Heritability and Number of Genes Controlling Leaf Rust Resistance in Four Cultivars of Wheat

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ABSTRACT

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Inheritance of leaf rust (*Puccinia recondita*) resistance in wheat (*Triticum aestivum*) was evaluated in two slow leaf-rusting cultivars (Borah and Wampum), a highly resistant cultivar (Wared), and a susceptible cultivar (Twin) using area under the disease progress curve as a measure of leaf rust resistance. Parental and F_1, F_2, and backcross populations of all possible single crosses between the four cultivars were evaluated in the field on a single plant basis in 1984, and 100 F_3 lines and 40–45 F_5 lines per cross were evaluated along with the parents in 1986. No discrete phenotypic classes were observed in the segregating populations of any cross. Based on quantitative analyses, each resistant cultivar contained at least two to three genes for leaf rust resistance, and the genes in each cultivar were different from those in the other two cultivars. Heritability estimates for leaf rust resistance, using three methods, ranged from 0.74 to 0.92 for Wared, 0.42 to 0.70 for Wampum, and 0.33 to 0.55 for Borah, when crossed with Twin. The cross between Borah and Wampum resulted in the lowest heritability estimates.

Additional key words: durable resistance, slow rusting.

The most economical and effective means of leaf rust control is 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 (9,22,24,31,32). Resistance expressed in the field by slow disease development (slow rusting) and in the greenhouse by its components (longer latent period, fewer and smaller uredia, and lower spore production) is considered to be potentially more durable. Slow rusting in wheat (*Triticum aestivum* L. em. Thell) to *Puccinia recondita* Rob. ex Desm., the causal agent of leaf rust, has been identified in a number of wheat cultivars (4,6,11,18,20,25,29). Kuhn et al (12) and Lee and Shaner (13,14) described the genetics of the inheritance of longer latent period using Mendelian ratios. Kuhn et al (12) reported that two partially recessive genes controlled the inheritance of longer latent period in Suwon 85. Lee and Shaner (13) reported that one to three genes, depending on the cross, controlled the inheritance of longer latent period in several wheat cultivars. Using a quantitative approach, Gavinlertvatana and Wilcoxson (6) estimated that 3–21 genes, depending on the cross, controlled slow leaf rusting. Heritability estimates for both slow leaf rusting and its components were considered high enough for selection of individuals with enhanced levels of leaf rust resistance (6,12,13).

This study was undertaken to determine the genetic control and heritability of the slow rusting resistances in Borah (CI 17267) and Wampum (CI 17691), two slow leaf-rusting spring wheat cultivars commercially grown in northwestern United States (18). Wared (CI 15926), a highly resistant cultivar also commercially grown in the Northwest, and Twin (CI 14588), a susceptible spring wheat cultivar, were included in the study.

MATERIALS AND METHODS

Seed from five individual plants of Borah, Wampum, and Wared and existing seed stocks of Twin were planted in November 1982 in 15-cm 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, Wampum, and Wared are awned, hard red spring wheats that are resistant to *P. recondita*. Twin is an awnless, soft white spring wheat. Reciprocal crosses were made in all combinations. Parental and F_1 seeds harvested in March 1983 were planted that same spring in the field in a crossing block to produce backcross, F_2, and additional F_1 seed. The F_1 plants (the male donor) were crossed with their respective female parents to produce the backcross generations. Individual seeds of the parental, F_1, F_2, and backcross populations were taped to 13-cm plastic stakes using 0.5-cm-wide strips of masking tape and planted in the field between 10 and 16 May 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 avoid the possibility of confusion with volunteer plants. The seeds were planted 20-cm apart in rows 2 m long, with a 45-cm spacing between the rows. Population sizes ranged from 24 to 61 plants per parent, 23 to 52 plants per F_1, 202 to 419 plants per F_2, and 28 to 63 plants per backcross, depending on the cross. The seeds were planted in five randomized blocks. 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 as such for data analysis, but instead were used to facilitate data collection, with data from one block collected each day and data from the entire experiment collected over a period of several days. The plots were irrigated for 1–3 hr in the late afternoon or evening on 6, 13, and 20 July to provide a more favorable environment for rust development. 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 (17).

