Yield Loss in Two Spring Oat Cultivars due to *Puccinia coronata* f. sp. *avenae* in the Presence or Absence of Barley Yellow Dwarf Virus

S. M. Bissonnette, C. J. D'Arcy, and W. L. Pedersen

Former graduate research assistant, professor, and associate professor, respectively, Department of Plant Pathology, University of Illinois, Urbana 61081.

Current address of S. M. Bissonnette: Champaign Extension Center, University of Illinois, 1401 D Regency Drive East, Savoy 61874.

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ABSTRACT

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Individual studies were done to estimate yield loss due to *Puccinia coronata* f. sp. *avenae* (crown rust) in the presence or absence of barley yellow dwarf virus (BYDV-PAV-IL) for two spring oat cultivars at two locations. Crown rust disease severity was assessed several times and related to yield and yield components. Linear critical point regression models were developed with analysis of covariance. Yield loss for each percent increase in crown rust severity (modified Cobb scale A) was 56.7 kg/ha for cv. Noble and 46.0 kg/ha for cv. Ogle. Test weight decrease for each percent increase in crown rust severity was 1.2 kg/m^3 for Noble and 1.1 kg/m^3 for Ogle. Ogle exhibited tolerance to yield loss from crown rust. Yield loss, due to each percent increase in crown rust severity in BYDV-infected plots, was 19.2 kg/ha for Noble and 28.7 kg/ha for Ogle. Test weight decrease, for each percent increase in crown rust disease severity, was not different from zero ($P \leq 0.05$) for Noble and 0.7 kg/m^3 for Ogle. Noble exhibited tolerance to yield loss from crown rust in BYDV-infected plots. The effect of BYDV on yield and reduction in test weight due to crown rust was not additive.

Additional keywords: *Avena sativa*, crop loss, multiple pathogen loss modeling.

Previous studies have evaluated the interactions between viral and fungal diseases (9,14,20,21,24,25). The effect of two diseases on a particular host can be additive or interactive. Zadoks and Schein (27) concluded that when two diseases are additive, each disease contributes to crop loss independently, and the final crop loss is the sum of the losses contributed by each disease separately. Interaction occurs when crop loss due to two diseases significantly deviates above or below the sum of the losses that would have been caused by each disease separately.

The effect of virus infection on fungal diseases varies (17). Initial infection of one pathogen may inhibit infection of a subsequent pathogen. Increased resistance to tobacco mosaic virus, expressed by the formation of fewer lesions, is exhibited in pinto bean (*Phaseolus vulgaris* cv. Pinto) inoculated with bean rust (*Uromyces phaseoli*) (10). Latch and Potter (14) found that Lemtal Italian rye grass (*Lolium multiflorum*) and S.24 perennial ryegrass (*Lolium perenne*) infected with ryegrass mosaic virus (RMV) and subsequently inoculated with crown rust (*Puccinia coronata* Corda) developed 75% less rust than plants not inoculated with RMV.

Another possible interaction between viruses and fungi is increased susceptibility to fungal infection. Sugar beets (*Beta vulgaris*) infected with beet mild yellowing virus showed increased susceptibility to natural infection by *Alternaria* compared to sugar beets not infected by the virus (21). Goodman et al (11) reported that barley yellow dwarf virus (BYDV) infection increased carbohydrate levels in the leaves of cereal plants. Because rusts typically require high levels of carbohydrates, as determined by Mains (16), Potter (20) proposed that BYDV infection of cereal plants could lead to enhanced susceptibility to rust diseases. Potter (20), evaluating the effect of BYDV infection of various cereals on

subsequent infection by their respective leaf rusts, found that fewer crown rust (*Puccinia coronata* Corda f. sp. *avenae* Eriks.) pustules developed on the distal portion of oat leaves (cv. Mostyn, susceptible to crown rust) infected with BYDV than on similar plants not infected with the virus. However, the number of pustules on the proximal leaf portions did not differ. The latent period of crown rust was not affected by BYDV infection of oats. Also, the latent period of leaf rust (*P. recondita* f. sp. *tritici*) apparently was not affected by BYDV infection on wheat (*Triticum aestivum* cv. Highbury, slow rusting). So, although increased susceptibility to rust in BYDV-infected plants was proposed, Potter's (20) results did not support the hypothesis.

Infection by one pathogen also may have no effect on subsequent infection by another pathogen. Latch and Potter (14) found that Lemtal Italian and S.24 perennial ryegrass infected with BYDV did not significantly alter susceptibility to subsequent infection by crown rust (*P. coronata*).

Previous studies on oats investigated the interaction between BYDV and crown rust from a mechanistic viewpoint (20). An empirical approach to studying this phenomenon is needed to determine the impact of these diseases on yield and yield components in a cropping situation. Development of empirical crop-loss models has been feasible for studying field phenomena involving more than one pathosystem (4).

Yield loss is the reduction in quantity and/or quality of yield (5). Loss methodology, as summarized by James (12), relies on producing epidemics representing several levels of disease severity so the quantitative relationship between potential increasing levels of disease and yield loss can be estimated effectively. Disease must be assessed regularly, and validated models must be developed to describe loss.

No known oat cultivars are immune to BYDV, and no oat cultivars that exhibit different quantitative levels of the virus when infected have been identified. Thus, it is impossible currently to establish different quantitative levels of BYDV disease severity or to maintain a disease-free control, which are both important requirements of developing a yield-loss model. However, different quantitative levels of crown rust can be established. Characterization of the relationship between BYDV and crown rust would be significant for breeding programs in which pathogens are screened dually and for regional yield-loss estimation. This study investigates the effect of crown rust infection alone and the dual infection of BYDV-PAV-IL and crown rust on oat yield and yield components. Preliminary reports have been published (2,3).

MATERIALS AND METHODS

Experimental design. Two independent studies were conducted in 1989 and 1990. The first study assessed the effect of crown rust alone on yield and yield components of two commercial spring oat (*Avena sativa* L.) cultivars. The second study assessed the effect of crown rust in the presence of BYDV-PAV-IL on yield and yield components of the same two spring oat cultivars: Ogle, which is tolerant, sensu Cooper and Jones (6), of BYDV-PAV and susceptible to crown rust infection, and Noble, which is sensitive to BYDV-PAV and susceptible to crown rust infection. Each cultivar was planted as a separate experiment for both the crown rust study and the crown rust plus BYDV yield-loss study. Standard agronomic practices were followed throughout the studies.

Field experiments were planted at the University of Illinois Agronomy/Plant Pathology South Farm at Urbana on 13 April 1989 and 27 March 1990 and also at the University of Illinois DeKalb Experiment Station at DeKalb on 11 April 1989 and 19 April 1990. Individual plots were planted with 40 g of seed per plot with a six-row cone-type planter and were 1.1 × 4.3 m. Experimental plots were separated by 1.1 × 4.3-m plots of spring oat cv. Hazel, which is resistant to crown rust and tolerant, sensu Cooper and Jones (6), of BYDV-PAV infection. Prior to machine harvest, experimental plots were trimmed to 2.4 m long. Moisture content was determined, and plot yields and test weights were standardized to a moisture content of 12.5%.

