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Inheritance of partial resistance to powdery mildew in spring wheat

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Summary. Four spring wheat (*Triticum aestivum* L.) cultivars exhibiting partial resistance to powdery mildew induced by *Erysiphe graminis* f.sp. *tritici* were crossed to a common susceptible cultivar to study the inheritance of resistance. The genetic parameters contributing to resistance were estimated by generation means analyses. Additive gene action was the most important genetic component of variation among generation means in all four crosses. Additive by additive effects were significant in one cross and both additive by additive and additive by dominance effects were significant in another. Dominance effects were not significant. The F2/F3 correlations in three crosses ranged from 0.27 to 0.43. Three additional crosses among resistant cultivars were employed to study the effectiveness of selection in improving resistance. By selecting the most resistant plants from the F2 and evaluating the progenies in the F4, increases in resistance ranging from 21% to 31% were obtained. In all crosses, there was transgressive segregation in both directions indicating that the genes conferring resistance to these cultivars differ and exhibit additive effects.

Key words: *Erysiphe graminis* f. sp. *tritici* – *Triticum aestivum* L. – Disease resistance – Additive gene action – Genetics of resistance

Introduction

The wide use of vertical resistance sensu Van der Plank (1963) against plant pathogens is due in part to its simpler inheritance which makes it readily amenable to plant breeding manipulations. Such resistance, however, is often short-lived due to selection in the pathogen population of specific races capable of overcoming the host's resistance.

Horizontal resistance (HR) offers a possible solution to the instability of vertical resistance, presumably because it is polygenic and hence requires a longer time before the pathogen can adapt to it (Parlevliet and Zadoks 1977). This does not mean that HR is permanent as some pathogens apparently have the potential to erode HR by selection for improved parasitic fitness (Rouse et al. 1980a; Villareal 1980). The polygenic inheritance of HR has been established for a wide array of host-pathogen systems (Parlevliet 1978; Skovmand and Wilcoxson 1975; Krupinsky and Sharp 1978; Kumar et al. 1982; Black 1970; Hooker 1967).

The use of HR in plant breeding has been limited because of the difficulty in detecting and selecting for it, particularly if major resistance genes are present. A procedure which has been successfully used for plant selection is to select for the components of resistance such as the latent period (Jones 1978; Parlevliet et al. 1980). The use of a statistical models for powdery mildew colonies that relate sporulation potential and infection efficiency has also been proposed by Rouse et al. (1980b) to detect relative levels of horizontal resistance in wheat. The effectiveness of these methods depends on the heritability of the components used as selection criteria and the ease and precision by which they are measured.

We have previously identified several spring wheat cultivars from our germplasm collection that exhibit reduced rates of powdery mildew development in field trials (Hautea 1986). At flowering, the disease reactions of these cultivars can be described as partial resistance in the sense that they are neither extremely susceptible nor completely resistant (Zadoks and Schein 1979). The objectives of the present study were to determine the inheritance and genetic control of partial resistance in these cultivars and to evaluate the effectiveness of early generation selection in increasing the levels of resistance in populations derived from crosses among the partially resistant cultivars.

Materials and methods

Three sets of experiments were conducted. In all experiments, disease severity was estimated on the flag and penultimate leaves, using the scale of James (1971), when all test plants had flowered. All plants flowered within one week of each other and disease assessment was done only once. Experiment 1 had the objective of estimating the heritability of partial resistance by parent-offspring regression. Three partially resistant cultivars, 'SD2868', 'Nadadores 63' and 'X6718', were crossed to the susceptible cultivar 'Powell'. The F1 plants were grown in the greenhouse in the spring of 1984 and the F2 seeds harvested. In the summer of 1984, 500 seeds of the F2 generation of each cross were drilled into 4-row, 5-m long plots in the field. All plots were surrounded by strips of the susceptible cultivar Powell. The cool, humid summer of 1984 was very favorable for powdery mildew development and natural infection occurred while the plants were still at the early tillering stage. F2 plants from each population that could be distinguished readily as separate plants were tagged. For the crosses X6718/Powell, SD2868/Powell, and Nadadores 63/Powell, respectively 125, 131, and 101 individual plants were tagged. Disease severity ratings on the flag and penultimate leaves were averaged, converted to arcsin square root to stabilize the variances (Snedecor and Cochran 1980) and used for subsequent analyses.