Rust intensities, based on the modified Cobb's scale for cereal rust (23), were recorded for individual plants on six different dates. Each recording date began on 11, 17, 24, and 31 July and 7 and 18 August. All data for a specific block were recorded within a 10–32-hr period for each of the six dates. Rust intensity during the first recording period ranged from 0 to 1%. Most plants were in the

jointing to boot stage during the first data collection period, and data collection ended when the plants began reaching maturity. The rust intensity recordings were based on measurements of area covered by rust and consisted of a range of values from 0 to 99%. Because of this, the scale of the rust intensity data was changed using an arcsin transformation (30). The area under the disease progress curve (AUDPC) was determined for each plant using the following formula:

$$\text{AUDPC} = {}_{i=1-5}\ \Sigma((x_i + x_{i+1})/2)t_i$$

in which x_i equals the rust intensity on date i and t_i equals the time in days between date i and date $i + 1$. The mean AUDPC values were calculated for the parental, F_1, and segregating populations of each cross and were used to characterize the inheritance of leaf rust resistance.

F_3 lines from 100 randomly selected F_2 plants of each cross were planted in the field in two replications on 12 May 1986. In each replication, 30–40 seeds per F_3 line were planted in 2-m long rows with a 45-cm spacing between the rows. A row of each parent of the cross was planted every 20 F_3 rows. Two rows of Twin were planted every 40 rows and as a border.

F_2 derived F_5 lines obtained by single seed descent from 40 to 45 of the 100 randomly selected F_2 plants of each cross used as progenitors of the F_3 lines were planted on 19 and 22 May 1986 in hill plots with three replications. Three to 15 seeds were planted per hill with the hill plots planted on a 30-cm spacing. Two hills of each parent were planted with each replication of the cross. Three rows of Twin were planted as a border.

To assure adequate infection, pots containing 15–20 Twin seedlings infected with race WPR-2 were transplanted 4-m apart in the border rows of the F_3 and F_5 plots on 31 May 1986, and the entire plots were uniformly dusted with urediospores of race WPR-2 mixed in talc at dusk on 11 and 29 June. The plots were irrigated for 1.5–2 hr before inoculation and periodically during the season to provide a more favorable environment for disease development. Based on evaluation of rust collections made throughout the season, only race WPR-2 was present in the plot.

Rust intensities were recorded for individual F_3 rows and F_5 hill plots. F_3 lines were recorded as homozygous or segregating at 1:1, 1:3, or 1:15 ratios. The average rust intensity for each F_3 line was based on the intensity values and the segregation ratios recorded. No attempt was made to identify segregation within the F_5 hill plots. The F_3 data were recorded on four dates and F_5 data were recorded on six dates. All F_3 and F_5 data for each replicate were recorded within 24 hr during each data collection period. The initial recording dates were 13 and 27 July and 4 and 10 August for the F_3 data and 10, 18, and 25 July and 1, 8, and 14 August for the F_5 data. Rust intensity data were transformed and area under the disease progress curve was measured for each F_3 row and F_5 hill plot in the manner described for the F_2 and backcross data.

Distributions of the F_2 and F_3 populations were tested for normality using the Kolmogorov-Smirnov test (30) and distributions of the F_5 populations were tested for normality using the Shapiro-Wilk statistic (26). Quantitative estimates of the number of genes segregating for leaf rust resistance were made using the Wright's formula (33). This formula was modified for use with the F_3 and F_5 data (Table 1). Each formula essentially estimates the gene number by dividing the square of the genotypic range by the genotypic variance. The genotypic variance was estimated by subtracting the environmental variance from the phenotypic variance of the segregating population used in the test. The genotypic range was estimated by two methods, the difference of the parental means and the phenotypic range of the segregating population. Narrow sense heritability values were calculated using the standard units method of Frey and Horner (5) and F_3/F_2 regression (10,16). Broad sense heritability values were calculated using F_5 variance components (6).

