

## Quantitative Determination of the Gene Action of Leaf Rust Resistance in Four Cultivars of Wheat, *Triticum aestivum*

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### ABSTRACT

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Gene action for resistance to leaf rust (*Puccinia recondita*) of wheat (*Triticum aestivum*) was studied in field plots using parental and F<sub>1</sub>, F<sub>2</sub>, and backcross plant populations from crosses of two slow-leaf-rusting cultivars (Borah and Wampum), a highly resistant cultivar (Wared), and a susceptible cultivar (Twin). Leaf rust intensity data were transformed to area under the disease progress curve (AUDPC). The inheritance of resistance as measured by AUDPC was recessive in Borah and partially recessive in Wampum and Wared. Based on joint scaling tests, inheritance of leaf rust resistance in Wampum best fit a simple additive genetic model

with no dominance or epistatic interaction; resistance in Wared best fit an additive-dominance model with no epistatic interaction; and resistance in Borah was best explained by a genetic model assuming significant additive × additive interaction. In crosses between the resistant cultivars, resistance was additive and the gene action was best explained by genetic models assuming significant interaction components. No significant differences were found between reciprocal F<sub>1</sub> or F<sub>2</sub> generations of any cross, indicating the absence of cytoplasmic inheritance for leaf rust resistance in these cultivars.

*Additional key words:* components of inheritance, durable resistance.

*Puccinia recondita* Rob. ex Desm., the causal agent of leaf rust of wheat (*Triticum aestivum* L.), is the most widely distributed and regularly occurring rust pathogen of wheat (4,5). Leaf rust is common in the northwestern United States, and under favorable environmental conditions it significantly damages most wheat cultivars grown in the region (15). Leaf rust is most economically and effectively controlled through the use of resistant cultivars. Resistance based on single dominant genes that produce a hypersensitive response is generally considered to be vulnerable to genetic changes in pathogen virulence (21,23,30,31). Resistance expressed in the field by slow disease development (slow rusting) and in the greenhouse by a long latent period, fewer and smaller uredia, and lower urediospore production is considered to be potentially durable (3,7,12,16,18,19).

Slow leaf rusting and durable resistance have been identified for several wheat cultivars (3,7,11,16,18,28). In most instances (7,10,11,12), inheritance of slow leaf rusting or its components is recessive or partially recessive, exhibits continuous variation in segregating populations, and is under oligogenic control. Kuhn et al (10) estimated that two partially recessive genes with equal effect controlled the inheritance of latent period in Suwon 85. Lee and Shaner (11,12) estimated that 2 to 3 recessive or partially recessive genes controlled the inheritance of latent period in six slow-rusting wheat cultivars, with transgressive segregation and additive effects exhibited in crosses between slow-rusting cultivars.

The leaf rust resistance of Borah (CI 17267) and Wampum (CI 17691), two wheat cultivars commercially grown in the northwestern United States, was characterized by Milus and Line (16) as having a longer latent period, fewer uredia per unit area, fewer urediospores per uredium, and smaller uredia than susceptible cultivars. The infection type (pustule size) in Borah and Wampum differs from that in other cultivars reported to be slow leaf rusting (7,9,18). Both Borah and Wampum exhibit a range of pustule sizes when inoculated with a single race of *P. recondita* (15,16). Infection types ranged from necrotic flecks with no sporulation to intermediate or high types. Milus and Line (16)

state, "The range of infection types is similar to the race-specific mesothetic or 'X' infection type of *Puccinia graminis* described by Stakman et al [26], but it may not consist of the complete range." Borah and Wampum were less resistant to leaf rust at lower temperatures than at higher temperatures (10–30 C vs. 2–18 C) (16). Race × cultivar interaction occurred, but at higher temperatures both Borah and Wampum were more resistant than susceptible cultivars for the races tested (15,16).

Little is known about the gene action of leaf rust resistance in wheat cultivars commercially grown in the northwestern United States, especially the slow rusting resistance expressed in some cultivars. This study was initiated to determine the gene action of leaf rust resistance in Borah and Wampum and in Wared (CI 15926), a cultivar that is highly resistant to races of *P. recondita* in the Pacific Northwest.