The spike from the primary culm of each tagged F2 plant was harvested separately to obtain the F3 families. For each cross, a random sample of 60 F3 families was obtained and evaluated in the field in the summer of 1985 in unreplicated 1-m rows. Five randomly selected plants per family were rated for disease severity and the ratings were averaged to obtain the mean family rating. Each F3 family could be traced directly to an individual F2 plant. The regression of the F3 family means to the F2 plant values was computed and multiplied by a factor of ⅔ to adjust for inbreeding in the F2 parents (Smith and Kinman 1965). The regression of the F3 to the F2 was also expressed in standard units which is equivalent to estimating the correlation coefficient between the two generations (Frey and Horner 1957).

Experiment 2 had the objective of determining the genetic control of partial resistance by generation means analyses. Each of the three resistant cultivars used previously and an additional cultivar, 'NK 715', were crossed as males to the susceptible cultivar Powell. For each cross, the susceptible parent and the resistant parent are hereafter referred to as P1 and P2, respectively. The F1 was backcrossed to P1 and P2 to produce the B1 and B2 generations, respectively. At the same time, the F2 plants were produced by selfing the F1.

Each cross was treated as a separate experiment during the field evaluation in the summer of 1985. Fifty seeds were planted for each of the parents and F1, 150 seeds for each of the backcrosses, and 300 seeds for the F2 at the rate of 25 seeds per 1-m row. One month after planting, the spreader rows of the susceptible cultivar 'Powell' were inoculated with a mixture of conidia of local isolates 27 (1, 2, 2+, 3c, 5, 6/3a, 3b, 4) and 28 (1, 2, 2+, 5/3a, 3b, 3c, 4, 6). Mildew assessment was carried out in June, 1985. The mean and variance of each generation were computed. These were used to estimate the genetic parameters m (midparent value), [d] (additive component), [h] (dominance component), [i] (additive × additive interaction), [j] (additive × dominance interaction), and [l] (dominance × dominance interaction) as described by Mather and Jinks (1977). A sequential model fitting procedure was adapted to find the model that best described the data. Selection of the best model was based on considerations of statistical significance of the parameters included, the coefficient of determination (R^2), the values of the residual mean squares, and the acceptability of the residual plots. An overall test for the adequacy of the models was a chi-square test of the residuals.

Experiment 3 was a simple selection experiment to evaluate the possibility of improving the levels of resistance over that of the partially resistant cultivars. Intercrosses were made among SD2868, X6718, and Nadadores 63 to produce three populations. In the summer of 1984, 500 seeds of the F2 from each population were planted into plots consisting of four rows, 5-m long and 30 cm apart. For the crosses SD2868/X6718, SD2868/Nadadores 63, and Nadadores 63/X6718, 161, 108, and 144 F2 plants, respectively, were tagged at random. Severity of powdery mildew was assessed on the main tiller of the tagged plants. At maturity, the tagged plants were harvested separately, hand-threshed, and divided into two F3 seedlots. Based on the frequency distributions of disease severity ratings, the 10% with the lowest disease ratings were selected. An equal portion of the seed from each selected plant was bulked to form the selected bulk, and the remaining seed was bulked with seed from each of the remaining F2 plants to form the random bulk. Random samples of seeds from the selected and random bulks were planted separately in the greenhouse for generation advance without selection. At maturity, 50 F3 plants were randomly selected from each of the random and selected bulks for each cross. The seeds from each F3 plant constituted a single F4 family. In the summer of 1985, the F4 families were evaluated in the field in a split-plot randomized complete block design with two replications, with crosses as main plots and selection treatments as subplots. Each subplot consisted of 50, 0.5-m rows arranged into five sections divided by a 1-m alley. One F4 family was planted to a row. In each section, the parental cultivars were included as checks and spreader rows of Powell were planted every three rows.

Disease assessments were done on two plants per row and the ratings were averaged and converted to arcsin square root. For each subplot the mean and variances of the 50 F4 families were computed. The analysis of variance was done to evaluate the effects of crosses, selection treatments, and cross by selection interaction. The gain due to selection was computed as the difference between the means of the selected and random lines expressed as percentage of the mean of the random lines.