RESULTS

Discrete classes were not observed within the segregating populations of any of the crosses (Figs. 1 and 2). Normal distributions occurred only in the Twin × Borah cross and in the F_5 population of the Twin × Wampum cross (Fig. 1). Transgressive segregation for susceptibility was observed in the crosses between resistant parents, indicating that the genes for leaf rust resistance in each parent may be different (Fig. 2). Because the segregating individuals did not separate into discrete classes, a quantitative rather than a Mendelian approach was used for analysis of the genetic control of leaf rust resistance.

Quantitative estimates of the numbers of genes segregating for leaf rust resistance were consistently lower when the difference between the parents, $(\bar{P}s - \bar{P}r)^2$, was used as a measure of the genotypic range, than when the phenotypic range was used to estimate the genotypic range (Table 2). When $(\bar{P}s - \bar{P}r)^2$ was used, the number of estimated genes varied from 0.9 to 2.2 for Borah, 1.3 to 2.8 for Wampum, and 1.0 to 2.6 for Wared, and the estimated number of segregating genes in resistant by resistant crosses was less than 1.0, with all but two of the estimates less than 0.5 genes (Table 2).

When the phenotypic range of the segregating population involved was used as an estimate of the genotypic, the number of

TABLE 1. Formulas used to estimate the number of genes (n) segregating for leaf rust resistance

Population tested	Formula used[a]
Backcross to the resistant parent (BC_R)	$n = \dfrac{(GR)^2}{4[V_{BC} - ((V_{PR} + V_{F1})/2)]}$
F_2	$n = \dfrac{(GR)^2\,[1.5 - 2h(1-h)]}{8(V_{F2} - (V_{PS} + V_{PR} + 2V_{F1})/4)}$ $h = (\bar{F}_1 - \bar{P}_R)/(\bar{P}_s - \bar{P}_R)$
F_3	$n = \dfrac{(GR)^2}{5.33\,[V_{F3} - (V_{PR} + V_{PS})/2]}$
F_5	$n = \dfrac{(GR)^2}{4.27\,[V_{F5} - (V_{PR} + V_{PS})/2]}$

[a] (GR) = Genotypic range, estimated as the phenotypic range of the segregating generation or the difference between the two parents $(\bar{P}_S - \bar{P}_R)$. $\bar{P}_R$ = the mean of the resistant parent, $\bar{P}_S$ = the mean of the susceptible parent, $\bar{F}_1$ = the mean of the F_1 generation, V_{PR} = the variance of the resistant parent, V_{PS} = the variance of the susceptible parent, V_{F1} = the variance of the F_1 generation, V_{BC} = the variance of the backcross generation, V_{F3} = the variance of the F_3 generation, V_{F5} = the variance of the F_5 generation, n = the estimated number of segregating genes.

TABLE 2. Estimates of the number of segregating genes for leaf rust resistance, as measured by area under the disease progress curve using the parental difference $(\bar{P}_s - \bar{P}_r)^2$ and the phenotypic range $(PR)^2$ as measures of the genotypic range