### MATERIALS AND METHODS

Seed from five individual plants of Borah, Wampum, and Wared, and existing seed stocks of the cultivar Twin (CI 14588) were planted in November 1982 in 15-cm round plastic pots filled with a potting mixture (6 parts peat, 2 parts perlite, 3 parts sand, 3 parts Palouse silt loam, 4 parts vermiculite by volume, with added lime, 14-14-14 Osmocote, and ammonium nitrate fertilizers) and grown in the greenhouse under metal halide lights to extend the photoperiod to 16 hr and to supplement natural daylight. Borah, Wared, and Wampum are awned, hard red spring wheats that are resistant to *P. recondita*. The resistance in Wared is expressed by a low infection type usually accompanied by necrosis. Twin is an awnless, soft white spring wheat that is susceptible to *P. recondita*. Reciprocal crosses were made in all combinations. Parental and F<sub>1</sub> seeds harvested in March 1983 were planted that same spring in the field in a crossing block to produce backcross, F<sub>2</sub>, and additional F<sub>1</sub> seed. The F<sub>1</sub> plants (the male donor) were crossed with their respective female parents to produce the backcross generations. Individual seeds of the parental, F<sub>1</sub>, F<sub>2</sub>, and backcross generations were taped to 13-cm plastic stakes using strips of masking tape 0.5 cm wide, and planted in the field in five randomized blocks between May 10 and 16, 1984, at Pullman, WA. This relatively late planting date limited the development of stripe rust (*Puccinia*

*striiformis*) so that it was not a factor in leaf rust assessment and extended the growing season to allow for maximum development of leaf rust. The seeds were planted while still attached to the plastic stakes to assure the identity of the single plants and to avoid the possibility of confusing them with volunteer plants. The seeds were planted 20 cm apart in rows 2 m long, with a 45-cm spacing between the rows. Depending on the cross, the number of plants that were evaluated ranged from 24 to 61 plants per parent, 23 to 52 plants per F<sub>1</sub>, 202 to 419 plants per F<sub>2</sub>, and 28 to 63 plants per backcross. One-fifth of each population was planted in each block, with the different populations randomly intermixed. Each individual plant was an experimental unit. Blocks were not used for data analysis, but instead were used to facilitate data collection.

Leaf rust developed naturally within the plots. Collections of *P. recondita* made during the 1984 growing season showed that the only race in the plots was WPR-2, as described by Milus and Line (15). The plots were irrigated 1–3 hr in the late afternoon or evening on July 6, 13, and 20 to provide a more favorable environment for rust development.

Rust intensities based on the modified Cobb's scale for cereal rust (22) were recorded for individual plants on six different dates: 11, 17, 24, 31 July, and 7 and 18 August. Data for a specific block were recorded within a period of 10–32 hr for each of the six dates. Rust intensity during the first recording period ranged from 0 to 1%. Because the ratings were measurements of leaf area and because the later intensities ranged from 0% to 99%, the scale of the rust intensity data was changed using an arcsin transformation (14,29). The area under the disease progress curve (AUDPC) was determined for each plant using the following formula:

$$\text{AUDPC} = \sum_{i=1}^{i=5} ((x_i + x_{i+1})/2)t_i$$

in which  $x_i$  = the transformed rust intensity on date  $i$  and  $t_i$  = the time in days between date  $i$  and date  $i+1$ . Mean AUDPC values were calculated for the parental, F<sub>1</sub>, and segregating populations of each cross, and they were used to characterize the inheritance of leaf rust resistance.

To test for the occurrence of cytoplasmic inheritance, the reciprocal F<sub>1</sub> and F<sub>2</sub> generations of each cross were compared. The method described by Falconer (6) was used to determine the degree of dominance for each cross and was calculated as the deviation of the F<sub>1</sub> from the midparent ( $h$ ), divided by the departure of the more susceptible parent from the midparent ( $d$ ). The joint scaling tests described by Mather and Jinks (14) were used to determine the gene action of leaf rust resistance in each resistant parent. The joint scaling tests estimated the midparent, genetic components, and digenic interaction components of a cross and used these estimates to fit the data to genetic models. The parental, F<sub>1</sub>, F<sub>2</sub>, and backcross means and variances of each cross were used in the test to determine the genetic components involved in the model tested. Each generation of each cross provides a parameter by which a genetic model can be tested (14). The more generations for which data are available, the more complex the model that can be tested. For example, a cross with parental, F<sub>1</sub>, and F<sub>2</sub> data can be used to test a model that includes the midparent value and the additive and dominance genetic components, but no interaction components. A cross that also includes information on the backcross populations can be used to test a genetic model with two interaction components (14). The genetic components estimated by the tests were the additive component ( $d$ ) and the dominance component ( $h$ ). Interaction components estimated were the additive × additive component ( $i$ ), the additive × dominance component ( $j$ ), and the dominance × dominance component ( $l$ ). The genetic components measured were an estimate of the net effect of all the loci at which the parents differ for the measured characteristic (14). The net effects for the genetic components were symbolized as  $[d]$ ,  $[h]$ ,  $[i]$ ,  $[j]$ , and  $[l]$ . In the joint scaling tests of Mather and Jinks (14), the component  $m$  is not an estimate of the midparent value as described by Falconer (6), but is an estimate of the mean value for all homozygous individuals in the parental and segregating generations.