Results

Parent-offspring regression

Two methods were used to estimate the heritability of resistance. The first was by the linear regression of the F3 family means on the parental F2 plant ratings. The coefficients obtained were significantly different from zero (Table 1). Smith and Kinman (1965) pointed out that the coefficients must be adjusted to account for inbreeding in the F2. The corresponding adjusted heritability estimates are shown in Table 1. The second approach was to use the standard unit regression method by Frey and Horner (1957). The standardization corrects for differences in scale caused by the fact that the two generations were grown in different environments. The relative estimates for the three crosses remained the same using the two methods.

Generation means analyses

In all crosses, P1 and P2 differed; hence, the model fitting procedure for estimating the genetic parameters could be conducted. The initial model that was fitted was a three-parameter model consisting of m, [d], and [h]. The estimates obtained for the four crosses are presented in Table 2. Because m should be an integral component of the model and estimates for m were significant for all crosses, only the importance of the other components will be evaluated hereafter. For the cross X6718/Powell only the additive component was significant. The chi-square value indicated that the model was adequate in explaining the observed variability. Likewise for the cross Nadadores 63/Powell, only the [d] component was significant. However, the chi-square value indicated that the three-parameter model was not adequate. For SD2868/Powell, neither the [d] nor the [h] component was important. For NK715/Powell, only the [d] component was important and accounted for 94% of the variation among generation means.

With the sequential model fitting approach, additional components were evaluated with the crosses where the three-parameter model was inadequate. Thus, the digenic, epistatic parameters [i], [j], and [l] corresponding to additive by additive, additive by dominance, and dominance by dominance interactions, respectively, were also fitted. These components were likewise evaluated with the two crosses where the three-parameter model was adequate, to determine if further improvements could be made. The final models chosen are presented in Table 3. As before, no other component except [d] was important in the cross X6718/Powell. For the cross Nadadores 63/Powell an additional component that proved important was the additive by additive interaction. The inclusion of [i] with [d] decreased the residual mean squares and resulted in an improved model. The case of SD2868/Powell is worth noting because neither [d] nor [h] was significant when evaluated previously and no interaction parameter was important. However, with a model that includes only m and [d], the residual mean squares decreased and the [d] component was judged significant. For NK715/Powell, the two additional interaction parameters [i] and [j] proved to be important. Their inclusion in the model together with [d] accounted for nearly all of the observed variation among generation means.

Table 1. Heritability estimates by F3/F2 regression of partial resistance to powdery mildew in three spring wheat crosses

Cross	Heritability*	
	b	Standard unit
X6718/Powell	0.142 (0.213*)	0.182 (0.273*)
Nadadores 63/Powell	0.214 (0.321**)	0.263 (0.394**)
SD 2868/Powell	0.322 (0.483**)	0.287 (0.431**)

* Values in parentheses are the computed coefficients before adjusting by the factor of 2/3. A single or double asterisk, respectively, indicates significance at the 0.05 and 0.01 levels of probability

Selection study

The F2 frequency distribution for the crosses SD2868/X6718, SD2868/Nadadores 63, and Nadadores 63/X6718 were approximately normal with mean disease severity ratings of 27.9, 31.4 and 41.8%, respectively. The means of the selected plants from these crosses were 12.8, 17.9, and 22.3%. The analysis of variance of the F4 ratings indicated that crosses and cross by selection interactions were not significant, but mean

Table 2. Estimates of the genetic components of variance among generation means of four spring wheat crosses using a three-parameter model

	X6718/Powell		Nadadores 63/Powell		SD 2868/Powell		NK715/Powell	
	estimate	p-value	estimate	p-value	estimate	p-value	estimate	p-value
m	25.2 ± 1.56	0.01	15.15 ± 2.24	0.01	21.76 ± 2.38	0.01	25.1 ± 1.03	0.01
[d]	4.65 ± 1.52	0.05	8.0 ± 2.16	0.03	6.34 ± 2.35	0.07	8.0 ± 1.0	0.01
[h]	0.22 ± 2.83	0.94	6.01 ± 4.24	0.25	0.56 ± 4.33	0.90	1.80 ± 1.96	0.42
X^2	4.916		8.325		12.368		1.872	
$p[X^2]$	0.1–0.25		0.025–0.05		0.005–0.01		0.5–0.75	
R^2(d/m)	0.7556		0.7606		0.714		0.9432	
R^2(h/d, m)	0.0005		0.0958		0.0016		0.0125	
R^2(d, h/m)	0.7561		0.8564		0.7156		0.9557	

m = mid-parent; [d] = additive component; [h] = dominance component

Table 3. Estimates of the genetic components of variation among generation means of four spring wheat crosses for the simplest adequate model