Cross[a]	Method[b]	Population tested				
		BC_R[c]	F_2	F_3	F_5	Range
Twin × Borah	$(\bar{P}_s - \bar{P}_r)^2$	0.9	1.7	2.2	1.6	1–2
	$(PR)^2$	3.2	6.2	4.6	6.6	3–7
Twin × Wampum	$(\bar{P}_s - \bar{P}_r)^2$	2.8	1.3	3.3	2.5	1–3
	$(PR)^2$	5.0	4.5	5.8	3.6	3–6
Twin × Wared	$(\bar{P}_s - \bar{P}_r)^2$	...[d]	1.0	2.6	1.8	1–3
	$(PR)^2$	...	3.3	3.5	2.6	2–4
Borah × Wampum	$(\bar{P}_s - \bar{P}_r)^2$	0.7	0.1	0.0	0.0	0–1
	$(PR)^2$	5.7	8.5	8.6	6.3	6–9
Borah × Wared	$(\bar{P}_s - \bar{P}_r)^2$	0.1	0.2	0.1	0.4	0–1
	$(PR)^2$	6.3	6.3	6.1	5.5	5–6
Wampum × Wared	$(\bar{P}_s - \bar{P}_r)^2$	0.0	0.0	0.1	0.6	0–1
	$(PR)^2$	2.1	4.9	7.8	6.5	2–8

[a] More susceptible parent listed first, more resistant parent listed second.
[b] Method used to estimate the genotypic range. $(\bar{P}_s - \bar{P}_r)$ = Parental difference, (PR) = phenotypic range.
[c] BC_R = Backcross to the more resistant parent.
[d] Insufficient data.

genes estimated to be segregating for leaf rust resistance was greater for resistant × resistant crosses than resistant × susceptible crosses (Table 2). The estimated number of genes ranged from 3.2 to 6.6 for Borah, 3.6 to 5.8 for Wampum, and 2.6 to 3.5 for Wared. Analysis of the resistant by resistant crosses showed 5.7 to 8.6 segregating genes in the Borah × Wampum cross, 5.5 to 6.3 in Borah × Wared, and 2.1 to 7.8 genes in Wampum × Wared, depending on the segregating population tested.

Broad sense heritability estimates, as measured by the variance components of the F_5 population, were generally higher than narrow sense heritability estimates obtained by the standard units method or the regression of the F_3 on the F_2 (Table 3). The highest heritabilities were obtained for the crosses involving Wared, while the cross between the slow rusting cultivars, Borah × Wampum, had the lowest heritability estimates. Narrow sense estimates of heritability were 0.33 and 0.55 for Borah, 0.42 and 0.70 for Wampum, and 0.74 and 0.92 for Wared (Table 3).

DISCUSSION

The lack of discrete classes in the segregating populations of the crosses may be due to low heritabilities, segregation of several genetic factors, or both (1). Normal distributions were evident only for the Twin × Borah cross and the F_5 population of the Twin × Wampum cross. This lack of a normal distribution may be due to the presence of dominance, epistasis, or linkage between the leaf rust resistance genes. Continuous variation, i.e., no discrete classes, in the segregating populations of crosses involving cultivars with slow rusting resistance has been reported for several cereal:rust-pathogen interactions (6,8,12,15,19,21,27,28) and has in some instances been cited as evidence of quantitative inheritance for disease resistance (6,8,27,28). Kuhn et al (12), however, warn against assuming quantitative inheritance solely on the basis of the presence of continuous variation in the segregating population, because the distribution of the segregating population is also influenced by the heritability of the trait being studied.

Transgressive segregation for susceptibility was observed in crosses between the resistant cultivars Borah, Wampum, and Wared (Fig. 2). This indicates that each of the resistant cultivars has different genes for leaf rust resistance. No transgressive segregation for resistance was observed in these crosses. However, in each cross at least one parent was highly resistant or expressed a mean area under the disease progress curve that fit into the most resistant category in the distribution of the segregating population. Only in the F_5 population of Borah × Wampum would it have been possible to identify more resistant types (Fig. 2). Larger population sizes in the F_3 and later generations, and more severe disease pressure, might have facilitated the identification of individuals that were more resistant than either parent. Transgressive segregation for susceptibility does not imply the existence of transgressive segregation for resistance, and the former should not be relied on as evidence of the latter. However, F_1 populations of the resistant × resistant crosses were more resistant than would be

