Barley Yellow Dwarf Virus Isolate-Specific Resistance in Spring Oats Reduced Virus Accumulation and Aphid Transmission

Stewart M. Gray, Dawn Smith, and Naomi Altman

Research plant pathologist, USDA, ARS, and associate professor, Department of Plant Pathology; research technician, Department of Plant Pathology; and assistant professor, Department of Plant Breeding and Biometry, Cornell University, Ithaca, NY 14853. Send all correspondence to the first author.
Accepted for publication 15 February 1993.

ABSTRACT

Gray, S. M., Smith, D., and Altman, N. 1993. Barley yellow dwarf virus isolate-specific resistance in spring oats reduced virus accumulation and aphid transmission. Phytopathology 83:716-720.

Resistance to barley yellow dwarf virus in a spring oat genotype was manifested as a reduction in accumulation of viral antigen in whole plants. The resistance was quantified for five isolates of BYDV from New York (MAV, PAV, SGV, RPV, and RMV) and found to be BYDV isolate specific. Similar levels of resistance were quantified for MAV, PAV, and SGV in which the reduction in viral antigen ranged from 58–63 percent, relative to levels in a susceptible genotype. RMV antigen was reduced up to 82 percent, but no resistance was expressed against the RPV isolate. Reduced viral antigen was correlated with reduced levels of transmission of MAV, PAV, SGV, and RMV, but not RPV. Further reductions in transmission efficiency were possible by limiting the acquisition access period. Resistance to circulative, nonpropagative, aphid-borne viruses manifested as a reduction in virus antigen may reduce the spread of disease among plants, especially if coupled with aphid resistance manifested as a feeding deterrent.

The barley yellow dwarf luteoviruses (BYDV) are responsible for serious economic loss in all major cereal crops worldwide. Despite intensive efforts during recent decades to identify high levels of resistance (3), only limited success has been achieved. In recent years, varying levels of resistance to BYDV, manifested as a reduction in viral antigen or viral RNA accumulation, have been reported for wheat, barley, and oat (2,10,11,18,21). The mechanisms of resistance are only beginning to be understood (10), and the resistance may be expressed at different levels within the same genotype, depending on the isolate of BYDV infecting the plant (2,9,18). It was suggested that a reduced virus concentration may translate to reduced aphid transmission efficiency and reduced virus spread (8,18). This correlation is well documented for nonpersistent viruses (5), but has received only limited attention for persistent viruses (1). Virus concentration can affect acquisition efficiency for some virus isolate-aphid vector combinations, but additional factors, such as length of feeding time or virus distribution in plants, may have more of an effect on overall transmission efficiency (6,14).

We described a resistance in a spring oat genotype that was manifested as a reduction in the accumulation of viral antigen. The resistance was examined in relation to its effectiveness against five BYDV isolates from New York. In addition, we examined the influence reduced viral antigen had on aphid transmission efficiency.

MATERIALS AND METHODS

Virus isolates, aphid vectors, and host genotypes. The BYDV isolates used in these studies included the previously characterized New York (NY) BYDV isolates referred to as PAV, MAV, RPV, RMV, and SGV (15,17). All isolates were maintained in 'Coast Black' oats (*Avena byzantina* K. Koch) as described by Rochow (15).

The aphids used in all experiments were clonally propagated from aphids originally collected and described by Rochow using his methods and rearing conditions (15). In all the studies, PAV and RPV were transmitted by *Rhopalosiphum padi*, MAV by *Sitobion avenae*, RMV by *R. maidis*, and SGV by *Schizaphis graminum*.

Plant genotypes included a winter oat cultivar, Coast Black, which is susceptible to all the NY isolates of BYDV, and a spring oat cultivar, Ogle, found to possess field resistance to PAV in New York (4). In addition, a spring oat breeding accession, IL86-5262, developed at the University of Illinois and kindly provided by Charles Brown, was included. IL86-5262 was field tested at Cornell University in 1987 and 1988 and found to possess high levels of field resistance to PAV (S. M. Gray, *unpublished*).

