Effects of Barley Yellow Dwarf Virus on Yield and Yield Components of Drilled Winter Wheat

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ABSTRACT

Hoffman, T. K., and Kolb, F. L. 1998. Effects of barley yellow dwarf virus on yield and yield components of drilled winter wheat. *Plant Dis.* 82:620-624.

Yield reduction in eight soft red winter wheat cultivars (*Triticum aestivum*) in response to barley yellow dwarf (BYDV) infection was evaluated in drilled plots. The experiment was conducted in 1993 and 1994 at the Crop Sciences Research and Education Center of the University of Illinois at Urbana-Champaign. Cultivars Caldwell, Cardinal, Clark, Howell, IL 87-2834, Tyler, and Pioneer brands 2548 and 2555 were selected for the study based on root system size, yield potential, and adaptation to local growing conditions. Plots were planted with a six-row drill to approximate conditions in growers' fields. A split-plot treatment design was used, with treatments as whole plots, and cultivars as subplots. The three treatments were BYDV-inoculated, natural BYDV infection, and a control (sprayed with Cygon to control naturally occurring aphids). Significant yield reductions in inoculated plots indicated the potential for severe yield loss due to BYDV infection under drilled conditions. The component of yield most severely affected by virus infection was number of kernels per spike. Kernel weight was affected but to a lesser extent than kernels per spike. Tiller number was generally not altered by infection but was positively correlated with yield in infected plots. Since kernels per spike and kernel weight were reduced by BYDV infection, it may be possible to select for tolerant genotypes by identifying lines in which these parameters are least affected by BYD disease pressure.

Barley yellow dwarf viruses (BYDV) are phloem-limited luteoviruses that infect members of the Poaceae family. Barley (*Hordeum vulgare* L.), wheat (*Triticum aestivum* L.), and oat (*Avena sativa* L.) are among the cultivated members of this family that are affected. The virus interferes with physiological processes within the plant which in turn cause the symptoms of chlorosis, stunting, and yield loss (17). Common effects of the virus on agronomic characteristics include reductions in yield, yield components, height, aboveground dry weight, and root growth (1,4,5,14).

Although major genes for resistance were found in barley soon after the discovery of BYDV, it was not until recently that major genes were reported in wheat. Tolerance exhibited by Anza and other wheat lines is conditioned by a partially effective gene, *Bdv1*, that has partially dominant gene action (3). Other genes for tolerance exist, but the variability in tolerance found in wheat is not as high as that found in barley and oat (25). Most of the tolerance in wheat appears to be quantitative in nature (7,27).

Cooper and Jones defined resistance as the ability of the host to reduce virus repli-

cation (10). Tolerance is defined as the ability of the host to exhibit few symptoms even in the presence of high virus titers. Studies on virus titer using enzyme-linked immunosorbent assay (ELISA) have indicated that genes for protection against BYDV in wheat generally condition tolerance rather than resistance (3).

Since high levels of resistance have not been found in wheat, tolerance may be an important mode of plant protection. Tolerance can play an important role in limiting yield loss and reduced grain quality due to disease (2).

The mechanisms of tolerance to BYDV in wheat are not well understood. A cultivar that appears to be tolerant in one environment may be less tolerant in another environment, thus complicating selection for tolerance. In characterizing tolerance to BYDV, it is important to consider the environmental conditions in which the cultivars are evaluated, including the level of infection (9).

Researchers have suggested that tolerance to BYDV in wheat should be characterized in terms of yield and components of yield (27). Yield of a tolerant cultivar would be reduced only slightly by infection. However, a very tolerant cultivar according to the definition above might also have low yield potential in general, making it unacceptable to the grower. Thus, it is important to look at absolute yields under BYDV infection, as well as relative yield reduction, when developing wheat cultivars for BYDV-prone areas.

Most research on the effects of BYDV on yield has been carried out in the greenhouse, in hill plots, or in single rows (1,4,7,12,23). The microenvironments under such conditions are different than the microenvironment in drilled wheat. It is important to know if the high yield losses demonstrated in the greenhouse and in hill plots are also exhibited under growing conditions more typical of grower's fields.

The purpose of this study was to evaluate the effects of BYDV infection on eight winter wheat cultivars tested in drilled plots. Percent grain yield reduction due to infection with BYDV was evaluated, but absolute grain yield was also an important criterion for evaluating the performance of the cultivars under BYDV infection.