Experimental design for all experiments was a randomized complete block with five replications and a factorial treatment design. Six treatments were applied to each experiment to achieve a range of crown rust epidemics. The first factor (crown rust) had two levels: uninoculated, and inoculated. The second factor (foliar fungicide) had three levels: not sprayed, fungicide sprayed 1 wk after rust inoculation, and fungicide sprayed 2 wk after rust inoculation. The fungicide Dithane M-45 (bis-dithiocarbamate, Rohm & Haas, Philadelphia) with Triton-B1956 as a spreader sticker (Rohm & Haas) was applied at two dates with a hand-held sprayer, 2.2 kg of product per hectare (20.4 g of product per plot). Although a randomized complete block design was used for these experiments, the purpose of the experiments was to generate a database for regression analysis of yield loss due to crown rust severity, not to test treatment differences. Experiments were assessed for crown rust severity at Zadoks growth stages: 73, 75, 77, and 83 at Urbana in 1989; 73, 75, 77, 83, and 87 at Urbana in 1990; 73 and 75 at DeKalb in 1989; and 73, 75, and 83 at DeKalb in 1990. Yield and yield-component data collected for both cultivars included number of panicles per meter row, number of spikelets per panicle, number of seeds per panicle, seed protein percent, test weight, and plot yield. Five random panicles per plot were collected at maturity, and both the number of spikelets per panicle and the number of seeds per panicle were determined. The means of these variables were used for analysis. In 1989, the seed protein percent for seed samples from each plot also was determined. Groat samples (5 g) from all plots were sent to D. Peterson (USDA-ARS) at the Cereal Crop Research Unit Madison, WI, for protein determination. Protein was determined by a near infrared reflectance procedure (Neotec GQA 41, Pacific Scientific, Silver Springs, MD).

Crown rust increase and field inoculation. A field collection of crown rust (*P. c. avenae*) was collected from infected oat plants at the University of Illinois Agronomy/Plant Pathology South Farm during June 1988. Urediniospore inoculum for field experiments was increased in the greenhouse by inoculating cv. Noble oats at growth stage 13 (26) with a suspension of 1 cm^3 of urediniospores in 500 ml of distilled water and two drops of Tween 80. Inoculum suspension (10 ml) was applied with an artists' airbrush to oats planted in flats, and the flats were placed in the greenhouse at ambient temperature. A plastic sheet was placed over inoculated plants to maintain high humidity and removed the next morning. Urediniospores were collected daily with a cyclone spore collector and stored in 5-cm^3 aliquots in glass vials at −80 C. Prior to field inoculation, the urediniospores were heat-shocked to break spore dormancy by allowing the vials to come to room temperature and then placing them in a 40-C water bath for 5 min. Vials were stored at 4 C for approximately 2 h. Prior to inoculation with crown rust, whole plots were sprayed with tap water with a hand-held sprayer. All crown rust inoculations in the field were done after 7:00 PM. Urediniospores (5 cm^3) were suspended in 1,000 ml of distilled water plus seven drops of Tween 80. Three 26-cm-diameter foci per plot were each inoculated with approximately 10 ml of the inoculum suspension with a hand-held spray bottle. A 75.8-L white plastic bag was secured over each inoculated area to maintain humidity; plastic bags were removed by 10:00 AM the next morning. Plots were inoculated with crown rust at growth stage 32 on 2 June 1989 and 22 May 1990 in Urbana and on 5 June 1989 and 30 May 1990 in DeKalb.

Aphid increase and field inoculation. Barley (*Hordeum vulgare* L. 'Hudson') was planted in clay pots in the greenhouse 6 wk before field inoculations. The potting mixture consisted of loam soil, peat moss, and perlite (4:1:1, v/v/v). At approximately growth stage 30, barley plants were infested with 20–30 viruliferous aphids (*Rhopalosiphum padi* L.) that had been reared on BYDV-PAV-IL–infected barley (cv. Hudson). Each pot containing aphid-infested plants was covered with a ventilated Plexiglas cage. Each new aphid colony was placed in a modified growth chamber, a potting bench covered with a Plexiglas box 1.1 m high with sliding Plexiglas doors and equipped with an air conditioner. The temperature was maintained near 22 C. On the day field plots were inoculated, the cages were removed in an aphid transfer

room, and the aphids were shaken from the plants onto white paper sprinkled with talcum powder. The aphids were placed in waxed-paper containers, covered, and stored at 4 C until field inoculation.

Viruliferous aphids were applied in seven evenly spaced foci per plot in 1989 and in four foci in 1990. A single focus was established by sweeping approximately 50–75 aphids from the waxed-paper container with a sable brush onto two to three plants in a given row in the plot. Plots of Noble and Ogle were inoculated on 17 and 11 May 1989 and 1990, respectively, in Urbana, and on 22 and 18 May 1989 and 1990, respectively, in DeKalb at growth stages 20–23. The viruliferous aphids were allowed to feed for 2 wk, and then plots were sprayed with Cygon 4 EC (dimethoate, American Cyanamide Co., Wayne, NJ) at 583 ml of product per hectare to kill the aphids.

Disease evaluation. Crown rust disease severity was assessed by the modified Cobb scale A (0–37), in which a severity rating of 37 refers to 100% relative infection and represents the maximum leaf area that can be occupied by rust pustules (19). Plots were evaluated for crown rust severity when crown rust infection was first observed on the flag leaf. Ten random flag and 10 random flag-1 leaves per plot were evaluated on each reading date. Plots at Urbana were evaluated every three days, and plots at DeKalb were evaluated weekly. Mean values of the 10 flag and flag-1 severity assessments for each plot on each reading date were used for regression analysis.

Infection with BYDV-PAV-IL was verified using a triple antibody sandwich enzyme-linked immunosorbent assay (TAS-ELISA) (7). Ten random flag-2 leaves per plot were collected in 1989, and three flag-2 leaves were collected from each plot in 1990. This resulted in both symptomatic and nonsymptomatic leaves being collected. For each cultivar, samples were collected at growth stage 32 at Urbana on 2 June 1989 and at growth stage 48 at DeKalb on 14 June 1989. In 1990, samples were collected at growth stage 38 at Urbana on 31 May and growth stage 68 at DeKalb on 27 June. These samples were stored at −80 C until evaluation with TAS-ELISA. Two leaves from the flag-2 leaves sampled from inoculated plots were chosen randomly for testing. Approximately one-half of each leaf was used to produce a 0.1-g tissue sample. Sap was extracted with a leaf-sap extractor, and TAS-ELISA was done immediately. The samples were arranged on the ELISA plates in the same design as the field from which they were collected. Plates were read automatically at 405 nm with an ELISA plate reader (Dynatech MR 700, Dynatech Laboratories, Inc., McLean, VA). At least two samples from uninoculated oats were run on each ELISA plate as negative controls. A sample was considered positive for BYDV-PAV-IL if sample absorbance was at least twice the mean of the negative control.