Virus antigen accumulation studies. Virus antigen measured by enzyme-linked immunosorbent assay (ELISA) and expressed as absorbance values (A_{405nm}) was quantified in plants 1–6 wk after inoculation. Ten-day-old seedlings of Coast Black, Ogle, and IL86-5262 were inoculated with the various isolates of BYDV by the appropriate aphid vector. Viruliferous aphids (10 per plant) were given a 96-h inoculation access period on the seedlings in a growth chamber maintained at 21 C. Aphids were killed by fumigation with DDVP (*O,O*-dimethyl-*O*-[2,2-dichlorovinyl] phosphate) in a closed chamber, and test plants were placed in a greenhouse. Six plants of each genotype were inoculated each week for 6 wk. Subjective evaluation of each plant for BYDV symptom expression was performed weekly by comparing infected plants to uninoculated plants grown under similar conditions. Leaf discoloration and overall plant height were evaluated. At the end of the 6-wk period, all plants were harvested by removing the aerial portions of the plants (i.e., 36 plants of each genotype; six plants from each week, 1–6 wk postinoculation). Sap was extracted from leaves and small stems of individual plants using a rolling leaf press. A 250-μl aliquot of sap from each sample was diluted 1:5 with phosphate-buffered saline (PBS), and 200 μl was loaded into duplicate wells of a microtiter plate previously coated with immunoglobulin (2 mg/ml, 2 h at 37 C) prepared against homologous purified virions. Double antibody sandwich ELISA (DAS-ELISA) was conducted as previously described (6). The production and specificity of the antisera to the NY-PAV, NY-MAV, and NY-RPV isolates have been described elsewhere (16). Antisera to the NY-RMV and NY-SGV isolates were produced in Richard Lister's laboratory (20). In our hands, the antisera to NY-RMV or NY-SGV only react with the homologous antigen in DAS-ELISA. To allow direct comparisons of absorbance values of unknown samples among plates, a twofold dilution series of purified virus diluted in healthy sap and rep-

resenting the linear portion of a standard curve was included on each plate. The absorbance values of the six standards plus a healthy sap control were monitored during the substrate reaction, and the entire plate was read when the standards reached a similar predetermined pattern of absorbance values ranging from $A_{405nm} = 1.5$ to $A_{405nm} = 0.05$ for the highest and lowest dilution, respectively. Absorbance values of unknown samples fell within the range of the standards a majority of the time.

Absorbance data (= viral antigen titer) were analyzed with analysis of variance (ANOVA) after a log transformation of the data. All analyses were done with the ANOVA or ONEWAY programs of Minitab (12). The relationship between weekly viral antigen titer and genotype was examined for each virus isolate individually using a completely random design. Genotype, week, and the genotype-by-week interaction were all tested against the error sum of squares. ANOVA was also used to compare 6-wk mean viral antigen titers between genotypes, and pairwise differences were calculated using Tukey's test with an error rate of $\alpha = 0.05$ (13).

Virus transmission studies. Five seedlings of Coast Black and IL86-5262 were inoculated with each of the five BYDV isolates as above and allowed to grow in the greenhouse for 3 wk. Twenty aphids (fourth instars for *R. padi* and *S. avenae*, first and second instars for *R. maidis* and *S. graminum*) were caged on the youngest fully expanded leaf (fourth or fifth) of the main tiller of each plant and allowed a 24-h acquisition access period (AAP). Single aphids were then transferred to individual, healthy oat seedlings (Coast Black) and allowed a 48 to 72-h inoculation access period. Aphids were killed by fumigation with DDVP in a closed chamber, and test plants were placed in a greenhouse and observed for symptom expression for 4–5 wk. Transmission efficiency was calculated as the proportion of 20 aphids transmitting virus from each source leaf. A mean transmission efficiency was calculated from the five source leaves. The entire experiment was conducted five times; therefore, transmission efficiency for each isolate/aphid combination was calculated using 500 aphids ($20 \times 5 \times 5$).

To determine the effect of the length of AAP on the transmission efficiency of BYDV from the resistant and susceptible genotypes, experiments similar to those described above were performed with the following changes. The transmission of RMV by *R. maidis* was tested using a 2 and a 6-h AAP; transmission of MAV by *S. avenae* was tested using a 6-h AAP; and transmission of RPV by *R. padi* was tested using a 2-h AAP. Individual experiments to determine the transmission efficiency from five individual source leaves of each genotype (20 aphids/source) were conducted four times.

To estimate the amount of virus antigen in each source leaf used in all the transmission experiments, the section of leaf enclosed by the cage was excised immediately after transfer of the aphids to indicator plants, and virus antigen content was immediately quantified by DAS ELISA as described above.