TABLE 3. Estimates of heritability as measured by area under the disease progress curve for leaf rust resistance in six crosses

Cross	Standard units	F_3/F_2 Regression	F_5 Variance components
Twin × Wared	0.74	0.77	0.92
Borah × Wared	0.77	0.62	0.87
Wampum × Wared	0.65	0.42	0.63
Twin × Wampum	0.55	0.42	0.70
Twin × Borah	0.37	0.33	0.55
Borah × Wampum	0.28	0.21	0.44

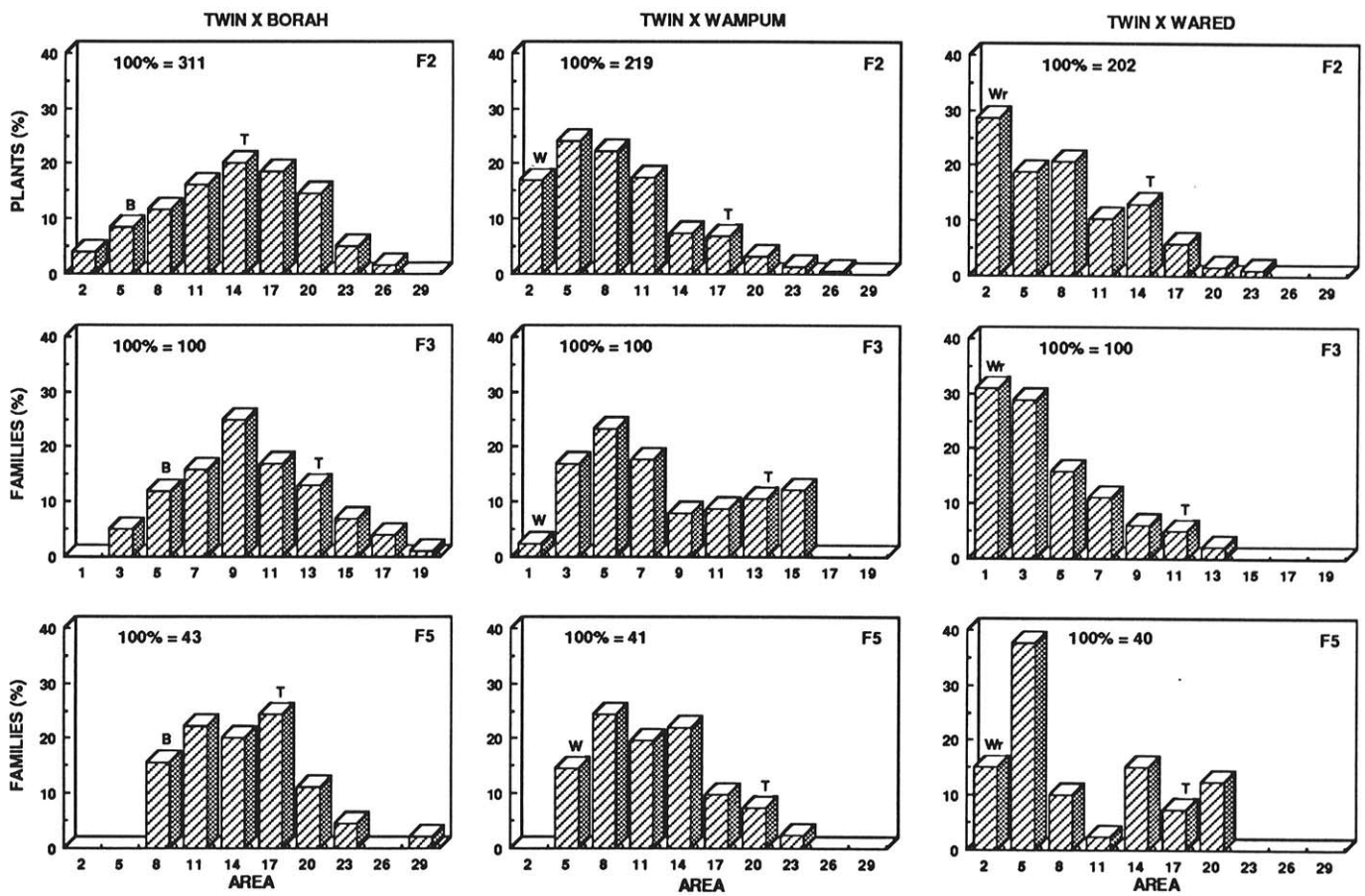

Fig. 1. Frequency distribution for area under the disease progress curve of crosses involving the susceptible cultivar Twin with the resistant cultivars Borah, Wampum, and Wared. The letters T, B, W, and WR, respectively, indicate the classes in which the means of parents Twin, Borah, Wampum, and Wared fall.

expected based on the observed resistance of the F_1 populations of the resistant × susceptible crosses (2). This indicates the ocurrence of additive gene action for resistance when Borah, Wampum, and Wared are crossed together.

The methods used to estimate the number of genes segregating for leaf rust resistance are derived from Wright's formula (33). The first method uses the difference of the parental means to estimate the genotypic range expected in a cross and assumes that no linkage exists between the loci involved, the effects of all loci involved are equal, no dominance, no epistasis, and all genes for resistance are in a single parent of the cross. Because this method assumes that all genes are in a single parent, it is an inappropriate test for crosses between two resistant parents. The effect of using this method to test resistant × resistant crosses can be seen in Table 2, where the estimates of gene numbers for these crosses indicate less than one segregating gene to be present. The difference in parental means for crosses between two resistant parents does not provide an accurate estimate of the expected genotypic range unless the two parents have the same genes for resistance. The presence of linkage, dominance, or unequal effects at different loci will cause an underestimation of the actual number of segregating genes present, while the presence of epistasis may cause either an overestimation or an underestimation of the actual number of segregating genes. The use of this formula provides, in most cases, a conservative estimate of the number of genes involved (3,15,19,28,33).