Statistical analysis. All statistical analyses were done using PC-SAS version 6.04 HD (Statistical Analysis Systems, SAS Institute Inc., Cary, NC); additionally, analysis of covariance was done following Littell et al (15). The relationship between yield or test weight and crown rust severity was examined by regression analysis. Critical point linear or quadratic models were produced and evaluated for each location and year for each experiment. For all cases, linear and quadratic models were fit with disease-severity assessments as the independent variable (x_i) by ordinary least squares regression. Multiple point models also were evaluated. Significance of the individual models was evaluated by the F statistic ($P \leq 0.05$), coefficients of determination (r^2), and significance of regression coefficients was evaluated with Students t statistics ($P \leq 0.05$).

To produce a generalized model describing the effect of yield loss due to crown rust, for either the crown rust or the crown rust plus BYDV studies over both years and both locations, analysis of covariance was used. Analysis of covariance relies on the assumption that all regression lines have the same slope. Testing for parallel slopes is equivalent to testing for no interactions in the generalized model (18). Based on disease assessments made at a given growth stage, data were pooled over the two locations and two years; the concomitant variable was mean crown rust severity, and the dependant variable was plot yield or test weight (adjusted for moisture). Thus, the locations and years were combined and newly described as four locations. Locations and blocks within locations were treated as qualitative variables, and locations had different slopes if the disease-location interaction was significant at ($P \leq 0.05$). If, for a given assessment date, the slope of the lines did not differ significantly among the locations, the data remained pooled, and the yield-loss models were developed from this pooled data. Differences in intercepts were taken into account by analysis of covariance.

Residual plots were evaluated to determine if any inconsistencies were present in the models, such as inconsistent variance, systemic lack of fit, or inadequacy of the model, that might suggest that transformations of Y or x_i might be appropriate (8).

Models were evaluated and validated using the prediction sum of squares (PRESS) statistic (1). The PRESS is $(Y - \hat{Y})/\{1 - [\text{var}(\hat{Y})/\text{var}(Y)]\}$, and the expected value of the PRESS is the variance. The total PRESS [Σ PRESS $= (n + m + 1)\ \sigma^2$] can be calculated by SAS with the P option and the CLI or CLM options in PROC REG or PROC GLM. If the total PRESS is calculated in this manner in SAS, the printed value must be divided by $n + m + 1$, in which n = the number of observations and m = the degrees of freedom of the parameters within the model (S. Carmer, *personal communication*).

Yield, yield components, and seed quality were evaluated by correlation analysis. Critical point models evaluating the effect of crown rust severity on number of seeds per panicle, number of spikelets per panicle, and seed protein percent also were developed and evaluated based on the same criteria as the yield- or test weight-loss models.

TABLE 1. Mean crown rust disease severities (percent) and disease ranges assessed at several growth stages on cvs. Noble and Ogle at two locations in 1989 and 1990 in Illinois

Cultivar and growth stage	Flag leaf[a]			Flag leaf-1[a]		
	Min	Max	Mean	Min	Max	Mean
Noble						
73	0.0	18.1	3.1	0.0	24.9	5.5
75	0.0	23.6	7.2	0.0	30.6	13.1
77	0.0	20.8	7.7	0.0	35.0	14.7
83	0.7	37.0	21.5	1.9	37.0	28.5
87	2.1	37.0	25.9	6.5	37.0	31.7
Ogle						
73	0.0	14.2	1.4	0.0	17.2	2.8
75	0.0	15.9	2.6	0.0	20.5	5.3
77	0.0	12.2	3.6	0.0	27.0	6.5
83	0.0	25.8	11.0	0.0	36.2	17.3
87	0.1	28.7	13.2	0.9	37.0	21.7

[a] Crown rust disease severity on flag or flag-1 leaves in each plot, assessed by the modified Cobb scale A (0–37).

TABLE 2. Mean crown rust disease severities (percent) and disease ranges for cvs. Noble and Ogle assessed at several growth stages on plots also infected with barley yellow dwarf virus (BYDV-PAV-IL) at two locations in 1989 and 1990 in Illinois

Cultivar and growth stage	Flag leaf[a]			Flag leaf-1[a]		
	Min	Max	Mean	Min	Max	Mean
Noble						
73	0.0	10.6	1.8	0.0	22.6	3.5
75	0.0	14.5	4.5	0.0	27.8	9.3
77	0.0	25.9	7.5	0.0	34.4	12.9
83	0.9	37.0	19.2	1.3	37.0	27.2
Ogle						
73	0.0	6.4	0.9	0.0	16.8	2.4
75	0.0	13.5	2.4	0.0	24.5	5.6
77	0.0	17.0	3.7	0.0	27.8	8.0
83	0.0	29.7	12.0	0.0	37.0	20.6

[a] Crown rust disease severity on flag or flag-1 leaves in each plot, assessed by the modified Cobb scale A (0–37).

RESULTS

Disease evaluation. The crown rust population used for these studies elicited a susceptible-type reaction on both Noble and Ogle. Fungicide treatments were effective in producing different epidemics of crown rust. In the crown rust yield-loss experiments on Noble and Ogle, disease ranges and mean crown rust severity were greater on flag-1 leaves than on flag leaves (Tables 1 and 2). Disease ranges and mean disease severity were lower for Ogle than for Noble (Table 1). The zero level of disease was maintained until growth stage 83 for cv. Noble and until growth stage 87 for cv. Ogle. Zero levels of disease also were less successfully maintained on flag-1 leaves than on flag leaves. Disease ranged from 0–37% on both Noble and Ogle, except on flag leaves of Ogle, where maximum disease severity was 28.7%.

In the yield-loss experiments involving both BYDV and crown rust, mean crown rust severity and disease ranges also were greater on flag-1 leaves than on flag leaves (Table 2). Crown rust disease ranges and mean disease severity were higher on Noble than on Ogle. Zero levels of crown rust on both flag and flag-1 leaves were maintained until growth stage 83 for Noble and for all assessments on Ogle. Crown rust ranged from 0–37% for both Noble and Ogle, except on flag leaves of Ogle, where observed maximum rust severity was 29.7%.

BYDV symptoms were visible in Noble and Ogle plots 2 wk after inoculation. All plots in the crown rust plus BYDV experiments for both Noble and Ogle developed characteristic symptoms of BYDV infection at all locations (Table 3). Noble exhibited more severe symptoms than Ogle.

The majority of plots in the crown rust plus BYDV experiments tested positive for BYDV-PAV-IL in both locations and years (Table 3), except the Urbana 1990 location, where 16 of 30 Noble and 10 of 30 Ogle plots tested positive for the virus. However, all plots had 100% visual incidence when crown rust assessments were made, and all were used to develop regression models for the crown rust plus BYDV experiments.