Two types of data were analyzed with ANOVA: the percentage of aphids that successfully transmitted the virus from each plant genotype; and the viral antigen titer in source leaves. All analyses were done with the GLM program of Minitab (12). A log transformation was used to transform the viral antigen titer data before analysis and the arcsin-square root transformation was used to transform the binomial transmission data before analysis. Untransformed data are presented in the tables and figures. The relationship between plant genotype and transmission, and between plant genotype and viral antigen titer, was examined for each virus isolate individually using a randomized complete block design. Each transmission experiment using five source leaves was treated as a replication. Accordingly, genotype was tested against the genotype by experiment sums of squares. The model was run both with and without absorbance values as a covariate to determine whether the effect of cultivar on transmission depended on viral antigen titer. The experiments using different AAP's were analyzed independently, and no attempt was made to include AAP as a variable in the ANOVA.

TABLE 1. Relative virus symptom expression[a] in three oat genotypes caused by five New York isolates of barley yellow dwarf viruses

Virus isolate	Oat genotype	Symptom type[b]
PAV	Coast Black	Y S
	Ogle	y S
	IL86-5262	NS[c]
MAV	Coast Black	Y S
	Ogle	y S
	IL86-5262	NS
SGV	Coast Black	y S
	Ogle	s
	IL86-5262	NS
RPV	Coast Black	Y S
	Ogle	y s[d]
	IL86-5262	NS
RMV	Coast Black	y s
	Ogle	s
	IL86-5262	NS

[a] Relative symptom intensity was assessed, on plants grown in a greenhouse, weekly from 1–6 wk following inoculation.
[b] Y = yellowing and/or reddening of most leaves on all plants; y = yellowing and/or reddening may occur on the first 1–3 leaves developing on an indicator plant 2–3 wk postinoculation. Symptoms never observed in new growth of plants >3 wk postinoculation; S = severe stunting; s = slight stunting; NS = no symptoms.
[c] 2 of 36 plants showed yellowing of 1–2 leaves.
[d] Yellow-red leaf discoloration was prominent on first one to two leaves, but new growth was asymptomatic.

RESULTS

Virus symptom expression. Symptom severity and type were BYDV isolate dependent in all genotypes (Table 1). Coast Black plants all exhibited classical BYDV reddening and stunting regardless of which BYDV isolate was infecting the plant. The severity of the symptoms was variable depending on the BYDV isolate; PAV, MAV, and RPV caused more severe symptoms than RMV or SGV. Symptom expression in Ogle was less severe than in Coast Black. PAV, MAV, and RPV all caused yellow-red leaf discoloration, but symptoms tended to ameliorate as the plants matured. Slight stunting was evident in all plants. Except for an occasional yellow leaf, all Ogle plants infected with RMV or SGV were symptomless. All IL86-5262 plants remained symptomless regardless of the infecting BYDV isolate, with the exception of one plant infected with PAV that exhibited slight yellowing 2–3 wk postinoculation.

Virus antigen accumulation. The pattern of virus antigen accumulation in plants over the 6 wk was variable within and among cultivars and BYDV isolates (Fig. 1). Analyses to determine differences in viral antigen titer utilized all data points, but compared mean antigen levels over the 6-wk period. Ogle and IL86-5262 both possess resistance to four of five BYDV isolates that is manifested as a reduction in the amount of viral antigen accumulating in leaf tissue; however, the level of resistance varies between plant genotype and among BYDV isolates. The reduction in relative levels of antigen accumulating in resistant versus susceptible genotypes over the 6-wk experiment were similar for PAV, MAV, and SGV. Relative to levels in susceptible Coast Black plants (set at 100 percent), mean levels of MAV antigen were reduced to 64 and 39% in Ogle and IL86-5262, respectively; PAV antigen was reduced to 57 and 35%, in Ogle and IL86-5262, respectively; and SGV antigen was reduced to 50 and 42% in Ogle and IL86-5262, respectively (Fig. 1). There was no significant difference ($P = 0.744$) in mean levels of RPV antigen accumulating in leaf tissue of the three genotypes. Levels of RMV antigen were reduced to 22 and 20% in Ogle and I186-5262, respectively, relative to levels in Coast Black (100 percent).

Pairwise comparisons of mean viral antigen titer between genotypes indicated antigen levels were significantly lower ($P = 0.05$) in both Ogle and IL86-5262 plants than in the susceptible Coast

Black plants for MAV, PAV, SGV, and RMV. Differences in viral antigen titer between Ogle and IL86-5262 were significant ($P = 0.05$) only for MAV and PAV (Fig. 1).