The rust intensity data were used to test eight genetic models

(Table 1). The most simple model ( $m[d][h]$ ) described by Mather and Jinks (14) estimated  $m$ , the additive genetic component  $[d]$ , and the dominance component  $[h]$ , while assuming that genetic interaction (epistasis) was nonsignificant. Genetic models assuming significant digenic interaction also were tested. The three interaction components, in various combinations, were included with  $m$ ,  $[d]$ , and  $[h]$  in the models assuming genetic interaction (Table 1). In addition, a model ( $m[d]$ ) was tested that estimated  $m$  and  $d$ , while assuming that the dominance component  $[h]$ , and any interaction components, were nonsignificant.

A chi-square test was used to determine the goodness of fit of each genetic model. The model was considered appropriate if the chi-square probability level was 0.05 or greater. Gene models estimating  $m$ ,  $[d]$ ,  $[h]$ , and a maximum of two interaction components were tested on data of the crosses Twin × Borah, Twin × Wampum, Borah × Wampum, and Wampum × Wared, while retaining one degree of freedom. Gene models estimating  $m$ ,  $[d]$ ,  $[h]$ , and a maximum of one interaction component were tested to the crosses Twin × Wared and Borah × Wared because only data for the backcross to one parent were available. For the gene models considered appropriate, as indicated by the chi-square test, individual genetic components were tested for significance using a student's  $t$ -test. Those genetic components estimated to be different than zero at  $P \leq 0.05$  were considered to contribute greatly to the model.

## RESULTS

There were no significant differences between the reciprocal F<sub>1</sub> or F<sub>2</sub> generations of any cross. Therefore, the reciprocal populations of the F<sub>1</sub> and F<sub>2</sub> generations were combined for analysis of the data.

Leaf rust intensity did not noticeably increase on any of the plants until the fourth data recording period, beginning 31 July (Fig. 1), and rust intensity did not noticeably increase on Borah or Wampum until the fifth data recording period, beginning 7 August. Leaf rust development on Wared was minimal, with a final intensity of <1%. For the Twin × Wampum, Twin × Wared, and Borah × Wared crosses, rust development on the F<sub>1</sub> and segregating populations was intermediate to development on the parents. For the Twin × Borah cross, rust development on the F<sub>1</sub>, F<sub>2</sub>, and backcross to Twin was similar to development on the susceptible parent, Twin, and development on the backcross to Borah was intermediate to development on Twin and Borah. Mean rust development on the F<sub>1</sub>, F<sub>2</sub>, and backcross populations was more rapid than development on either parent in Borah × Wampum and Wampum × Wared (Fig. 1).

The mean AUDPC of the F<sub>1</sub> for the Twin × Borah cross was

TABLE 1. Genetic models used to test the gene action of leaf rust resistance in crosses of Borah, Wampum, Wared, and Twin

Model	Description
$m[d]$	additive gene action $[d]$ (no dominance or epistatic interaction)
$m[d][h]$	additive gene action $[d]$ , dominance $[h]$ , (no epistatic interaction)
$m[d][h][i]$	additive gene action $[d]$ , dominance $[h]$ , additive × additive interaction $[i]$
$m[d][h][j]$	additive gene action $[d]$ , dominance $[h]$ , additive × dominance interaction $[j]$
$m[d][h][l]$	additive gene action $[d]$ , dominance $[h]$ , additive × dominance × dominance interaction $[l]$
$m[d][h][i][j]$	additive gene action $[d]$ , dominance $[h]$ , additive × additive interaction $[i]$ , additive × dominance interaction $[j]$
$m[d][h][i][l]$	additive gene action $[d]$ , dominance $[h]$ , additive × additive interaction $[i]$ , dominance × dominance interaction $[l]$
$m[d][h][j][l]$	additive gene action $[d]$ , dominance $[h]$ , additive × dominance interaction $[j]$ , dominance × dominance interaction $[l]$

similar to that of Twin (Table 2). The degree of dominance for Twin  $\times$  Borah was 1.33 (Table 3), suggesting the occurrence of heterosis and overdominance for susceptibility. The mean AUDPC values of the F<sub>2</sub> and the backcross to Twin were also similar to that of Twin and were higher than the mean AUDPC value of Borah, while the mean AUDPC of the backcross to Borah was intermediate to Twin and Borah (Table 2).