	X6718/Powell		Nadadores 63/Powell		SD 2868/Powell		NK 715/Powell	
	estimate	p-value	estimate	p-value	estimate	p-value	estimate	p-value
m	25.3 ± 0.74	0.01	19.94 ± 0.99	0.01	22.02 ± 1.17	0.01	26.35 ± 0.05	0.01
[d]	4.65 ± 1.32	0.02	7.70 ± 1.28	0.01	6.38 ± 2.02	0.03	9.05 ± 0.08	0.01
[h]	–		–		–		–	
[i]	–		– 6.33 ± 1.87	0.04	–		– 1.50 ± 0.10	0.01
[j]	–		–		–		– 7.46 ± 0.30	0.01
[l]	–		–		–		–	
X^2	3.694		2.88		9.33		0.009	
$p[X^2]$	0.25–0.50		0.50–0.75		0.05–0.10		0.995	
R^2	0.756		0.95		0.714		0.999	

m = mid-parent; [d] = additive component; [h] = dominance component; [i] = additive × additive interaction; [j] = additive × dominance interaction; [l] = dominance × dominance interaction

Table 4. Mean disease severity of F3-derived F4 families from random and selected F2 plants from crosses of three partially resistant cultivars

Cross	Random	Selected	Gain (%)	Realized herita-bility**
SD 2868/ X6718	23.89* (103.84)	16.31 (100.87)	31.73	50.1
SD 2868/ Nadadores 63	21.22 (97.96)	15.98 (72.99)	24.70	38.8
Nadadores 63/ X6718	30.39 (132.14)	23.84 (128.25)	21.60	33.6

* Data are arcsin transformed severity values. These are means of 2 replications of 50 F4 families. Values in parentheses are pooled variances among families

** Realized heritability (%) was computed by expressing the difference between the selected and random lines as proportion of the selection differential in the parental F2 population

disease severity of lines derived from the random and selected bulks difered. For each cross, the gain from selection was computed as the difference between the selected and random lines and expressed as a proportion of the mean of the random lines. The mean disease ratings and the corresponding estimated gain for each cross are shown in Table 4. In all crosses, selection resulted in a decrease in the mean disease severity ratings; i.e., improved resistance, ranging from 21.6 to 31.7%. As noted previously, however, the absence of a significant cross by treatment interaction indicated that the gains observed were not statistically different among crosses.

Expressing the difference between the selected and random lines as proportion of the selection differential in the F2 parental population gave realized heritability

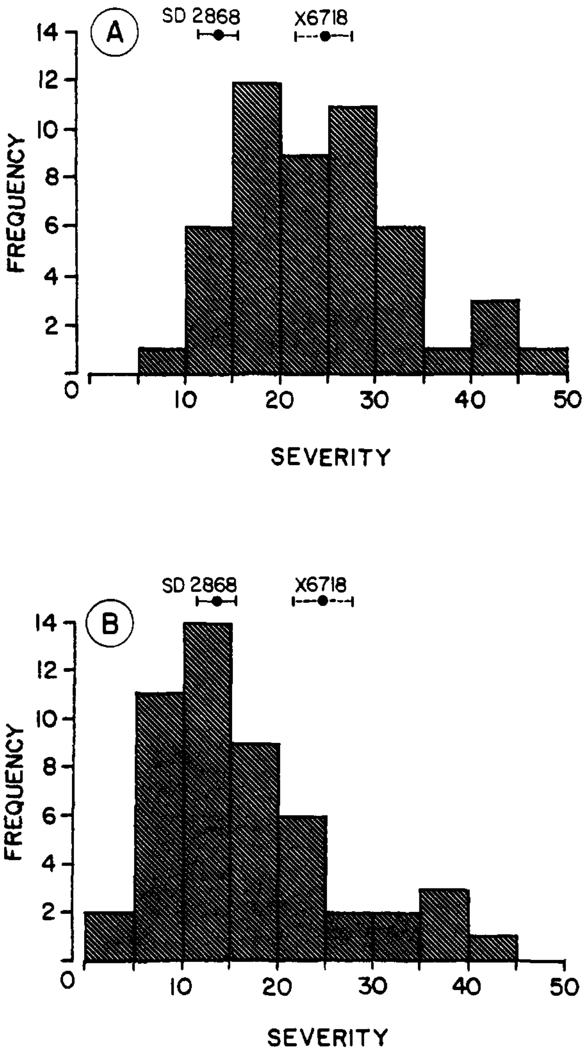

Fig. 1. Frequency distribution of severity ratings on 50 F4 families from random (**A**) and selected (**B**) bulks from the cross SD 2868/X6718