Our experience indicates that IL86-5262 was more difficult to inoculate with RMV by *R. maidis* than Ogle or Coast Black. The percentage of IL86-5262 plants inoculated with RMV by *R. maidis* and having an ELISA value above healthy background was 27% compared with 55 and 88% infection of Ogle and Coast Black, respectively. The percent infection of all genotypes with the other BYDV isolate-vector combinations was 100 percent. Inoculation of the three genotypes with RMV using *R. maidis* was repeated using 15–20 viruliferous aphids per plant. Infection levels were 96, 96, and 88% for Coast Black, Ogle, and IL86-5262, respectively. Plants from the second experiment were used to determine the accumulation of RMV antigen in the three genotypes.

Virus transmission. Virus source tissue was chosen by leaf position and time after inoculation to maximize differences in viral antigen (on the basis of ELISA) between resistant IL86-5262 and susceptible Coast Black tissue. Generally, the youngest fully expanded leaf was used on plants 3 wk postinoculation. In all experiments there was significantly less viral antigen ($P < 0.05$) in source tissue from IL86-5262 than Coast Black plants (Table 2). Mean viral antigen titer was reduced by 67, 82, 65, 45, and 89 percent for PAV, MAV, SGV, RPV, and RMV, respectively, in the resistant IL86-5262 relative to susceptible Coast Black tissue. The differences between mean viral antigen titers in IL86-5262 and Coast Black plants were consistent in all five replicates of experiments using the five virus isolates (*data not shown*).

Mean transmission efficiency was consistently lower from the resistant IL86-5262 tissue relative to Coast Black for each of the virus isolate-aphid vector combinations (Table 2). Transmission efficiency of RPV by *R. padi* was significantly lower from IL86-5262 than Coast Black with ($P = 0.002$) or without ($P = 0.028$) viral antigen as a covariate indicating viral antigen titer in the source tissue was not responsible for the difference in transmission efficiency. Transmission efficiencies of MAV by *S. avenae* and RMV by *R. maidis* were significantly lower from the IL86-5262 tissue when transmission data were analyzed independent of viral antigen titer (MAV, $P = 0.048$; RMV, $P = 0.004$). When viral antigen titer was used as a covariate in the analysis, differences in transmission efficiency from IL86-5262 and Coast Black virus sources were not significantly different (MAV, $P = 0.322$; RMV $P = 0.187$), indicating that viral antigen titer did contribute sig-