MATERIALS AND METHODS

This study was conducted at the Crop Sciences Research and Education Center of the University of Illinois at Champaign-Urbana, during the 1993 and 1994 growing seasons. Cultivars included in the study were Caldwell, Cardinal, Clark, Howell, IL 87-2834, Tyler, and Pioneer brands 2548 and 2555. These cultivars were selected for the experiment based on adaptation to local conditions and root fresh-weight data obtained from a hydroponic study of root growth (21). Mian characterized Cardinal, Howell, 2555, and Tyler as large-rooted and Caldwell as small-rooted. Clark was intermediate in root fresh-weight. IL 87-2834 and 2548 were included as high-yielding, well-adapted cultivars. Clark (22) and Caldwell (24) are considered early maturing. Pioneer 2555 heads about the same time as Caldwell (15) and 2548 about 1 day later (16). Howell, Cardinal, IL 87-2834, and Tyler are midseason for maturity (18,19,26).

Plots were planted on 1 October 1992 and 5 October 1993. Kernel weight of each seed lot was determined prior to planting so that all cultivars were planted at the same rate (342 kernels m⁻²). Plots were 2.43 m long and consisted of six rows spaced 17.8 cm apart. Prior to planting, nitrogen in the form of ammonium nitrate at 44.8 kg ha⁻¹ was applied to experimental fields. An additional 44.8 kg ha⁻¹ was top-dressed in the spring of each year.

A split-plot design with four replications was used for the experiment. Whole plots were BYDV treatments, and the eight cultivars were the subplots. The three treatments were BYDV-inoculated, natural BYDV infection (no treatment applied),

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Accepted for publication 11 February 1998.

Publication no. D-1998-0319-02R
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and Cygon R400 (0,0-dimethyl S-[-N-(methylcarbamoyl) methyl] phosphorodithioate) sprayed as a control. The insecticide sprayed treatment was used to minimize any naturally occurring infection by viruliferous aphids. An Illinois strain of the virus, BYDV-PAV-IL, was used for the inoculated treatment. Buffer zones, one plot wide, were planted between whole plots to act as barriers against aphid movement and insecticide drift. When plants were at the two-leaf stage, the insecticide was applied to the control plots at a rate of 194 g a.i. ha⁻¹ in 278 liters of water. The same rate was applied in the spring when plants became photosynthetically active and again in mid-May to protect against late-season infection.

In the fall, after the control plots were sprayed, viruliferous oat-bird cherry aphids (*Rhopalosiphum padi*) carrying BYDV-PAV-IL were applied to plots designated to receive the virus treatment. An equal volume of corn meal was mixed with the aphids to aid in even distribution throughout the plot. The aphid-corn meal mixture was applied using a small plastic container with holes drilled in the lid. To ensure virus infection, aphids were applied to the inoculated plots several times. Applications were 1 to 2 weeks apart, depending on the availability of viruliferous aphids. An estimated 2.4 and 1.7 aphids per plant were applied in the first and second year, respectively. Based on previous studies, this technique ensured a very high level of infection (85 to 100% of the plants infected with BYDV) (13).

To control rust and other fungal diseases, all plots were sprayed with Punch (1-[[bis(4-fluorophenyl)methylsilyl]methyl]-1H-1,2,4-triazole) at Feekes GS 8 (20) using a rate of 91 g a.i. ha⁻¹ in 94.5 liters of water. A surfactant, Latron B-1956 (Rohm & Haas, Philadelphia, PA), was used at a rate of 0.037 liters ha⁻¹.

In 1993, wheat soilborne mosaic virus (WSBMV) symptoms developed in the field. Symptoms were most severe in the fourth replication, so it was excluded from the analysis. In the second year, plots in a low area of the field were damaged by standing water, so the first replication was excluded from the analysis. Thus, data analysis in each year was based on three replications.

Visual BYDV symptoms were rated based on the percentage of plants per plot exhibiting symptoms. Tiller counts were made on a 61-cm section of row in each plot. Yield data were obtained by harvesting the entire plot using a research combine. Analysis of variance and correlations were performed using SAS. Cultivar and treatment effects were considered fixed, and year and replication effects were considered random.

RESULTS AND DISCUSSION

Weather conditions in the 2 years of the study were quite different. The spring of

the first year was cool and wet; whereas the second year was warmer and dryer. In the first year, only 55 growing degree days (base 10°C) had accumulated by the end of April, and there were approximately 77 cm of rainfall from January to July, distributed evenly throughout the 6 months. In the second year, 88 growing degree days had accumulated by the end of April, with almost half of the 52 cm of rain from January to July falling in April. In general, both seasons were favorable for wheat production, and yields were not limited by disease. Thus, except for WSBMV in part of the field in 1993, yield loss due to BYDV was not confounded with yield loss due to other pathogens.

