultivated grasses a potential source of economically important BYDV infections for two reasons. First, the PAV-type specific resistance incorporated in small grains (for example, the *Yd₂* gene in barley) can be overcome by RPV types and mixed infections (Griesbach and Falk, 1988). Aphids transmitting RPVs or mixed types to plants at the seedling stage have great potential for causing economic damage even to resistant cultivars. Second, depending on the availability of water (either through rain or irrigation), these weed species could serve as seasonal bridging hosts for aphids after fall aphid flights, since potentially viruliferous aphids could then multiply on these grasses until the small grain crops emerge in November and December. Thus, grasses have the potential to serve as primary sources of inoculum in California, and can become a component in the epidemiology of economically important BYDV infections.

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