TABLE 3. Triple antibody sandwich enzyme-linked immunosorbent assay (TAS-ELISA) results testing cvs. Noble and Ogle for barley yellow dwarf virus (BYDV-PAV-IL) at two locations in Illinois in 1989 and 1990[a]

Cultivar and location	Negative control[b]	Absorbance range	+BYDV-PAV-IL no. of plots[c]
Noble			
DeKalb 1989	0.006	0.308–0.915	30/30
Urbana 1989	0.030	0.019–0.810	25/30
DeKalb 1990	0.014	0.017–0.494	28/30
Urbana 1990	0.041	0.034–>1.800	16/30
Ogle			
DeKalb 1989	0.006	0.073–0.960	30/30
Urbana 1989	0.030	0.157–0.938	30/30
DeKalb 1990	0.014	0.053–0.400	30/30
Urbana 1990	0.041	0.029–0.945	10/30

[a] Visual incidence of plants exhibiting characteristic leaf-tip necrosis, chlorosis, leaf reddening, leathery leaves, and stunting was 100%.
[b] Negative control was the average absorbance of at least two samples from uninoculated oat plants. Plates were read at 405 nm with an automatic ELISA plate reader.
[c] Sample positive for BYDV-PAV-IL if absorbance was twice the mean of the negative control.

Yield-loss models. Predictor-location interactions for the yield-loss models were not significant ($P \leq 0.05$). Therefore, pooled data from four locations (2 locations × 2 years) were used to develop linear models to predict yield loss, using crown rust-severity assessments in the presence or absence of BYDV at given growth stages.

The model, developed for the Noble crown rust study, predicted that for each percent increase in rust severity there will be a 56.7 kg/ha loss of yield (Fig. 1; Table 4). The proportion of variation in yield explained by this model was 0.84. This model was developed from rust-severity assessments made on flag leaves at growth stage 75. The model developed for the Ogle-crown rust experiments predicted that for each percent increase in rust severity there will be a 46.0 kg/ha decrease in yield (Fig. 2; Table 4). This model was developed from rust assessments made on the flag-1 leaf at growth stage 75. The proportion of variation in yield explained by the model was 0.67.

In the presence of BYDV, the rate of yield loss was positively affected, although it was much less compared to plots without BYDV. The yield-loss model developed for the Noble-crown rust plus BYDV experiments predicted that for each percent increase in rust severity, yield will be reduced by 19.1 kg/ha (Fig. 3; Table 4). The proportion of the variation in yield explained by the model was 0.51. This model was developed from rust assessments made at growth stage 73 on flag-1 leaves. The model developed for the Ogle-crown rust plus BYDV experiments was developed based on only three locations: DeKalb 1989, DeKalb 1990, and

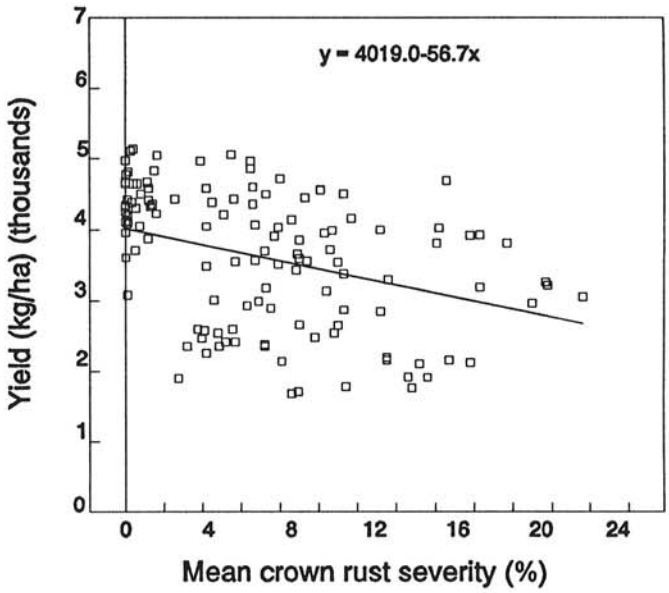

Fig. 1. Regression model to predict yield loss of Noble oats as a function of mean crown rust severity on the flag leaf at growth stage 75. Plotted data for mean disease severity are 120 observations from two trials of Noble oats in 1989 and two trials in 1990 used to develop the regression model.

TABLE 4. Regression models to predict oat yield (kilograms per hectare), using crown rust disease severity

Experiment[a]	Cultivar	Intercept	b[b]	F	t	r^2	MSE[c]	PRESS[d]
Crown rust	Noble	4,019.0	−56.7	26.1***	−8.0***	0.84	171,800.3	177,172.5
Crown rust	Ogle	4,818.8	−46.0	10.0***	−5.9***	0.67	193,043.4	198,223.0
Crown rust + BYDV-PAV-IL	Noble	2,546.3	−19.1	5.1***	−2.0*	0.51	209,004.2	213,830.6
Crown rust + BYDV-PAV-IL	Ogle	4,521.4	−28.7	11.1***	−3.1**	0.69	253,824.1	237,862.8

[a] Crown rust-Noble and crown rust-Ogle models developed from crown rust assessments on the flag and flag-1 leaves, respectively, at growth stage 75. Crown rust + barley yellow dwarf virus (BYDV-PAV-IL)–Noble and crown rust + BYDV-PAV-IL–Ogle models developed from crown rust assessments made on the flag-1 leaf at growth stages 73 and 75, respectively. * = $P \leq 0.05$, ** = $P \leq 0.01$, and *** = $P \leq 0.0001$.
[b] Partial regression coefficient.
[c] Mean square error.
[d] Predicted residual estimated sum of squares.

Urbana 1990. The Urbana 1989 location had significant storm damage that caused severe lodging and subsequent seed loss due to birds and rodents. The model predicted that for each percent increase in rust severity there would be a 28.7 kg/ha decrease in yield (Fig. 4; Table 4). The model was developed from rust assessments made on flag-1 leaves at growth stage 75. The proportion of variation in yield explained by the model was 0.69.

For each model developed, the partial regression coefficients were significantly different from zero, and the PRESS was a reasonable estimate of the mean square error (Table 4). Residual plots for Noble and Ogle in the crown rust experiments plotted either against x_i or $\hat{Y}$ showed no departures from normal, so the least squares models appear to be valid.

For the crown rust plus BYDV experiments, the residual plot for Noble plotted against x_i showed a fairly random pattern. However, at high crown rust severity, yield is consistently over predicted. Residuals plotted against predicted yield exhibit a random pattern, although deviations from the regression are larger in the middle range of predicted yields than at high or low predicted yields. Residual plots of Ogle in the crown rust plus BYDV studies showed a random pattern for either the residuals plotted against the predictor variable or the predicted yield.