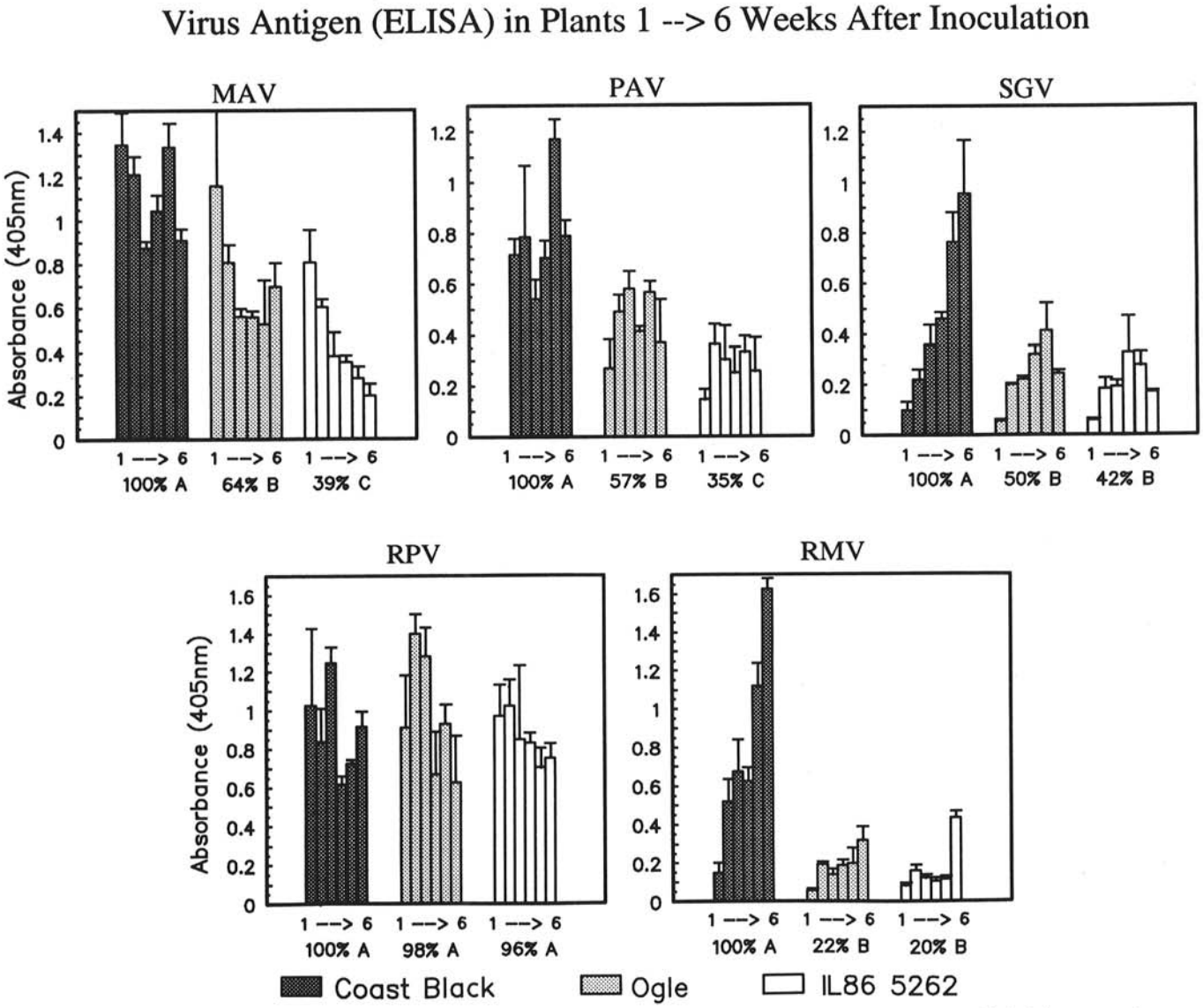

Fig. 1. The temporal pattern of accumulation of barley yellow dwarf virus (BYDV) antigen, as determined by enzyme-linked immunosorbent assay, in a susceptible oat genotype, Coast Black, and two oat genotypes possessing isolate-specific resistance to BYDV, Ogle and IL86-5262. Mean levels of antigen ($n = 3$–6) accumulating in the aerial portions of plants 1–6 wk postinoculation are indicated for five New York BYDV isolates. Bars from left to right (in each six-bar group) represent wk 1–6, respectively. Percentages given below each six-bar group indicate the 6-wk mean level of virus antigen relative to 6-wk mean antigen levels in the susceptible Coast Black genotype. Percentages followed by the same letter are not significantly different ($P = 0.05$) in pairwise comparisons of 6-wk mean levels of antigen.

nificantly to the differences in transmission efficiency. Differences in transmission efficiency of PAV by *R. padi* or SGV by *S. graminum* from IL86-5262 or Coast Black were not significant (PAV, $P=0.177$) or barely significant (SGV, $P=0.07$) when transmission data were analyzed independent of viral antigen titer. If viral antigen titer was used in the analysis, the levels of significance were $P = 0.997$ and $P = 0.485$ for PAV and SGV, respectively. This relatively large decrease in levels of significance for PAV and SGV transmission efficiencies when viral antigen titer was used in the analyses suggests that in addition to other unknown factors, the reduction in virus titer may have had a significant effect on the ability of aphids to acquire virus from IL86-5262 plants.

Reducing the length of AAP reduced the transmission efficiency of the three BYDV isolate-aphid vector combinations examined (Table 3). The transmission efficiency of RMV by *R. maidis* was 6.8 and 20.0% when given a 6-h AAP and 0 and 2.5% when given a 2-h AAP from IL86-5262 and Coast Black, respectively. Due to the low mean transmission rate and large numbers of aphids not transmitting virus, no further analysis was done on data resulting from the 2-h AAP experiment. In contrast to the transmission study on RMV using a 24-h AAP, the difference in transmission efficiency of RMV from either source using a 6-h AAP was not significantly different, although transmission efficiency may have been influenced by viral antigen titer. The transmission efficiencies of MAV by *S. avenae* were 38.6 and 50% when given a 6-hr AAP on IL86-5262 and Coast Black, respectively (Table 3). Differences in transmission efficiencies between the two sources were not significantly different (MAV, $P = 0.084$), and viral antigen titer did not significantly influence transmission efficiency. The transmission efficiency of RPV by *R. padi*, given a 2-hr AAP, was 20.5 and 23.2% from IL86-5262 and Coast Black, respectively. The difference was not significant ($P = 0.250$), and viral antigen did not significantly influence transmission efficiency.

The viral antigen titer differences between IL86-5262 and Coast Black for the MAV, RPV, and RMV were significant and similar to those described previously (Table 3).