Neither the simple additive ( $m[d]$ ) nor the additive-dominance ( $m[d][h]$ ) genetic models fit the data of Twin  $\times$  Borah (Table 4). All genetic models that included the additive  $\times$  additive component [ $i$ ] fit the data. Both the additive component [ $d$ ] and the additive  $\times$  additive component [ $i$ ] contributed significantly to the these models. In addition, a model including the additive  $\times$  dominance component [ $j$ ] and the dominance  $\times$  dominance component

[ $l$ ],  $m[d][h][j][l]$ , fit the data. All individual components contributed significantly to this model (Table 4).

There was slight dominance for susceptibility ( $h/d = 0.09$ ) in the Twin  $\times$  Wampum cross (Table 3). The F<sub>1</sub> value was very near the midparent, indicating that resistance to leaf rust was additive. The AUDPC values of the backcross generations were intermediate to the F<sub>1</sub> and their respective backcross parents, which also suggested that resistance is additive in Wampum (Table 2). All models to which the data of this cross were tested showed an acceptable fit (Table 4). For all models, however, only the additive genetic component [ $d$ ] was significant.

Susceptibility was partially dominant ( $h/d = 0.23$ ) in the Twin  $\times$  Wared cross (Table 3). The relationship among the mean AUDPC values of the different generations was similar to that in