Loss models for test weight. Predictor-location interactions were not significant ($P \leq 0.05$). Therefore, pooled data from two locations and two years were used to develop linear models to predict test weight loss, using crown rust-severity assessments in the presence or absence of BYDV at given growth stages.

The model developed for the Noble-crown rust study predicted that for each percent increase in rust severity there will be a

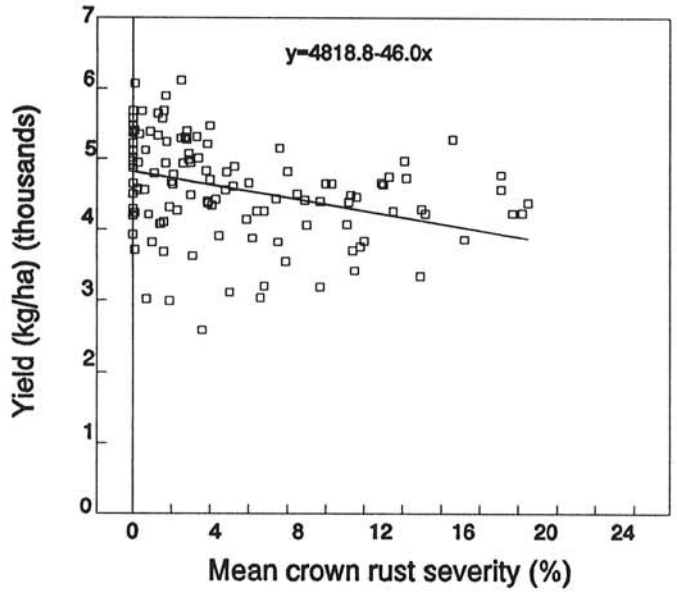

Fig. 2. Regression model to predict yield loss of Ogle oats as a function of mean crown rust severity on the flag-1 leaf at growth stage 75. Plotted data for mean disease severity are 120 observations from two trials of Ogle oats in 1989 and two trials in 1990 used to develop the regression model.

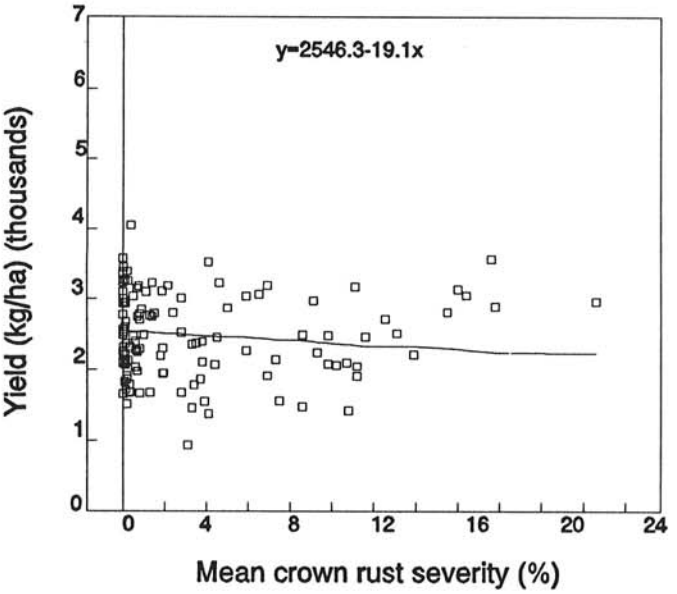

Fig. 3. Regression model to predict yield loss of Noble oats infected with barley yellow dwarf virus as a function of mean crown rust severity on the flag-1 leaf at growth stage 73. Plotted data for mean disease severity are 120 observations from two trials of Noble oats in 1989 and two trials in 1990 used to develop the regression model.

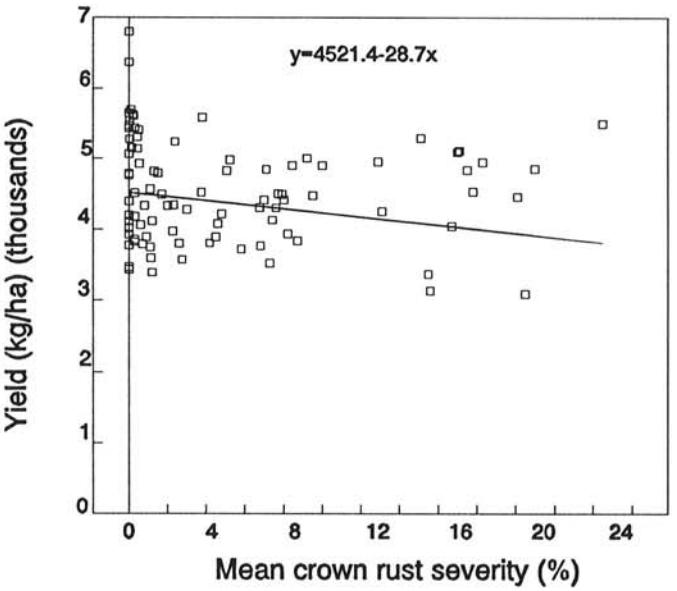

Fig. 4. Regression model to predict yield loss of Ogle oats infected with barley yellow dwarf virus as a function of mean crown rust severity on the flag-1 leaf at growth stage 73. Plotted data for mean disease severity are 90 observations from one trial of Ogle oats in 1989 and two trials in 1990 used to develop the regression model.

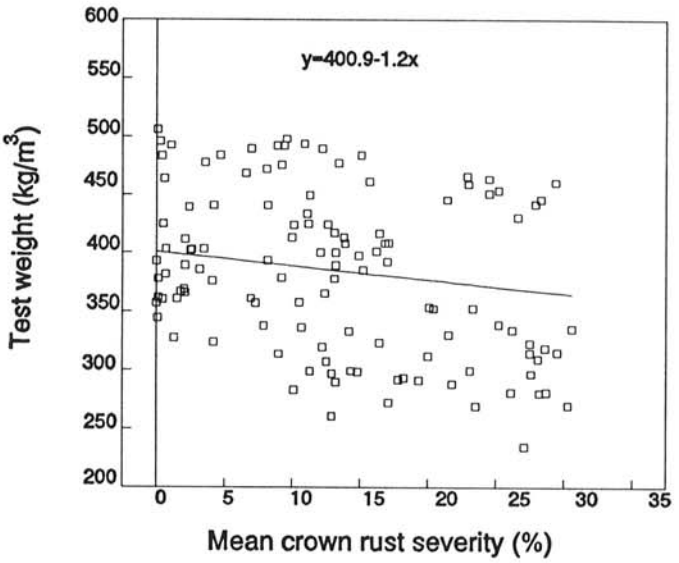

Fig. 5. Regression model to predict test weight of Noble oats as a function of mean crown rust severity on the flag-1 leaf at growth stage 75. Plotted data for mean disease severity are 120 observations from two trials of Noble oats in 1989 and two trials in 1990 used to develop the regression model.