Plots were rated for symptom expression by estimating the percentage of plants exhibiting BYDV symptoms. Although enough aphids were applied to each plot for potential infection of all plants, visual symptom ratings as low as 17% were recorded for some of the inoculated plots (Table 1). An average of 90% of the plants in inoculated plots were found to be infected with BYDV by ELISA in experiments using the same inoculation technique at the same locations (13). Thus, visual ratings in the present study are likely

to have underestimated the number of infected plants per plot. It is likely that many of the plants not exhibiting visual symptoms were infected. It is not unusual for symptoms in BYDV-infected plants to be negligible (3).

A significant year by treatment interaction for symptom expression indicated that the environment influenced symptom expression. Symptom expression in inoculated plots was much higher in 1993. The cool, wet conditions that year may have been responsible for the higher level of symptom expression observed. More severe BYDV symptom expression is common in cooler environments (11). Since control plots and naturally infected plots did not exhibit many differences for symptom expression or for other parameters, no data are presented for the naturally infected plots, and all comparisons will be made between the inoculated and control plots.

Although symptom expression was negatively correlated with yield and positively correlated with yield reduction in 1994, symptoms were positively correlated with yield in 1993 (Table 2). These results demonstrate the unreliability of symptom expression for selecting higher yielding or

Table 1. Percentage of wheat plants expressing symptoms of barley yellow dwarf virus (BYDV) infection in drilled field plots

Cultivars	Symptom expression			
	1993		1994	
	Control	Inoc. ^a	Control	Inoc.
Caldwell	0	78	0	50
Cardinal	0	55	1	48
Clark	0	82	1	63
Howell	0	82	3	40
IL87-2834	0	85	0	17
2548	0	57	0	33
2555	0	82	2	50
Tyler	0	80	0	38

^a Inoculated in the fall with aphids carrying BYDV-PAV-IL.

Table 2. Correlations among selected characteristics measured on eight barley yellow dwarf virus infected wheat cultivars in 1993 (top value) and 1994 (bottom value)

	Yield	Yield reduction ^a	Number of tillers	Kernels per spike	Kernel weight	Harvest index
Symptoms	0.68*** ^b -0.56**	NS ^c 0.40*	0.44* -0.45*	NS NS	0.46* NS	NS NS
Yield	...	NS -0.68***	0.44* 0.39*	NS NS	0.68*** NS	NS NS
Yield reduction	...	...	NS NS	NS NS	NS NS	NS NS
Number of tillers	...	...	...	NS NS	NS -0.43*	NS NS
Kernels per spike	...	...	...	...	NS NS	0.57** NS
Kernel weight	...	...	...	...	...	0.55** 0.52**

^a Yield reduction in infected plots compared with control plots.

^b * = {probability > |r| under the hypothesis that Rho = 0} ≤ 0.05. ** = {probability > |r| under the hypothesis that Rho = 0} ≤ 0.01. *** = {probability > |r| under the hypothesis that Rho = 0} ≤ 0.001.

^c Not significant.

more tolerant (based on percent yield reduction) cultivars in some environments. A number of researchers have stated that chlorosis is an unreliable symptom for evaluation of BYDV tolerance in wheat (5,6). Our results confirm this and indicate that selection for reduced symptoms may in fact select lower yielding lines in some environments. Comeau suggested that in wheat, it is more important to make com-

parisons with check plants for characteristics such as tillering, height, grain fill, and biomass data (8).

A year by treatment interaction was observed for grain yield, suggesting that the environment contributes to the effect of the virus on grain yield. Grain yields of both control and inoculated treatments were consistently higher in 1994 than in 1993 (Fig. 1). Control plots had an average yield

of 6,014 kg ha⁻¹ in 1994, compared with 4,997 kg ha⁻¹ in 1993. Although grain yields were higher in 1994, percent yield reductions were also higher (Table 3). BYDV inoculation resulted in average yield reductions of 33% in 1994 and 25% in 1993. These results suggest that relative yield reductions may be greater in environments where yield potential is higher. The highest yield reduction was 36% for

Fig. 1. Effect of barley yellow dwarf virus on winter wheat. Grain yield in 1993 (A) and 1994 (B); number of kernels per spike in 1993 (C) and 1994 (D); thousand kernel weight in 1993 (E) and 1994 (F); harvest index in 1993 (G) and 1994 (H). Dark bars are controls and light bars are barley yellow dwarf virus infected plots. An asterisk indicates a difference between control and infected treatments at $P = 0.05$. Cultivars are Caldwell (Cal), Cardinal (Car), Clark (Cla), Howell (How), IL87-2834 (IL), 2548 (48), 2555 (55), and Tyler (Tyl).