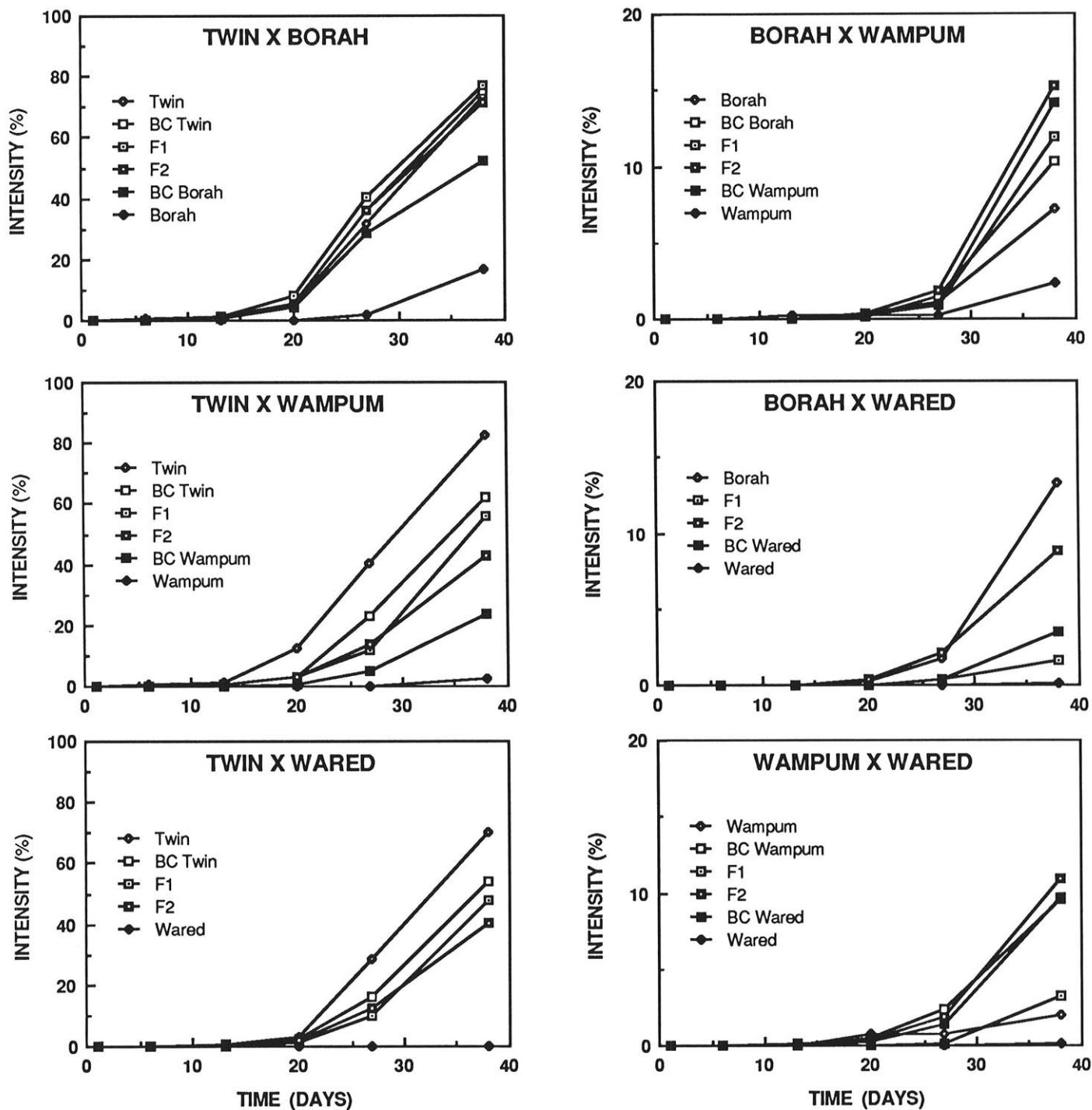


Fig. 1. Development curves for leaf rust on parental, F<sub>1</sub>, F<sub>2</sub>, and backcross plants of six wheat crosses.

TABLE 2. Mean area under the disease progress curve (AUDPC) for each population of six crosses

Population	AUDPC					
	Twin × Borah	Twin × Wampum	Twin × Wared	Borah × Wampum	Borah × Wared	Wampum × Wared
P <sub>1</sub> <sup>a</sup>	13.04	15.54	12.03	2.06	3.32	1.38
BC <sub>1</sub>	13.56	10.47	8.96	2.61	... <sup>b</sup>	2.71
F <sub>1</sub>	14.64	9.09	7.47	2.83	1.02	1.21
F <sub>2</sub>	13.22	8.02	6.95	3.06	2.01	2.41
BC <sub>2</sub>	10.29	4.76	...	2.82	0.94	2.07
P <sub>2</sub>	3.41	1.37	0.16	1.37	0.16	0.18

<sup>a</sup>P<sub>1</sub> corresponds to the first parent and P<sub>2</sub> corresponds to the second parent in each cross. BC<sub>1</sub> corresponds to the backcross to P<sub>1</sub>. BC<sub>2</sub> corresponds to the backcross to P<sub>2</sub>.

<sup>b</sup>Insufficient data.

Twin × Wampum. The F<sub>1</sub> mean was intermediate to the two parental means, and the mean of the backcross to Twin was intermediate to the means of the F<sub>1</sub> and Twin (Table 2). As in the Twin × Wampum cross, all models tested to the data showed an

TABLE 3. Degree of dominance (*h/d*) for each of six crosses

Cross	<i>m</i> <sup>a</sup>	<i>h</i>	<i>d</i>	<i>h/d</i>
Twin × Borah	8.23	6.41	4.81	1.33
Twin × Wampum	8.46	0.64	7.08	0.09
Twin × Wared	6.10	1.38	5.93	0.23
Borah × Wampum	1.72	1.11	0.34	3.26
Borah × Wared	1.74	-0.72	1.58	-0.46
Wampum × Wared	0.78	0.43	0.60	0.72

<sup>a</sup>*m* = The midparent; *h* = the deviation of the F<sub>1</sub> from the midparent; and *d* = the departure of the susceptible parent from the midparent.

TABLE 4. Chi-square goodness of fit test and probability of fit of six crosses using eight different genetic models, and fit of the individual genetic components for models with acceptable chi-square fit