TABLE 5. Regression models to predict oat test weight (kilograms per cubic meter) using crown rust disease severity

Experiment[a]	Cultivar	Intercept	b[b]	F	t	r^2	MSE[c]	PRESS[d]
Crown rust	Noble	400.9	−1.2	108.5***	−7.1	0.96	245.5	252.7
Crown rust	Ogle	415.2	−1.1	37.9***	−4.3***	0.83	218.6	226.8
Crown rust + BYDV-PAV-IL	Noble	377.7	−0.2	81.3***	−0.8NS	0.94	253.4	261.7
Crown rust + BYDV-PAV-IL	Ogle	410.2	−0.7	69.4***	−3.3***	0.93	124.0	117.7

[a]Crown rust-Noble and crown rust-Ogle models developed from crown rust assessments on flag and flag-1 leaves, respectively, at growth stage 75. Crown rust + barley yellow dwarf virus (BYDV-PAV-IL)–Noble and crown rust + BYDV-PAV-IL–Ogle models developed from crown rust assessments made on the flag-1 leaf at growth stage 75. * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.0001$, and NS = not significant.
[b]Partial regression coefficient.
[c]Mean square error.
[d]Predicted residual estimated sum of squares.

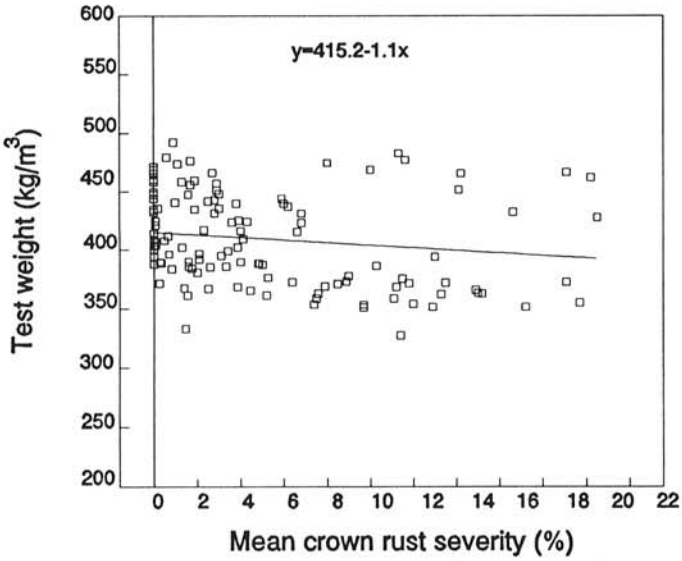

Fig. 6. Regression model to predict test weight of Ogle oats as a function of mean crown rust severity on the flag-1 leaf at growth stage 75. Plotted data for mean disease severity are 120 observations from two trials of Ogle oats in 1989 and two trials in 1990 used to develop the regression model.

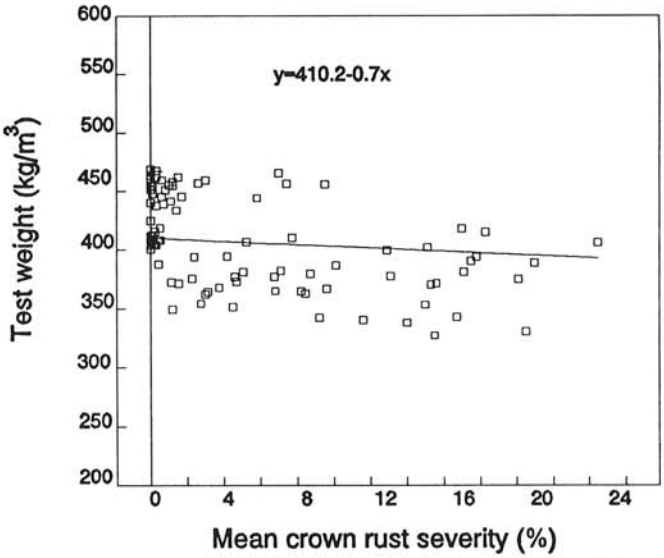

Fig. 7. Regression model to predict test weight of Ogle oats infected with barley yellow dwarf virus as a function of mean crown rust severity on the flag-1 leaf at growth stage 75. Plotted data for mean disease severity are 90 observations from one trial of Ogle oats in 1989 and two trials in 1990 used to develop the regression model.

TABLE 6. Correlation between adjusted yield and yield components for cvs. Noble and Ogle in the crown rust study in two locations in 1989 and 1990 in Illinois

Cultivar and dependent variables[a]	Spikelets/ panicle	Seeds/ panicle	Protein	Test weight
Noble				
Yield	−0.22*[b]	−0.10	0.32**	0.67***
Spikelets/panicle	—	0.94***	−0.89***	−0.43***
Seeds/panicle	—	—	−0.87***	−0.29***
Protein	—	—	—	0.82***
Ogle				
Yield	−0.30**	−0.24**	−0.06	0.23**
Spikelets/panicle	—	0.98***	0.38**	−0.00
Seeds/panicle	—	—	0.39**	0.11
Protein	—	—	—	−0.17

[a]All plot yields and test weights were standardized to 12.5% moisture and extrapolated to kilograms per hectare or kilograms per cubic meter, respectively. Mean number of spikelets or seeds per panicle was estimated by averaging the number of spikelets or seeds on five randomly sampled panicles per plot. Mean seed protein percent on a dry basis was determined from 5-g groat samples from each plot.
[b]* = $P \leq 0.05$, ** = $P \leq 0.01$, and *** = $P \leq 0.0001$.

1.2 kg/m^3 decrease in test weight (Fig. 5; Table 5). The proportion of variation in test weight explained by this model was 0.96. The model was developed from rust-severity assessments made on flag-1 leaves at growth stage 75. The model developed for the Ogle-crown rust experiments predicted that for each percent increase in rust severity there will be a 1.1 kg/m^3 decrease in test weight (Fig. 6; Table 5). The proportion of variation in test weight explained by this model was 0.83. This model was developed from rust-severity assessments made on flag-1 leaves at growth stage 75.

For the crown rust plus BYDV yield-loss experiments, increasing rust severity also led to increased reduction in test weight but less so than in the absence of BYDV. No model with a slope different from zero was developed for the Noble-crown rust plus BYDV yield-loss experiments ($P \leq 0.05$). The model shown in Table 5 was typical of the Noble models evaluated. The model for the Ogle-crown rust plus BYDV yield-loss experiments was developed from crown rust assessments made on flag-1 leaves at growth stage 75. For each percent increase in rust severity, there will be a 0.7 kg/m^3 decrease in test weight (Fig. 7; Table 5). The proportion of variation in test weight explained by the model was 0.93.

Partial regression coefficients differed significantly from zero, and the PRESS values were reasonable estimates of the mean square error (Table 5). Residual plots for Noble and Ogle in the crown rust experiments plotted either against x_i or $\hat{Y}$ showed no abnormalities in the data.