The second method uses the phenotypic range of the segregating population as an estimate of the genotypic range. This method also assumes that there is no linkage, no epistasis, no dominance, and that there are equal effects at all loci, but it does not assume that all the genes for resistance are in one parent. For this reason, this method can be used to estimate the number of segregating genes in a cross between two resistant cultivars. If the parents do not have common genes for resistance, the method estimates the sum of the resistance genes in both parents. Because of environmental effects on the phenotypic range, especially in the F_2 and backcross populations, this method may overestimate the actual number of segregating resistance genes. The effect of the environment can be more pronounced on the F_2 and backcross populations than on the F_3 or the F_5 populations because of the lack of replication in the F_2 and the backcross. In this study, individual plants were evaluated in the F_2 and backcross populations while replicated lines were evaluated in the F_3 population and replicated hill plots were evaluated in the F_5 population. Individual plants tend to be more vulnerable to environmental influence than rows or hill plots. The advantage of using the phenotypic range as a measure of the genotypic range is that the numbers of segregating genes obtained for the data from susceptible × resistant crosses can be compared with gene numbers estimated for resistant × resistant crosses. Estimates of gene numbers were higher for resistant × resistant crosses than for resistant × susceptible crosses (Table 2). This corroborates the conclusion that Wampum, Borah, and Wared contain different resistance genes, which was based on the presence of susceptible types in the segregating populations of the resistant × resistant crosses.

Because the method using the parental difference as a measure of the genotypic range often underestimates the number of genes and the method using the phenotypic range as a measure of the genotypic range tends to overestimate the number of genes, it was concluded that upper and lower ranges of these two methods, respectively, provide reasonable estimates of the number of segregating resistance genes (Table 2). Based on these analyses, Wampum, Borah, and Wared would each contain two to three, and possibly more, genes for leaf rust resistance.