TABLE 2. Comparison of barley yellow dwarf viral antigen titer (measured by ELISA) in leaf tissue of two oat genotypes and the transmission efficiency of aphid vectors acquiring virus from the two source tissues

Virus isolate[a]	Oat genotype[b]	Viral antigen titer[c] (A_{405})	Transmission efficiency[d]
PAV	Coast Black	0.672 ± 0.104	84 ± 4.8
	IL86-5262	0.223 ± 0.042	76 ± 6.4
		$P = 0.010$	$P = 0.177$ (0.997)
MAV	Coast Black	0.544 ± 0.033	81 ± 2.6
	IL86-5262	0.099 ± 0.012	68 ± 2.9
		$P < 0.001$	$P = 0.048$ (0.332)
SGV	Coast Black	0.530 ± 0.138	59 ± 9.3
	IL86-5262	0.183 ± 0.031	46 ± 12.1
		$P = 0.012$	$P = 0.070$ (0.485)
RPV	Coast Black	0.378 ± 0.049	63 ± 8.0
	IL86-5262	0.206 ± 0.033	52 ± 7.8
		$P = 0.005$	$P = 0.002$ (0.028)
RMV	Coast Black	0.350 ± 0.083	69 ± 6.8
	IL86-5262	0.040 ± 0.006	38 ± 4.8
		$P < 0.001$	$P = 0.004$ (0.187)

[a] Barley yellow dwarf virus (BYDV) isolates from New York (NY) and transmitted by their efficient aphid vector; RPV – *Rhopalosiphum padi*, RMV – *R. maidis*, PAV – *R. padi*, MAV – *Sitobion avenae*, and SGV – *Schizaphis graminum*.

[b] Plants were inoculated 3–4 wk before use as a source, and the youngest fully expanded leaf was used (fourth or fifth leaf). Coast Black plants are considered to be susceptible to all five NY-BYDV isolates. IL86-5262 plants possess varying levels of resistance to the five NY-BYDV isolates expressed as a reduction in viral antigen titer.

[c] Values are the mean ± standard error of mean absorbance data (A_{405nm}) read directly from ELISA plates (two wells per sample). Five plants were used for each experiment, and each experiment was replicated five times ($n = 25$). *P* value indicates the significance level of the difference between the two values.

[d] Aphids were allowed a 24-h acquisition access period before being transferred to Coast Black oat seedlings (one aphid per seedling) for a 5–7 day inoculation access period. The transmission efficiency represents the mean percentage ± standard error ($n = 500$) of infected indicator plants for five experiments repeated over time and using five source plants (leaves) for each experiment. Twenty indicator plants were used to determine the transmission efficiency from each source leaf. *P* values indicate the signifiance level of the difference between the transmission efficiencies from Coast Black oats and oat breeding line IL86-5262. The *P* values in parentheses were calculated with viral antigen titer data as a covariate in the analysis.

DISCUSSION

Resistance or tolerance to BYDV in small grains is generally assessed on the basis of symptoms induced by one isolate (4,7, 10,11). Rarely are multiple isolates used to assess resistance (2,9,18,21). Studies of this nature have shown a correlation between degree of resistance (measured by yield parameters or virus titer) and symptom severity (7,10), although exceptions do exist (18). Our findings generally agree with previous studies that a susceptible cultivar, e.g., Coast Black, will show symptoms when infected with any of the NY-BYDV isolates, whereas genotypes with various levels of resistance to BYDV, e.g., Ogle or IL86-5262, will show reduced or no symptoms. In addition, our work has shown that symptom appearance and/or severity may not reflect the level of resistance to virus accumulation in the plant and that virus resistance is BYDV isolate specific. None of the NY-BYDV isolates produced consistent symptoms in IL86-5262, yet clearly resistance levels, with regard to viral antigen titer, range from very high, in the case of RMV, to completely susceptible, in the case of RPV. Symptom expression in Ogle is also not reflective of viral antigen titer. RPV infection induces milder symptoms than PAV or MAV, yet the resistance to virus accumulation in whole plants was not detected for RPV.

Transmission efficiency from the resistant IL86-5262 plants was reduced for all five NY-BYDV isolates, but viral antigen titer did not contribute significantly to the reduction in transmission of RPV. Gray et al (6) also found that transmission of NY-RPV by *R. padi* was not influenced by viral antigen titer. A commonality of both studies was the inability to examine virus sources that varied widely with respect to viral antigen titer. It is likely that the transmission efficiency of RPV by *R. padi* can be influenced by virus concentrations but that the virus concentrations necessary to show this have not been used.