Plots of residuals in the Ogle-crown rust plus BYDV experiments also showed a random pattern of the residuals plotted against the predictor variable. The residuals plotted against the predicted test weight showed some clumping, which indicated gaps in the predictor variable.

Relationship among yield, yield components, and seed quality. Stored seed samples from 1990 experiments were infested by rodents and, thus, could not be evaluated for seed protein percent. In the Noble-crown rust study, spikelets per panicle and seed

protein were weakly but significantly correlated to yield (Table 6). Test weight was positively correlated to yield ($R = 0.67$). Seeds per panicle and spikelets per panicle were highly correlated ($R = 0.94$). Spikelets per panicle and seeds per panicle were both highly negatively correlated to seed protein percent ($R = -0.89$ and -0.87, respectively). Spikelets per panicle and seeds per panicle had low negative but highly significant correlations to test weight ($R = -0.43$ and -0.29, respectively). Seed protein was highly positively correlated to test weight ($R = 0.82$; Table 6). For Ogle, spikelets per panicle, seeds per panicle, and test weight were correlated to yield, but the correlations were low ($R = -0.30$, -0.24, and 0.23, respectively). The seed protein percent also had low correlation to yield ($R = 0.32$). Spikelets per panicle and seeds per panicle were highly correlated. In contrast to Noble, spikelets per panicle and seeds per panicle for Ogle showed low correlation to seed protein percent ($R =$ 0.38 and 0.39, respectively). Seed protein was not correlated to test weight.

The correlations of yield and the other observed yield components for the crown rust plus BYDV studies for both cultivars differed from the crown rust studies. For cv. Noble, yield was correlated to seed protein percent ($R = -0.46$) but not to spikelets or seeds per panicle or test weight (Table 7). Spikelets and seeds per panicle were highly correlated. Spikelets and seeds both had low negative correlations to seed protein percent ($R = -0.41$ and -0.37, respectively) compared to Noble that was not BYDV infected. Spikelets and seeds per panicle had low negative correlations to test weight. Seed protein had a low positive correlation to test weight. Correlation analysis of the crown rust plus BYDV studies for Ogle showed that seeds and spikelets per panicle were highly correlated. Spikelets per panicle and test weight had very low negative correlations (Table 7).

In the crown rust studies, the ranges and means of yield, spikelets and seeds per panicle were all higher in Ogle than in Noble (Table 8). The range of seed protein percent was larger for Noble than Ogle; however, the average seed protein was the same. The range of test weights in Noble was greater than in Ogle, and the mean test weight of Ogle was greater than Noble.

In the crown rust plus BYDV experiments, the ranges and means for yield were higher for Ogle than Noble (Table 8). The range of spikelets per panicle was lower in Ogle than Noble, although the mean of Ogle was higher. The range of seeds per panicle was larger for Noble than Ogle; however, the mean number of seeds per panicle of Ogle was greater than that of Noble. The range of and mean seed protein percent was higher in Noble than Ogle. The range in test weight was larger in Noble than Ogle, but again the average test weight of Ogle was greater than Noble.

Average yield, spikelets and seeds per panicle, and test weight for both cultivars were lower in the presence of BYDV than in the absence of BYDV. Comparatively, seed protein percent was higher in crown rust plus BYDV experiments than in crown rust experiments.

Loss models of yield components or protein. In only one experiment did disease severity explain variation in one of these parameters. The variation in seed protein percent was explained best by crown rust severity assessed on the flag leaf at growth stage 75 for Noble in the crown rust experiments only. The model developed indicated that for each percent increase in crown rust severity there will be a 0.032 decrease in seed protein percent ($Y = 18.86 - 0.032\ X_2$). The F statistic was 29.5 ($P \leq 0.0001$), t was -2.3 ($P \leq 0.05$), and the r^2 was 0.86.

TABLE 7. Correlation between adjusted yield and yield components for cvs. Noble, in two locations in 1989 and 1990, and Ogle, in one location in 1989 and two locations in 1990, in the crown rust barley yellow dwarf virus (BYDV-PAV-IL) study in Illinois

Cultivar and dependent variables[a]	Spikelets/ panicle	Seeds/ panicle	Protein	Test weight
Noble				
Yield	−0.17[b]	−0.08	−0.46**	0.10
Spikelets/panicle	—	0.95***	−0.37**	−0.40***
Seeds/panicle	—	—	−0.41***	−0.43**
Protein	—	—	—	0.38***
Ogle				
Yield	0.02	0.01	−0.28	0.00
Spikelets/panicle	—	0.94***	0.15	−0.21*
Seeds/panicle	—	—	0.13	−0.11
Protein	—	—	—	−0.18

[a] All plot yields and test weights were standardized to 12.5% moisture and extrapolated to kilograms per hectare or kilograms per cubic meter, respectively. Mean number of spikelets or seeds per panicle was estimated by averaging the number of spikelets or seeds on five randomly sampled panicles per plot. Mean seed protein percent on a dry basis was determined from 5-g groat samples from each plot.
[b] * = $P \leq 0.05$, ** = $P \leq 0.01$, and *** = $P \leq 0.0001$.

DISCUSSION

The intention of this study was to develop realistic yield-loss models for two commercial oat cultivars to predict the impact of crown rust alone and crown rust with BYDV-PAV-IL on spring oat yield. Crown rust epidemics were successfully established in all experiments. A broader range of disease was represented on flag-1 leaves earlier in the season than on flag leaves. Because all plots were inoculated with crown rust before flag-leaf

TABLE 8. Means and ranges of dependent variables from the crown rust crop-loss and crown rust + barley yellow dwarf virus (BYDV-PAV-IL) experiments done for cvs. Noble and Ogle at two locations in 1989 and 1990 in Illinois

Experiment and dependent variables[a]	Noble			Ogle		
	Min	Max	Mean	Min	Max	Mean
Crown rust						
Yield	1,685.0	5,130.0	3,610.0	2,586.0	6,119.0	4,574.0
Spikelets	16.7	47.0	32.9	22.9	59.6	34.9
Seeds	26.7	85.7	53.7	40.0	96.2	60.6
Protein	16.2	21.4	18.7	17.3	21.0	18.7
Test weight	234.3	505.7	383.0	327.4	492.1	409.3
Crown rust + BYDV-PAV-IL						
Yield	934.1	4,058.0	2,478.0	2,529.0	6,809.0	4,362.0
Spikelets	16.6	46.0	28.2	14.0	41.0	29.1
Seeds	25.6	79.8	45.9	26.4	71.6	51.1
Protein	19.0	23.4	21.0	18.2	20.5	19.4
Test weight	253.2	477.2	375.9	327.2	468.2	406.6

[a] All plot yields and test weights were standardized to 12.5% moisture and extrapolated to kilograms per hectare or kilograms per cubic meter, respectively. Mean number of spikelets or seeds per panicle was estimated by averaging the number of spikelets or seeds on five randomly sampled panicles per plot. Seed protein percent on a dry basis was determined from 5-g groat samples from each plot.

emergence, all rust on the flag leaves was due to secondary spread or natural infection. Crown rust epidemics on either flag or flag-1 leaves of individual cultivars did not seem to differ between crown rust experiments and crown rust plus BYDV experiments.