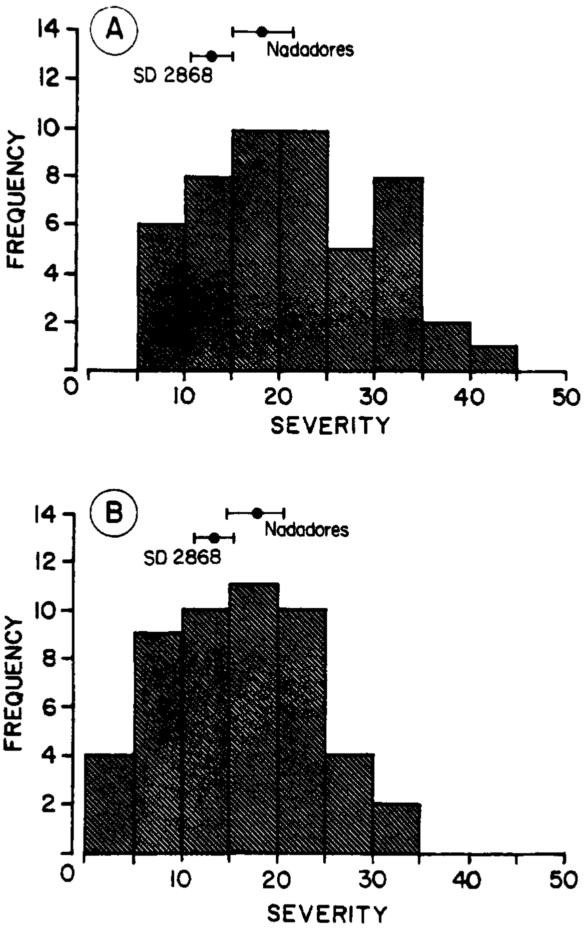

Fig. 2. Frequency distribution of severity ratings on 50 F4 families from random (A) and selected (B) bulks from the cross SD 2868/Nadadores 63

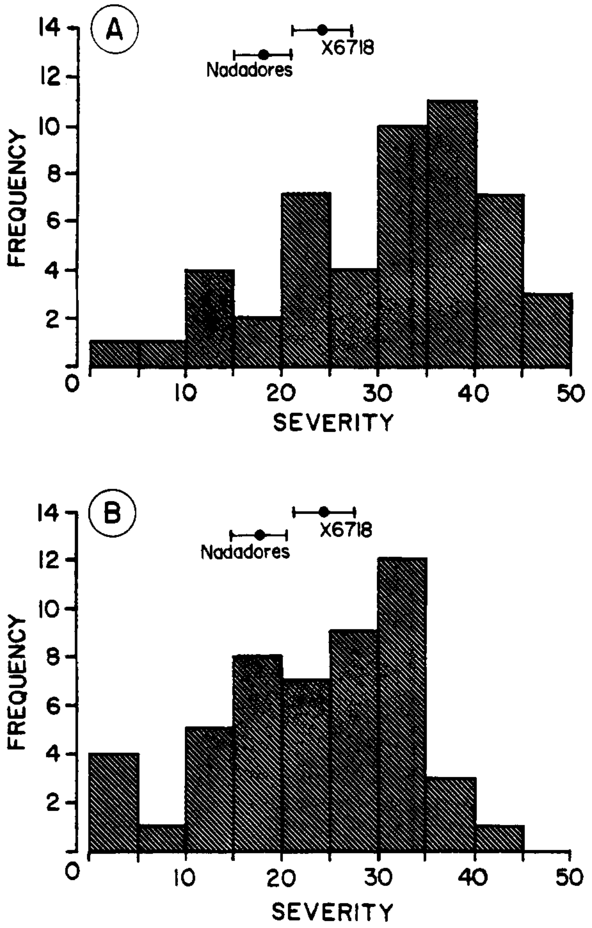

Fig. 3. Frequency distribution of severity ratings on 50 F4 families from random (A) and selected (B) bulks from the cross Nadadores 63/X6718

estimates ranging from 34 to 50%, depending on the cross (Table 4). This indicated that one cycle of selection did not reduce the variability in any of the three populations.