Clark in 1994. This reduction represented a loss of 2,081 kg ha⁻¹. All cultivars tested exhibited significant yield reduction due to BYDV infection in at least 1 year of the study. Yield losses as high as 36% show the potential for severe yield loss due to BYDV infection in drilled plots. These results were artificially induced by fall infection and large numbers of aphids, but they illustrate the potential damage that is possible on drilled winter wheat when viruliferous aphid infestation is severe. Additional research will be required to determine yield loss under lower levels of infection.

Cultivars exhibiting the highest percent yield loss due to BYDV infection were not necessarily the ones exhibiting the lowest yields. Among the cultivars tested, high-yielding cultivars under control conditions were often higher yielding under inoculated conditions regardless of their level of tolerance (percent yield reduction).

Yield is the product of three components: number of spikes per unit area, number of kernels per spike, and kernel weight. These components were evaluated to determine which were most severely affected by BYDV infection. Both kernels per spike and kernel weight were reduced by infection (Fig. 1), but BYDV rarely caused a decrease in tillers per unit area (data not shown).

Reductions in number of kernels per spike ranged from 11 to 30%, while kernel weight reductions ranged from 3 to 19% (Table 3). For all cultivars across years, reductions in kernels per spike were greater than reductions in kernel weight or number of tillers. This indicated that the greatest proportion of yield loss consistently resulted from a reduction in the size of the spike.

Variability was observed among the eight cultivars for both number of kernels per spike and kernel weight under BYDV pressure. Based on the cultivars tested, maintaining kernels per spike and kernel weight under BYDV infection seems to be important for minimizing yield loss due to BYDV. Spike weight in durum wheat (*Triticum durum*) is considered a good indicator of BYDV tolerance (6). Correlation analysis within the inoculated treatment did not show a strong correlation

between kernels per spike and yield. There was, however, a strong correlation between kernel weight and yield in infected plots in 1993 (Table 2).

Although tiller numbers were generally not reduced in inoculated plots compared with control plots (Table 3), tiller number per unit area was correlated with yield in infected plots in both years of the study (Table 2). This suggests that although BYDV did not significantly reduce tiller number, those varieties that tillered more tended to be higher yielding under BYDV infection.

Infection with barley yellow dwarf virus reduced the harvest index of some cultivars although most were not reduced (Fig. 1). Significant differences in harvest index between control and inoculated plots occurred in two cultivars in 1993 and three cultivars in 1994. Large reductions in harvest index occur if virus infection has a greater effect on grain yield than on biomass. Thus, for most cultivars tested, the relative reduction in biomass was similar to the reduction in grain yield.

Yields in this study were severely reduced by artificially induced BYDV infection in drilled plots. Symptom expression did not appear to be a reliable variable for measuring tolerance to BYDV in the wheat cultivars tested. Although none of the cultivars exhibited a high level of tolerance to BYDV, analysis of yield components suggested possible selection schemes for increasing BYDV tolerance in wheat. Selection for higher spike weight in BYDV-infected population may be one way of selecting for tolerance to BYDV in wheat, confirming what has been suggested by others (6). Although tiller numbers were generally not reduced in this study, cultivars that had higher numbers of tillers were usually the ones that were higher yielding under BYDV infection. Thus, high tiller number may also be an important characteristic for wheat varieties grown in BYDV-prone environments.

ACKNOWLEDGMENTS

We thank L. L. Domier and G. R. Gregerson for maintaining the virus strain and for providing aphid vectors during both years of the experiment.

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Table 3. Percentage of change in yield and yield components due to barley yellow dwarf virus infection in eight wheat cultivars (compared with control)

Cultivar	1993				1994			
	Yield	Tillers	Kernels per spike	Kernel weight	Yield	Tillers	Kernels per spike	Kernel weight
Caldwell	-21	+2	-19*	-6	-35*	-4	-23*	-5
Cardinal	-7	-2	-27*	-12*	-33*	+6	-27*	-8
Clark	-22	+5	-17*	-11*	-36*	-12	-11	-4
Howell	-34*	-2	-30*	-13*	-35*	+4	-18	-16
IL 87-2834	-26*	+10	-22*	-12*	-29*	0	-17	-3
2548	-27*	-3	-30*	-14*	-35*	-12	-21*	-19
2555	-29*	+12	-23*	-6	-35*	-24	-23*	-9
Tyler	-24*	+11	-21*	-13*	-26*	+6	-23*	-6

* = significant difference ($P = 0.05$) between the control (sprayed with Cygon) and inoculated treatments based on Fisher's protected LSD.

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