The sampling scheme used to verify BYDV infection in 1989 was adequate for ELISA detection of BYDV-PAV-IL. In 1990, however, the number of leaves collected from each plot was reduced from 10 to three, which was not adequate for ELISA verification of BYDV for all Ogle and Noble plots in Urbana. Despite this, all plots infected with BYDV-PAV-IL were symptomatic of BYDV infection.

Linear critical point models best described yield loss due to crown rust. The critical point yield-loss models developed from these studies indicate a significant negative relationship between increasing severity of crown rust, in the presence of or absence of BYDV-PAV-IL, and spring oat yields.

Noble and Ogle are both susceptible to crown rust; however, the rate of yield loss for each percent increase in crown rust severity was greater in Noble (56.7 kg/ha) than in Ogle (46.0 kg/ha). The models were developed from similar crown rust disease assessments ranging from 0 to 23.6% for Noble and 0 to 20.5% for Ogle. Under a similar range of crown rust, the predicted yield loss is greater in Noble than in Ogle. This is consistent with definitions of tolerance (22,27).

This relationship is different in the presence of BYDV. The rate of yield loss due to crown rust in BYDV-infected plots is greater for Ogle (28.7 kg/ha) than Noble (19.2 kg/ha). Whereas the rate of yield loss due to crown rust decreased for each cultivar with the addition of BYDV, the mean crown rust-severity assessments were not very different from experiments that did not involve BYDV. In situations in which these two pathogens are evaluated simultaneously, this apparently induced resistance to yield loss due to crown rust could have serious consequences. The potential yield loss due to crown rust in the absence of BYDV could be significantly underestimated.

BYDV had a great effect on the yield-loss models, especially on the intercepts. The estimated intercept for Noble, which is sensitive to BYDV, decreases from 4,019.0 kg/ha for the model predicting yield loss due to crown rust alone to 2,546.3 kg/ha in the model for crown rust with BYDV. Similarly, in Ogle, which is tolerant, sensu Cooper and Jones (6), of BYDV, the estimated intercept is reduced from 4,818.8 kg/ha to 4,521.4 kg/ha when BYDV is present.

In the case of Noble, the variation in yield explained by crown rust severity is much higher in the crown rust study ($r^2 = 0.84$) than in the crown rust plus BYDV study ($r^2 = 0.51$). This was not the case for Ogle, in which the variation in yield explained by crown rust was not changed by the addition of BYDV ($r^2 = 0.67$ and 0.69, respectively).

Based on the change in rate of yield loss due to crown rust in the crown rust plus BYDV studies, the relationship between crown rust and BYDV is not additive, which agrees with greenhouse studies by Potter (20). This rate change can be characterized as induced resistance, not to infection or to secondary spread, but to yield loss from crown rust. Johnson and Allen (13), working with *P. striiformis*, suggested that the effects of induced resistance could retard the development of rust diseases in the field, much like the use of multilines. They suggested that inoculation with a nonvirulent race may delay the onset of sporulation with a virulent race and also reduce spore mass produced. In the case of BYDV and crown rust, although BYDV reduces the rate of yield loss due to crown rust, the initial impact of BYDV on yield is so great that utilizing possible induced resistance to curtail further loss due to crown rust seems improbable. However, the mechanism may be of interest if a milder strain of BYDV were present.

The critical point models developed for reduction in test weight show a significant negative relationship between increasing severity of crown rust in the presence or absence of BYDV-PAV-IL and test weight of spring oats. The rate of decrease in test weights, for each percent increase in crown rust severity, did not differ between Noble (1.2 kg/m^3) and Ogle (1.1 kg/m^3) in the crown rust studies.

This relationship is different in the presence of BYDV. The rate of test weight decrease for each percent increase in crown rust did not differ from zero for Noble. This indicates that when Noble is infected with BYDV no decrease in test weight is realized by increasing severity of crown rust. The rate of decrease in test weight in Ogle decreased from 1.1 kg/m^3 to 0.7 kg/m^3 in the presence of BYDV. As with the yield-loss models, the rate of test weight loss due to crown rust decreased with the addition of BYDV for each cultivar and similarly, the mean crown rust-severity assessments hardly differed from experiments that did not involve BYDV.

The impact of BYDV on the test-weight models, as evidenced in the intercepts, is not as large as for the yield-loss models. In Noble, the estimated y-intercept decreased from 400.9 kg/m^3 for the model predicting test weight loss due to crown rust alone to 377.7 kg/m^3 for the model for crown rust plus BYDV. In Ogle, which is tolerant, sensu Cooper and Jones (6), of BYDV, the estimated intercept was reduced from 415.2 kg/m^3 to 410.2 kg/m^3 when BYDV was present. In the case of both Noble and Ogle, the variation in test weight explained by crown rust severity did not differ between studies.

For all models, location effects were significant as tested with the blocks within locations error term. Although intercepts varied between locations, the rate of yield or test weight loss due to crown rust between locations did not differ. Therefore, locations were pooled, and models were developed with analysis of covariance.

The PRESS statistic was an effective tool for selecting and validating a predictive model. For the models presented, the PRESS statistics calculated were good estimators of the individual error variances. However, as with many statistical techniques to develop a best regression, there is no test to determine if the PRESS for a given regression is better than another. It remains at the discretion of the investigator to choose a best model.

Overall, seeds and spikelets per panicle and seed protein percent were not good indicators of yield or test weight for either cultivar. However, spikelets and seeds per panicle had low but consistent negative correlations to test weight in both Noble studies.

The average yield and yield components were greater in the crown rust studies than in the crown rust plus BYDV studies. Ogle did better than Noble in both the crown rust and the crown rust plus BYDV studies in terms of average yield and yield components. Overall, average seed protein percent was higher in the crown rust plus BYDV studies than in the crown rust studies for both cultivars, contrasting with Potter (20) who found that crude protein content of plants infected with both crown rust and BYDV did not differ from plants infected with crown rust alone.

Groat protein is an important characteristic of oat seed. Singleton et al (23) found that rust infection generally lowered the percentage of groat protein in oats but that this reaction was variable depending on crown rust severity. Higher crown rust severity generally led to lower protein, which may suggest a quantitative relationship. Based on correlation and regression analysis in this study, the relationship is variable between cultivars. The critical point regression model developed for Noble to describe the effect of crown rust on seed protein percent indicated a significant negative effect of crown rust on seed protein percent. However, it was the only acceptable model developed for either Noble or Ogle, and the relationship existed at only one critical point. Although the model is statistically acceptable, the validity is questionable because it may apply to any other cultivar or critical point. Apparently, there is no quantitative relationship between spikelets and seeds per panicle and crown rust severity. The relationships may be wholly qualitative.

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