Cross	Model <sup>a</sup>	Chi <sup>2</sup> value	P <sup>b</sup>	Component fit <sup>c</sup>
Twin × Borah	<i>m</i> [ <i>d</i> ]	79.4	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ]	16.1	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ]	2.8	0.26	[ <i>d</i> ],[ <i>i</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ]	10.4	0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>l</i> ]	9.2	0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>j</i> ]	0.3	0.57	[ <i>d</i> ],[ <i>i</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>l</i> ]	1.2	0.28	[ <i>d</i> ],[ <i>i</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ][ <i>l</i> ]	3.3	0.07	[ <i>d</i> ],[ <i>h</i> ],[ <i>j</i> ],[ <i>l</i> ]
Twin × Wampum	<i>m</i> [ <i>d</i> ]	5.9	0.21	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ]	4.8	0.19	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ]	3.5	0.18	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ]	4.4	0.11	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>l</i> ]	2.2	0.33	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>j</i> ]	2.6	0.11	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>l</i> ]	1.9	0.17	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ][ <i>l</i> ]	0.6	0.45	[ <i>d</i> ]
Twin × Wared	<i>m</i> [ <i>d</i> ]	5.6	0.14	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ]	1.6	0.44	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ]	1.4	0.24	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ]	0.1	0.76	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>l</i> ]	1.6	0.20	[ <i>d</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>j</i> ]	...	...	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>l</i> ]	...	...	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ][ <i>l</i> ]	...	...	...
Borah × Wampum	<i>m</i> [ <i>d</i> ]	30.4	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ]	16.9	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ]	1.8	0.42	[ <i>i</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ]	11.7	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>l</i> ]	5.0	0.08	[ <i>h</i> ],[ <i>l</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>j</i> ]	0.1	0.82	[ <i>i</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>l</i> ]	1.7	0.19	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ][ <i>l</i> ]	2.6	0.11	[ <i>h</i> ],[ <i>l</i> ]
Borah × Wared	<i>m</i> [ <i>d</i> ]	18.9	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ]	10.3	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ]	0.03	0.87	[ <i>d</i> ],[ <i>h</i> ],[ <i>i</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ]	8.8	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>l</i> ]	1.1	0.23	[ <i>d</i> ],[ <i>l</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>j</i> ]	...	...	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>l</i> ]	...	...	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ][ <i>l</i> ]	...	...	...
Wampum × Wared	<i>m</i> [ <i>d</i> ]	111.7	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ]	97.3	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ]	4.4	0.11	[ <i>d</i> ],[ <i>h</i> ],[ <i>i</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ]	97.3	<0.01	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>l</i> ]	0.004	>0.99	[ <i>d</i> ],[ <i>h</i> ],[ <i>l</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>j</i> ]	4.4	0.04	...
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>i</i> ][ <i>l</i> ]	0.002	0.96	[ <i>d</i> ],[ <i>l</i> ]
	<i>m</i> [ <i>d</i> ][ <i>h</i> ][ <i>j</i> ][ <i>l</i> ]	0.001	0.97	[ <i>d</i> ],[ <i>h</i> ],[ <i>l</i> ]

<sup>a</sup>*m* = Estimated mean of all homozygous individuals; [*d*] = additive component; [*h*] = dominance component; [*i*] = additive × additive interaction component; [*j*] = additive × dominance interaction component; and [*l*] = dominance × dominance interaction component.

<sup>b</sup>The model was considered to fit if *P* ≥ 0.05.

<sup>c</sup>The individual components listed differed significantly from zero at *P* = 0.05 and thus contributed significantly to the model.



acceptable fit (Table 4). Because data for the backcross to only one parent were available, no genetic models assuming two interaction components could be tested. When the individual genetic components of the models were tested, only the additive genetic component [*d*] was significant.

The degree of dominance for the Borah × Wampum cross was 3.26, indicating extreme overdominance for susceptibility (Table 3). All genetic models that included either the additive × additive component [*i*] or the dominance × dominance component [*l*], or both, fit the data of this cross (Table 4). For the genetic models that include [*i*] but not [*l*], only the individual component [*i*] contributed significantly to the models, while in the genetic models that included [*l*] but not [*i*], only [*h*] and [*l*] contributed significantly to the models. No individual components were found to significantly contribute to the genetic model that included both [*i*] and [*l*],  $m[d][h][i][l]$ .

The mean AUDPC of the F<sub>1</sub> for the Borah × Wared cross was intermediate to the parental means (Table 2). Resistance was partially dominant, as indicated by the negative degree of dominance value, -0.46 (Table 3). Genetic models assuming additive × dominance ( $m[d][h][i]$ ) and dominance × dominance ( $m[d][h][l]$ ) components fit these data (Table 4). The individual components [*d*], [*h*], and [*i*] contributed significantly to the first model, while [*d*] and [*l*] contributed significantly to the second. No models assuming two interaction components could be tested because only data for the backcross to one parent were available.

The degree of dominance for the Wampum × Wared cross was 0.72, indicating partial dominance for susceptibility (Table 3). As in the Borah × Wampum cross, however, the parental and F<sub>1</sub> means were not significantly different (Table 2). The three genetic models that include the dominance × dominance component [*l*] fit the data of this cross (Table 4). The additive genetic component [*d*], the dominance component [*h*], and the dominance × dominance interaction component [*l*] contributed significantly to models assuming a dominance × dominance interaction ( $m[d][h][l]$ ) and both additive × dominance and dominance × dominance interactions ( $m[d][h][i][l]$ ), while the individual components [*d*] and [*l*] contributed significantly to the genetic model assuming both additive × additive and dominance × dominance interaction ( $m[d][h][i][l]$ ). In addition, the genetic model that included the additive × additive component [*i*],  $m[d][h][i]$  also fit the data. For this model the individual components [*d*], [*h*], and [*i*] contributed significantly.