The reduction in viral antigen titer in IL86-5262 did contribute to the significant reduction in transmission efficiency of MAV, PAV, SGV, and RMV; however, the magnitude of the difference in viral antigen titer between IL86-5262 and Coast Black tissue was not reflective of the difference in transmission efficiency. In general, transmission efficiency was high for all aphid-virus combinations regardless of virus source or viral antigen titer. The most striking example was the ability of 38 percent of *R. maidis* individuals to transmit RMV from IL86-5262 tissues that had a mean viral antigen titer not significantly above healthy background as determined by ELISA.

It was not determined if fewer aphids were acquiring the MAV, PAV, SGV, and RMV from the IL86-5262 tissue and reducing the probability of transmission or if all aphids were acquiring less virus, which reduces their ability to transmit. The latter explanation is more probable on the basis of the findings of Barker and Harrison (1) and van den Heuval et al (19), in which aphids were found to acquire less virus when fed either on plants with a lower virus titer or an artificial diet containing less virus. The acquisition of less virus by most aphids rather than the acquisition of virus by fewer aphids is somewhat supported by the fact that reducing the AAP reduces the transmission efficiency of aphids regardless of the source (Table 3). If the reduction in transmission was due to fewer aphids acquiring virus, there should be fewer

TABLE 3. Effect of acquisition access period on aphid transmission efficiency of selected barley yellow dwarf virus (BYDV) isolates from two oat genotypes

Virus isolate/ aphid vector[a]	Oat genotype	Length of ASP[b] (h)	Virus antigen titer[c] (A_{405})	Transmission efficiency[d]
MAV/ *Sitobion avenae*	IL86-5262	6	0.150 ± 0.087	38.6% ± 5.9
	Coast Black		0.713 ± 0.087	50.0% ± 6.1
			$P = 0.013$	$P = 0.084$ (0.121)
RPV/ *Rhopalosiphum padi*	IL86-5262	2	0.248 ± 0.041	20.5% ± 5.5
	Coast Black		0.478 ± 0.060	23.2% ± 6.1
			$P = 0.012$	$P = 0.250$ (0.293)
RMV/ *R. maidis*	IL86-5262	6	0.049 ± 0.026	6.8% ± 4.7
	Coast Black		0.428 ± 0.107	20.0% ± 6.5
			$P = 0.007$	$P = 0.126$ (0.653)

[a] BYDV isolates and aphid clones characterized and maintained from New York.
[b] Acquisition access period.
[c] Values are the mean ± standard error of mean absorbance data (A_{405nm}) read directly from ELISA plates (two wells per sample). Five plants were used for each experiment, and each experiment was replicated four times ($n = 20$). P value indicates the significance level of the difference between the two values.
[d] Following the acquisition access period, aphids were transferred to BYDV-susceptible Coast Black indicator seedlings (one aphid per seedling) for a 5 to 7 day inoculation access period. The transmission efficiency represents the mean percentage ± standard error ($n = 400$) of infected indicator plants for four experiments repeated over time and using five source plants (leaves) for each experiment. Twenty indicator plants were used to determine the transmission efficiency from each source leaf. P values indicate the significance level of the difference between the transmission efficiencies from Coast Black oats and oat breeding line IL86-5262. The P values in parentheses were calculated with viral antigen titer data as a covariate in the analysis.

aphids transmitting from the resistant source relative to the susceptible source regardless of the AAP. Reducing the AAP appears to have reduced the amount of virus acquired from either source to levels below a threshold necessary for transmission. The reduction in viral antigen titer effectively increases the time necessary for aphids to acquire enough virus for transmission. This hypothesis is supported by the finding of Gray et al (6), who showed that the effect of virus titer was only important at short AAP and that, given enough time, an aphid could acquire enough virus to become viruliferous regardless of the titer.

It is important that programs screening for BYDV resistance recognize the limitations of using symptom severity as a sole selection criteria and the probability that resistance to one BYDV isolate may not indicate resistance to all isolates of BYDV. Screening should be done against all BYDV isolates common to the particular geographic region, and selection should be made not only on yield considerations, but also on increasing resistance to the virus to minimize the potential for the crop to serve as a symptomless reservoir for BYDV. The results of this study suggest that virus antigen concentration may be a useful screening technique to identify and distinguish virus resistance from tolerance. As previously discussed, reduced viral antigen titer correlates with reduced symptoms and increased yield in many instances. Additionally, this study and others (1,6,19) indicate that a reduction in viral antigen titer can significantly reduce the transmission efficiency of certain luteovirus isolates by their respective aphid vectors. Since the effect of titer on transmission efficiency is dependent on the length of AAP, it would be beneficial to combine this type of resistance with one that limits the length of time an aphid will feed on a plant (14).