The gain from selection can be easily visualized in Figs. 1–3 which illustrate the frequency distribution of severity ratings of the 50 F4 lines for each cross and selection treatments. In all crosses, a shift in the distribution towards lower severity values is apparent. Transgressive segregation also occurred in all crosses. Transgressive segregants are herein defined as those which exceeded or fell below the means of the higher or lower parent, respectively. The 95% confidence interval for the means of the parents in each cross are shown for comparison. Transgressive segregation occurred in both directions but more transgressive segregants for susceptibility were observed with the lines derived from the random bulk. This indicates that, for some reason, there was a preferential loss of desirable segregants when selection was not done.

Discussion

The heritability estimates obtained in the study were generally low but significantly different from zero. Using either direct or standard unit regression, the highest heritability estimate obtained was 32%. Comparing heritabilities estimated by the two methods provides a means of determining the degree to which environment influences phenotypic variability (Frey and Horner 1957). For each cross, the rather close agreement between the heritability estimates based on the two methods suggest that environmental influences did not affect the phenotypic variances in parents and progenies to a large extent. The significant estimates obtained indicate the genetic control of partial resistance in the crosses evaluated, but the generally low estimates suggest that selection for improved resistance would be relatively difficult when individual F2 plants are the selection units in the resistant by susceptible crosses used in the study.

Generation means analyses showed that additive gene action was the most important component of genetic variation and that no dominance component was significant. The absence of dominance effects implies that resistance in these cultivars is not conditioned by the known major resistance genes which have been rendered ineffective by matching virulence genes in the pathogen population. The results still indicate that genetic factors other than the major resistance genes are responsible for the observed resistance.

Significant digenic epistatic components were observed in two crosses. Only additive by additive interaction was important in one cross while both additive by additive and additive by dominance interactions were important in another. In all cases, these parameters had negative values indicating that the epistatic effects were in the direction of improved resistance. Such significant interactions could have biased the estimates of m and [d] in the crosses Nadadores/Powell and NK715/Powell but probably only to a slight degree as the additive effects accounted for the larger portion of the observed variability. The generation means model assumes that only two alleles are present at a locus within a mating. Being a disomic allohexaploid, significant epistatic effects in wheat may reflect interactions between alleles at homeologous loci (MacKey 1970). Additive intergenomic interactions imply that the interacting alleles can be fixed in homozygous genotypes and, because the observed interactions were for improved resistance, may possibly be utilized in breeding for powdery mildew resistance in wheat.

The occurrence of transgressive segregants demonstrated the multigenic nature of resistance in the varieties used. Without information on the number of genes conferring resistance to each parent, we can only infer that there are at least unique genetic factors for resistance in the different cultivars for transgressive segregation to have occurred. This may not be surprising considering that the components of resistance differ in the parental cultivars used in the crosses; SD2868 has the longest latent period; Nadadores has the lowest infection efficiency; and X6718 has moderate levels of expression of all resistance components (Hautea 1986).

In other host-pathogen systems, latent period alone could be under the control of multiple genes (Parlevliet 1976; Kuhn et al. 1980; Lee and Shaner 1985a). In fact, transgressive segregation for longer latent period has been documented in these host-pathogen systems (Lee and Shaner 1985b; Parlevliet and Kuiper 1985). Because the latent period is only one component of resistance, independent genetic control of the other components would result in multigenic control of resistance. The fact that the transgressive segregants were recovered in a relatively low sample size of 50 F4 families suggests that resistance genes are independently inherited.

The observed response to selection in crosses among three partially resistant cultivars demonstrated that mass selection could be effective in increasing the levels of powdery mildew resistance in these populations. Effective mass selection for polygenically controlled resistance has also been reported against stripe rust in wheat (Krupinsky and Sharp 1979) and leaf rust in barley (Parlevliet and Kuiper 1985). One cycle of selection did not reduce the population variances and results suggested that another cycle of selection could result in further gains. An important requirement for success is the proper choice of parents that could contribute complementary factors and/or components of resistance. Further studies should focus on the specific components of resistance in the transgressive segregants.

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