When Borah, Wampum, and Wared are crossed with one another, the leaf rust resistances act additively. This can be seen by comparing the F<sub>1</sub> means of the different crosses (Table 2). For example, the F<sub>1</sub> mean of Twin × Borah was 14.64 and of Twin × Wampum was 9.09. Because there are susceptible plants in the F<sub>2</sub> population of Borah and Wampum (1), one would not expect these two cultivars to have common genes for resistance. If the resistance in Wampum was epistatic to that in Borah, an F<sub>1</sub> mean of approximately 9.09 for Borah × Wampum would be expected. The F<sub>1</sub> mean, however, was 2.83, significantly lower than 9.09, indicating additive gene action (Table 2). The F<sub>1</sub> means of Borah × Wared and Wampum × Wared also were lower than expected. If the leaf rust resistance in each parent acted independently and if they did not share any genes for resistance, the expected F<sub>1</sub> means of Borah × Wared and Wampum × Wared should be at least 7.45, which is the F<sub>1</sub> mean of Twin × Wared. Instead, the F<sub>1</sub> means of Borah × Wared and Wampum × Wared were 1.02 and 1.21, respectively (Table 2), also indicating additive gene action.

## DISCUSSION

The lack of significant differences between reciprocal F<sub>1</sub> and F<sub>2</sub> generations indicated that there was no cytoplasmic (maternal) inheritance in any of the crosses. Genetic models assuming epistatic interaction and models assuming no epistatic interaction both adequately described the gene action in the Twin × Wampum and Twin × Wared crosses at a chi-square probability level of 0.05 (Table 4). For each cross, however, only the additive genetic component [*d*] contributed significantly to the models, which

supported the conclusion that the simple models adequately described the data. According to Mather and Jinks (14), if a simple model provides a good fit to the data, there is no basis for assuming a more complex situation. The leaf rust resistance in both Wampum and Wared appeared to be additive with no significant dominance or epistatic effects, fitting a simple additive model ( $m[d]$ ). In both crosses (Twin × Wampum and Twin × Wared), the degree of dominance was consistent with the results of the joint scaling tests. Only slight dominance for susceptibility ( $h/d = 0.09$ ) was shown in the Twin × Wampum cross (Table 3). This would explain why the additive model ( $m[d]$ ) gave a better fit to the data than the additive-dominance model ( $m[d][h]$ ) (Table 4). The degree of dominance was greater in the Twin × Wared cross ( $h/d = 0.23$ ), even though the dominance component [*h*] was not significant (Table 4). This may explain why the additive-dominance model showed a better fit than the additive model. The fact that the leaf rust development curves for the F<sub>1</sub> generations of Twin × Wampum and Twin × Wared were intermediate to the parents and that the development curves of the backcross generations were intermediate to the F<sub>1</sub> generation and the respective parent (Fig. 1) also supported the interpretations using the joint scaling tests.

Inheritance of leaf rust resistance in Borah is best explained by a model assuming additive × additive genetic interaction ( $m[d][h][i]$ ). A significant additive × additive interaction component indicates an interaction between the homozygous conditions of the loci involved, and thus the resistance in Borah may be explained by complementary genes. Mendelian ratios for the F<sub>2</sub> and backcross to Borah fit a model for two complementary genes (2), which is consistent with a genetic model assuming epistatic interaction. Although the degree of dominance for Twin × Borah was 1.33, indicating heterosis and overdominance for susceptibility (Table 3), the F<sub>1</sub> mean was similar to that of the susceptible parent (Table 2). It is therefore possible that the gene action may be one of complete dominance, rather than overdominance, for susceptibility. Two complementary resistance genes, with one or both recessive, would result in an F<sub>1</sub> similar to the susceptible parent.

The degree of dominance in Borah × Wampum was 3.26, which is an indication of extreme overdominance for susceptibility (Table 3). However, what appears as overdominance is more likely due to the dispersion of the different resistance genes possessed by Borah and Wampum.