LITERATURE CITED

1. Barker, H., and Harrison, B. D. 1986. Restricted distribution of potato leafroll virus antigen in resistant potato genotypes and its effect on transmission of the virus by aphids. Ann. Appl. Biol. 109:595-604.
2. Brettel, R. I. S., Banks, P. M., Cauderon, Y., Chen, X., Cheng, Z. M., Larkin, P. J., and Waterhouse, P. M. 1988. A single wheatgrass chromosome reduces the concentration of barley yellow dwarf virus in wheat. Ann. Appl. Biol. 113:599-603.
3. Cooper, J. I., and Jones, A. T. 1983. Responses of plants to viruses: Proposals for the use of terms. Phytopathology 73:127-128.
4. Cooper, D. C., and Sorrells, M. E. 1983. Field reaction of eight oat lines to the PAV isolate of barley yellow dwarf virus. Cereal Res. Commun. 11:263-268.
5. Gray, S. M., Moyer, J. W., Kennedy, G. G., and Campbell, C. L. 1986. Virus-suppression and aphid resistance effects on spatial and temporal spread of watermelon mosaic virus 2. Phytopathology 76:1254-1259.
6. Gray, S. M., Power, A. G., Smith, D. M., Seaman, A. J., and Altman, N. S. 1991. Aphid transmission of barley yellow dwarf virus: Acquisition access periods and virus concentration requirements. Phytopathology 81:539-545.
7. Habekuss, A. 1988. Beziehungen zwischen Symptomausprägung und Viruskonzentration im Wirt-Virus-System Wintergerste-Gerstengelbverzwergungs-Virus. Arch. Phytopathol. Pflanzenschutz 24:453-458.
8. Jedlinski, H., Rochow, W. F., and Brown, C. M. 1977. Tolerance to barley yellow dwarf virus in oats. Phytopathology 67:1408-1411.
9. Jones, A. T., and Catheral, P. L. 1970. The effect of different isolates on the expression of tolerance to barley yellow dwarf virus in barley. Ann. Appl. Biol. 65:147-152.
10. Larkin, P. J., Young, M. J., Gerlach, W. L., Waterhouse, P. M. 1991. The Yd2 resistance to barley yellow dwarf virus is effective in barley plants but not in their leaf protoplasts. Ann. Appl. Biol. 118:115-125.
11. Lorens, G. F., Falk, B. W., and Qualset, C. O. 1989. Inheritance of resistance to barley yellow dwarf virus detected by Northern blot analysis. Crop Sci. 29:1076-1081.
12. Minitab Inc. 1991. Minitab Reference Manual, Release 8. Minitab Inc., State College, PA.
13. Neter, J., Wasserman, W., and Kutner, M. H. 1990. Applied Linear Statistical Models. 3rd Edition. Irwin Publishers, Homewood, IL.
14. Power, A. G., Seaman, A. J., and Gray, S. M. 1991. Aphid transmission of barley yellow dwarf virus: Inoculation access periods and epidemiological implications. Phytopathology 81:545-548.
15. Rochow, W. F. 1969. Biological properties of four isolates of barley yellow dwarf virus. Phytopathology 59:1580-1589.
16. Rochow, W. F., and Carmichael, L. E. 1979. Specificity among barley yellow dwarf viruses in enzyme immunosorbent assays. Virology 95:415-420.
17. Rochow, W. F., and Muller, I. 1971. A fifth variant of barley yellow dwarf virus in New York. Plant Dis. Rep. 55:874-877.
18. Skaria, M., Lister, R. M., Foster, J. E., and Shaner, G. 1985. Virus content as an index of symptomatic resistance to barley yellow dwarf virus in cereals. Phytopathology 75:212-216.
19. Van den Heuvel, J. F. J. M., Boerma, T. M., and Peters, D. 1991. Transmission of potato leafroll virus from plants and artificial diets by *Myzus persicae*. Phytopathology 81:150-154.
20. Webby, G., Lister, R. M., and Gray, S. M. 1989. Purification of the RMV and SGV isolates of barley yellow dwarf virus for antiserum production. (Abstr.) Phytopathology 79:1174.
21. Xin, Z. Y., Brettell, R. I. S., Cheng, Z. M., Waterhouse, P. M., Zppels, R., Banks, P. M., Zhou, G. H., Chen, X., and Larkin, P. J. 1988. Characterization of a potential source of barley yellow dwarf virus resistance for wheat. Genome 30:250-257.