The populations ranged from 202 to 419 F_2 plants, 100 F_3 lines, and 40 to 45 F_5 lines, depending on the cross. Mendelian analysis

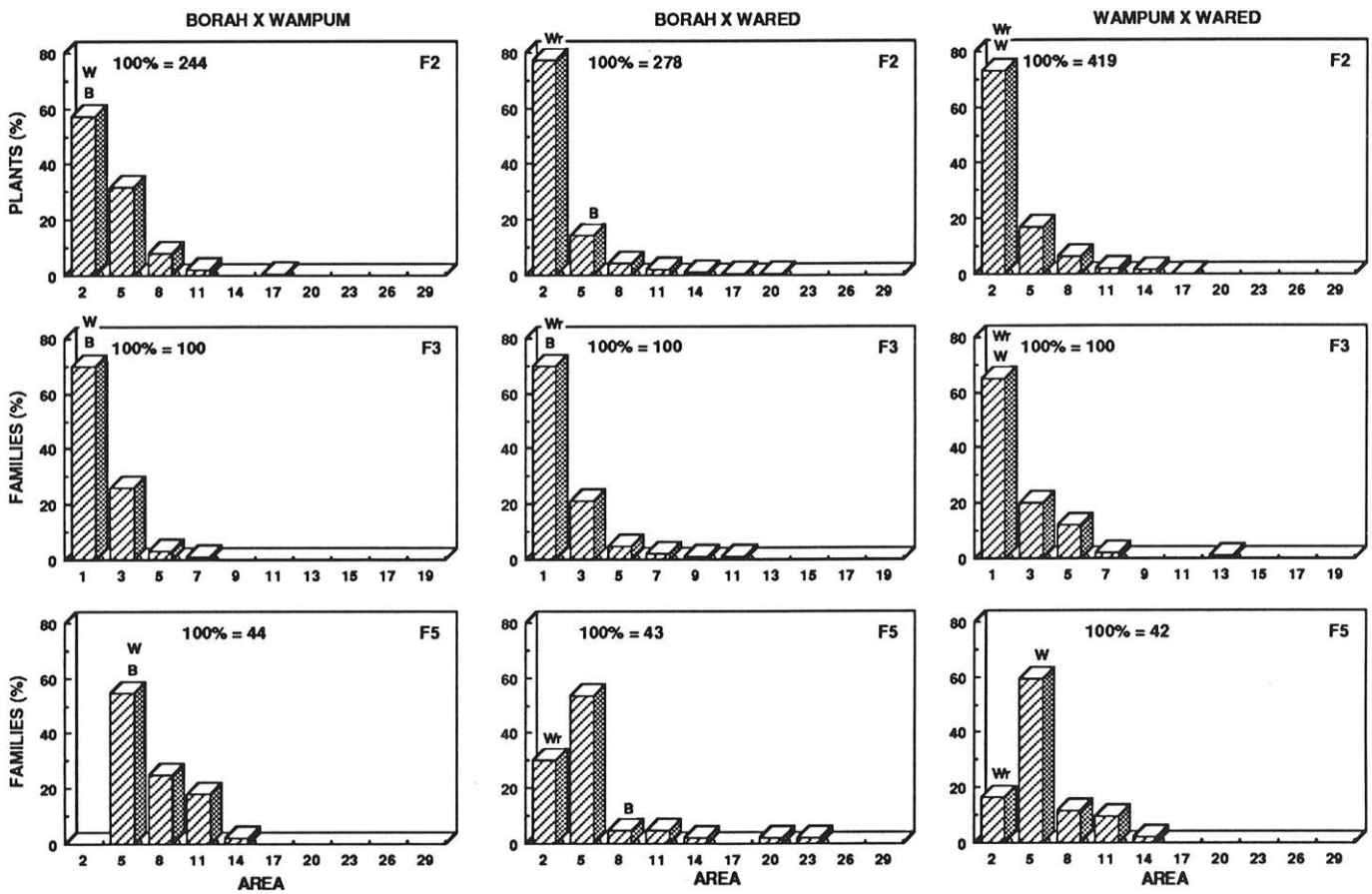

Fig. 2. Frequency distribution for area under the disease progress curve of resistant × resistant crosses involving Borah, Wampum, and Wared. The letters B, W, and WR, respectively, indicate the classes in which the means of the parents Borah, Wampum, and Wared fall.