The joint scaling tests assume that all loci segregating for a measured character (i.e., leaf rust resistance) are associated in a single parent (14). Therefore, when analyzing resistant × resistant crosses, the joint scaling tests cannot be expected to accurately describe the gene action involved. However, they can be used to observe certain patterns. In the resistant × resistant crosses, all of the genetic models that included the dominance × dominance interaction component, [*l*], adequately fit the data (Table 4) and, in all but one of these models, [*l*] was significant. A significant dominance × dominance interaction component indicates an interaction between the heterozygous states of the loci involved. This would help explain the lower than expected AUDPC values of the F<sub>1</sub> populations of the resistant × resistant crosses. Also, all but one of the genetic models including the additive × additive interaction component, [*i*], fit the data for the crosses between resistant parents, indicating interaction between homozygous conditions of the loci involved. It appears that the additive gene action occurring for resistance to leaf rust in the crosses between resistant cultivars is significantly affected by epistatic interaction when the loci for resistance are in the homozygous and heterozygous conditions.

If the additive gene action is due to interaction between alleles at different loci, as implied by the relationship of the F<sub>1</sub> means of the crosses between Wampum, Borah, and Wared, and by the joint scaling tests, then transgressive segregation is expected. Additive gene action resulting in transgressive segregation has been reported for both hypersensitive leaf rust resistance (24) and slow leaf rusting (12). Wismer (32) observed transgressive segregation in a cross between the cultivars Oro (highly susceptible to leaf rust) and

Tenmarq (moderately susceptible). Segregation in the F<sub>4</sub> indicated that the inheritance was controlled by multiple factors (32).

Borah and Wampum are slow-leaf-rusting cultivars, as shown by their leaf-rust development curves (Fig. 1). The inheritance of resistance was completely recessive in Borah and slightly recessive in Wampum. Lee and Shaner reported that the inheritance of latent period in six slow-leaf-rusting cultivars was controlled by recessive or partially recessive genes (11). Kuhn et al (10) reported that two partially recessive genes controlled the inheritance of latent period in Suwon 85. Recessive or partially recessive control of slow rusting has been reported for several rust/cereal interactions (3,10,11,13,17,19,25). The slow leaf rusting in wheat cultivars has been considered by many workers to be race nonspecific (3,7,9,10,11,28). However, the slow leaf rusting of Borah and Wampum differed from that reported for other slow-leaf-rusting cultivars in that the components of slow rusting in Borah and Wampum showed race specificity (16) that was expressed by a shift in degree of susceptibility. Parlevliet (20) also reported differential interaction of slow-leaf-rusting barley cultivars to *Puccinia hordei*. According to Parlevliet (19,20), the slow leaf rusting in these barley cultivars is under polygenic control and has been quite stable.

Even though the leaf rust resistance in Borah and Wampum is race specific, that resistance has not been completely overcome (16). In the field, neither cultivar has been severely attacked by *P. recondita*. Johnson (8) defines durable resistance as "... resistance that remains effective during its prolonged and widespread use in an environment favorable to the disease. The test for durable resistance must include two elements, time (long) and area (large)." By these criteria, we do not know whether Borah or Wampum possess durable resistance. WPR-2 was the predominant race in eastern Washington in 1979 (15). Tests of field collections indicated that this was still true in 1984 (M. E. Bjarko, unpublished). However, spring wheat is grown on a relatively small percentage of the area planted to wheat in eastern Washington, and the major winter wheat cultivars grown in this region are susceptible to WPR-2 (15). Therefore, selection pressure for the pathogen to change may be minimal. This must be considered when determining whether the resistance observed in a particular cultivar is durable or not. However, the nature of the resistances in Borah and Wampum (longer latent period, smaller uredia, and lower urediospore production) would indicate that both contain potentially durable resistance and should be reasonable choices as sources of desirable leaf rust resistance.

Wared, in contrast to Borah and Wampum, has such a high degree of leaf rust resistance that it cannot be considered to be a slow-rusting cultivar. The nature of its resistance indicates it is probably race specific (21,23,30,31). Statler (27) reported that Wared probably carries the leaf rust resistance genes *Lr2a* and *Lr10*, and possibly *Lr2c*. *Lr10* is ineffective against the races of *P. recondita* thus far identified in the Pacific Northwest, while *Lr2a* is effective against WPR-1 and WPR-2 (15). Wared may also contain an adult-plant resistance gene (R. F. Line, unpublished) The resistance in Wared has not been overcome by races of *P. recondita* found in the Pacific Northwest.

Borah, Wampum, and Wared are commercial cultivars with desirable agronomic characteristics. The additive gene action exhibited in the crosses between these cultivars suggests that it should be possible to identify progeny with greater leaf rust resistance than that found in the parental cultivars. It should be possible to select slow-leaf-rusting lines with good agronomic qualities and potentially durable leaf rust resistance.

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