depends on the identification of individuals in each phenotype, especially the extreme phenotypes. With three segregating genes, a population of 191 individuals is required to be assured (at $P = 0.05$) of obtaining at least one individual in the extreme classes (7). Neither the F_3 nor the F_5 populations were large enough to identify three or more genes at this level ($P = 0.05$) of confidence. The small sizes of the F_3 and F_5 populations studied could also account for the lack of transgressive segregation for resistance. Quantitative estimates depend on the sample population being representative of the reference population in terms of population mean and variance. Quantitative estimates of the number of leaf rust resistance genes present were similar whether the F_2, F_3, or F_5 populations were used (Table 2). This indicates that although the F_3 and F_5 populations were not large enough for Mendelian analysis, they provided adequate information for a quantitative estimation of gene number. It is also possible that Borah, Wampum, and Wared may have common genes for resistance to leaf rust. Because susceptible types were observed in the segregating generations, however, the effects of these genes must be comparatively small.

Using the formula of Wright (33), Milus and Line (19) estimated that two to three genes for durable resistance to stripe rust were present in Luke, Nugaines, and Gaines wheats. Luke et al (15) estimated 2.16 genes for crown rust resistance in Red Rustproof oats. Skovmand et al (28) estimated that 2–12 genes segregate for slow stem rusting in wheat, depending on the cross. Gavinlertvatana and Wilcoxson (6) estimated 3–21 genes for slow leaf-rusting in spring wheat, depending on the cross. Using a Mendelian approach, Kuhn et al (12) estimated that two genes controlled the inheritance of longer latent period in Suwon 85 wheat to leaf rust. Lee and Shaner (13,14) estimated that one to three genes controlled the inheritance of longer latent period in wheat to leaf rust, depending on the cross.

As would be expected, broad sense heritability estimates based on the variance components of the F_5 population were higher than the narrow sense estimates. The three estimates of heritability all resulted in similar rankings among the crosses (Table 3). Heritability estimates were highest for the crosses involving Wared. Wared is highly resistant to leaf rust and its resistance appears to be readily identifiable in the segregating populations. Heritability estimates indicate it may be possible to select for individuals containing higher numbers of resistance genes and thus obtain enhanced resistance to leaf rust in the crosses of Borah × Wared and Wampum × Wared. It should be kept in mind, however, that the high level of resistance already present in Wared may make it difficult to identify such individuals. Narrow sense heritabilities, estimated by the standard units method and the regression of the F_3 onto the F_2, were both less than 0.30 in the cross between the two slow rusting cultivars, Borah and Wampum (Table 3). Selection for enhanced leaf rust resistance would probably be more difficult in this cross than in the crosses involving Wared. Replicated tests of the F_5 and later generations, using larger populations sizes than reported here, with severe disease pressure, would facilitate such selection. We are aware of no other published reports estimating the narrow sense heritability of slow leaf-rusting as measured by area under the disease progress curve.

This study revealed that slow leaf-rusting in Borah and Wampum is controlled by different genes. Two to three genes, or possibly more, control slow leaf-rusting in each parent. Transgressive segregation for susceptibility, but not for resistance, was observed. This may have been due to the small size of the F_3 and F_5 populations and to the inability to differentiate between individuals with high degrees of resistance. Narrow sense heritability estimates indicated that selection for lines with increased numbers of genes for leaf rust resistance, and thus broader based resistance to leaf rust, can be made, although not without effort.

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